Santa Barbara County Oak Restoration Program August 1994 - August 2005 Final Report

Principal Investigators: Bruce E. Mahall, Frank W. Davis, Claudia M. Tyler University of California at Santa Barbara

Submitted to: County of Santa Barbara Department of Planning and Development Energy Division October 2005

Acknowledgements

This program was funded by an endowment established as mitigation for oaks removed during construction of the All American Pipeline. The fund is administered by the Santa Barbara County Department of Planning and Development, Energy Division. We thank Sedgwick Reserve's present manager, Michael Williams, and former managers, Mark Reynolds and Virginia Boucher for their assistance and sustained support of our use of large portions of the reserve for this project. We are tremendously grateful to Mike Hall of California State Polytechnic University at San Luis Obispo, and his students, especially Tomo Anderson, Jonathon Kreillich, Bart Cremers, and Adrian Cuzzick, for managing all aspects of the cattle grazing program, including water system and fence installation and maintenance from 1995 - 2002; this program was supported by the Cal Poly Foundation. We also thank John Solem from Wise Acres Ranch for conducting cattle grazing in our experimental paddocks at Sedgwick Reserve from 2002 -2005. This project has been possible thanks to the help of many generous and hardworking assistants and volunteers, including: Rusty Brown, Shelly Cole, Melanie Dunbar, Nathan Gale, Judy Kim, Bill Kuhn, Dennis Odion, Anuja Parikh, Cara Peace, Rick Skillin, Peter Slaughter, Lisa Thwing, Doug Wreden, and the staff and docents at Sedgwick Reserve. We thank county staff from the Santa Barbara County Energy Division for their support and advice, especially Tricia Backelin, Chris Price, Kristen Getler, Laura Sawicki, Amy Sabbadini, Michelle Pasini, Joddi Leipner, John Day, Nancy Minnick, and Alice McCurdy. We also thank the staff at UCSB's Institute for Computational Earth System Science, especially Kathy Scheidemen, John Sanchez, Imelda Moseby, and Claudia Kashin for their administrative support. Finally, we wish to acknowledge the University of California's contributions of vital financial, legal, and intellectual support, and a commitment to community service.

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The Santa Barbara County Oak Restoration Program 1994 – 2005 Final Report

EXECUTIVE SUMMARY

INTRODUCTION

The Santa Barbara County Oak Restoration Program was funded as alternative mitigation for the loss of more than 2000 oaks during installation of the All American Pipeline (AAPL). As described in the original request for proposals, this program was intended to promote the regeneration of oak habitats within Santa Barbara County through fencing and cattle grazing management. Initiated in 1995 by investigators at the University of California at Santa Barbara, the Oak Restoration Program was designed as a program of research and restoration that would give practical guidance to resource managers and land owners concerned with management and restoration of local oak woodlands. This report provides a summary of the research findings and work completed within the initial 10-year contract period.

PROGRAM OBJECTIVES AND ACCOMPLISHMENTS

The Santa Barbara County Oak Restoration Program has been designed to achieve multiple objectives: to restore oak habitat, and to conduct a long-term ecological investigation that would improve our understanding of the role of cattle and other ecological factors in limiting or promoting establishment of oaks in large-scale, landscape-level environments. While establishing oaks in residential settings is generally straightforward and successful, efforts to replace oak habitats for landscape-level mitigation in Santa Barbara County and throughout the state have faced significant challenges, and have often resulted in failure. Thus, the goal of the Santa Barbara County Oak Restoration Program was not only to plant oaks, which had been attempted previously with mixed results, but to improve our understanding of the factors limiting establishment of oaks in large-scale rangeland settings.

This program represents a long-term commitment by the principal investigators, the University of California at Santa Barbara, and the UC's Natural Reserve System to: 1) restore several hundred acres of valley oak savanna and blue oak woodlands on Sedgwick Reserve, a 5896-acre ranch at the base of Figueroa Mountain; 2) conduct large-scale grazing and related experiments that will give practical guidance to resource managers and land owners in Santa Barbara County who are concerned with management and restoration of local oak woodlands; 3) disseminate findings in the form of presentations, onsite demonstration projects, and literature that is directed towards locals landowners and resource managers. Summarized below are the program's main accomplishments to date.

RESTORING OAK HABITAT

Although the emphasis of planting activities has been on conducting largescale experiments, restoration of oak savanna and woodlands at the site is an integral component of the program. As a result of our planting experiments (1996 -2002) there are currently 793 new oaks within five age classes: a total of 220 coast live oaks, *Quercus agrifolia*, and 573 valley oaks, *Q. lobata*, within the program area of 525 acres at Sedgwick Reserve in the Santa Ynez Valley. All plantings have been done in areas that are suitable for establishment of oaks, and that will be maintained as natural oak savanna and woodland habitats in the future.



HISTORICAL MAPPING OF OAKS AT SEDGWICK

Mapping the modern and historical distribution of oak woodlands at the Sedgwick Reserve was an important first step in designing the restoration experiment. We used archival air photos to measure changes in oaks between 1943 and 1989. Over the 46-year survey period there was a gradual but steady decline in oak population: 897 out of 5,343 canopy trees disappeared. Average stand densities declined from 5.5 to 4.4 trees per acre. No recruitment of new canopy oaks was observed in the 962 acre study area during the time period 1943-1989. Our historical analysis of oaks on the Sedgwick Reserve indicates that large areas of the reserve have supported higher oak densities in the recent past and would thus be good candidates for oak restoration. Oak woodlands on the reserve have experienced a range of land use histories providing an opportunity to study oak restoration methods in areas that have undergone complete tree removal, mechanical tillage under the tree canopies, and/or livestock grazing.

LARGE-SCALE PLANTING EXPERIMENTS

The primary effort of The Santa Barbara County Oak Restoration Program has been to conduct replicated large-scale planting experiments in four different years to determine the effects of cattle and other ecological factors on oak seedling establishment in oak savannas and woodlands. In 33 large experimental plots we planted acorns collected from valley oak and coast live oak on the site. Fifteen of these large plots are controls, open to cattle grazing, fifteen exclude cattle with the use of electric fence, and three are ungrazed in large ungrazed pastures. Within the plots, experimental treatments included: 1) protection from small mammals such as gophers and ground squirrels, 2) protection from large animals such as cattle, deer, and pigs, and 3) no protection from mammalian grazers. In winters 1997, 1998, 2000, and 2001, we planted approximately 1000 acorns of each species. Acorns and seedlings did not receive supplemental water.



Coast live oak (L) and valley oak (R) saplings protected from both small and large mammals.

Results indicate that several factors play a role in limiting or promoting seedling recruitment of oaks. First, rainfall levels in late winter and early spring significantly impact rates of establishment and survival. Abundant rainfall, as seen in the El Niño year 1998, was associated with highest seedling emergence and survivorship, and very low rainfall resulted in low seedling emergence, as seen in 1996 - 1997, and in increased seedling mortality as observed in 2002. Second, as observed in all four planting years, and at all planting sites, seed predation and herbivory by small mammals (most likely gophers and ground squirrels) significantly reduces oak seedling recruitment. Third, herbivory by insects such as grasshoppers may reduce seedling survivorship across all treatments in some years, as observed in 2000 - 2001. Fourth, acorn and seedling survivorship is not negatively impacted by winter/spring livestock grazing. In fact, survivorship of protected seedlings was slightly higher in areas grazed by cattle than in ungrazed areas. Contrary to our expectations, establishment and survival of coast live oak was lower than that of valley oak for all four planting trials. The results of these experiments also provide guidance for those planting oaks in similar conditions by indicating the range of survival and growth one might expect if acorns are planted using these treatments.

SUMMER DROUGHT PHYSIOLOGY OF OAK ADULTS & SEEDLINGS

We conducted preliminary physiological measurements in the fall of 1997 to assess water availability and drought stress in adult valley oak and coast live oak trees.

We hypothesized that the trees would be under great water stress due to the long interval since rainfall (January - November 1997), and that there might be differences between the two species. Contrary to our expectations, we found that mature trees of the two species had very similar water availabilities, and that the values indicated a relative lack of water-stress. This suggests that mature trees of both species may be using the same, deep water sources. We also found that natural seedlings (~ one or two years old) had significantly less water available to them, and there was considerable water stress for seedlings relative to the adult trees found in the same location. These measurements support our hypothesis that water stress was a dominant cause of mortality for seedlings establishing in 1996 - 1997. They also suggested that further study of plant water relations could provide information about factors limiting natural regeneration of oaks.

We began studies of the physiology of coast live oak and valley oak seedlings in 2002 to examine the effects of annual summer drought on seedling survival and transition to the sapling stage. During summers of 2002, 2003 and 2004, we measured water availability, rates of photosynthesis, and chlorophyll fluorescence characteristics of selected seedlings (planted in 1997-1998) and neighboring adults.



Measuring physiological characteristics of oak trees and seedlings.

There were similarities and important differences between the two species. The established (four- to six-yr-old) seedlings of both species showed no evidence of severe drought stress, even during a year (2002) of half average rainfall. However, valley oak seedlings had lower water availability and higher photosynthetic rates than coast live oak seedlings overall. We suspect that differences between the two species could be due to differences in root architectures, with coast live oaks developing extensive lateral roots plus deep, vertical roots, and valley oak developing primarily deep, vertical roots.

Supporting our previous findings, the adults of these two species did not differ in measurements of water availability, which were high, indicating these trees utilize a substantial source of perennially available ground water. In both species there were large differences between seedlings and adults of the same species, with seedlings having lower water availability and lower photosynthetic rates than those of nearby adults. However, it appears a few of these plants have attained access to a similar or the same

source of water available to the adults, and thus the population of seedlings in this study may be just on the verge of reaching substantial water sources, leading to consequent increases in growth rates. Observing the physiological characteristics of these oak seedlings over time will allow us to better understand what controls the seedling to sapling transition.

PATTERNS OF NATURAL OAK SEEDLING ESTABLISHMENT

In order to determine the spatial and temporal patterns of natural oak seedling establishment we surveyed a sub-sample of our experimental plots in savannas to locate naturally occurring oak seedlings in three different years. The numbers of natural seedlings varied considerably among years. For example in 1998, a year of high acorn production followed by a very wet winter (El Niño) resulted in relatively high natural establishment. However, most of these seedlings did not survive, as evidenced by the low numbers of seedlings present in 2004. Another finding is that natural recruitment of valley oak is the lowest of the three species recorded, even though the only species of mature oak trees within the plots was valley oak. We conducted more extensive and detailed surveys in one year. One finding was that there were very few valley oak seedlings produced per area of valley oak tree canopy present, compared to both coast live oak and blue oak. Although canopy cover in the plots average 12% overall and was predominately valley oak, most seedlings were blue oaks. We also found that the majority of natural seedlings were located in areas grazed by cattle. However, the relationship between grazing and natural seedling recruitment may vary among oak species; while there were more live oak seedlings found in ungrazed plots than in grazed plots, both valley oaks and blue oaks were more abundant in grazed plots. Another pattern we detected was that seedlings were strongly aggregated under or near adult trees. In nearly all plots, most seedlings were found under tree canopy rather than in the open grassland.

ADDITIONAL EXPERIMENTS: RAPTOR POSTS AND WATERING

Since results of our large-scale planting experiments indicated that two factors, above-average rainfall, and protection from seed predation and herbivory by small mammals, are associated with high rates of oak seedling recruitment, we established two experiments to study potential means of influencing these factors in the field. We conducted a pilot study to investigate whether the addition of artificial raptor perches (large wood poles) would lead to a reduction **i**n small mammal activity and thus to a decrease in oak seedling mortality. The results of this pilot study support our previous findings that small mammals significantly reduce emergence and establishment. However the addition of artificial perches to attract predators did not reduce small mammal activity. We also conducted a pilot study to investigate the effects of supplemental water on valley oak and coast live oak seedling establishment. We have

not yet detected any significant differences in establishment survival rates among watering treatments. However for coast live oak we found significant effects of treatment on seedling height; seedlings that received water were significantly taller than controls. In 2003 – 2004, rainfall was above average. Thus, our finding that watering treatments did not improve emergence may have been due to the fact that there was enough natural precipitation to ensure germination; even emergence in the unwatered treatment was very high. We suggest that supplemental watering could yield very different results in a year with below-average rainfall.

EFFECTS OF CATTLE GRAZING ON UNDERSTORY VEGETATION

To characterize the understory vegetation and to examine effects of cattle grazing on the herbaceous vegetation of oak savannas and woodlands we established permanent sampling quadrats within our large experimental plots in May 1996, and have recorded all plant species present and their percent cover almost every spring from 1996 to 2003.



Cattle graze at Sedgwick winter through spring, reducing abundance of non-native grasses.

Our main findings to date from this long-term vegetation monitoring are: 1) historical pattern of land use and physical terrain appear to be the dominant factors affecting species composition; 2) variation between years in community diversity and composition is related to rainfall patterns; 3) moderate cattle grazing (winter/spring) appears to have positive effects on diversity and proportion of native species in the community; and 4) *Bromus diandrus*, ripgut brome, increased with removal of cattle.

A PRESCRIPTION FOR ESTABLISHING OAKS

Based on results of our field experiments to date, we developed a prescription for establishing oaks in large landscape or rangeland settings in Santa Barbara County. These methods can be adapted as appropriate to various planting environments. We include recommendations on acorn collection, site selection, planting schedule and methods, and seedling protection. We also provide expected rates of growth and survival, based on our findings. If seedlings are protected from both small and large mammals, but unwatered, seedling survival rates for valley oak may be as high as 37% to six-years-old, and for coast live oak as high as 30% to six-years. Growth of such seedlings may average ~10 cm per year, with a range of 0 to 18 cm per year.

PUBLIC OUTREACH

The outreach activities of the Santa Barbara Oak Restoration Program have been conducted since early in the project and on an ongoing basis to reach a diversity of people, including landowners, ranchers, school groups, policy-makers, restorationists, scientists, and other members of the community. Literally thousands of individuals have visited the experiments and restoration areas established for this program. Outreach has included site tours, public workshops, lectures, website development, and media coverage. Complementary research on oaks has been conducted at Sedgwick as a direct result of this program.



Students plant oaks and other native species in restoration plots at Sedgwick.

FUTURE WORK

We have demonstrated the relative importance of factors that limit the establishment and survival of oak seedlings, or the transition from acorn to seedling. The next unknown in the life-stage of an oak is: what limits the recruitment of saplings in rangelands, or what controls the transition from seedlings to saplings? We believe this transition may be the most important bottleneck in oak recruitment in this woodland system, and the Santa Barbara Oak Restoration Program is now in a unique position to be able to address this critical problem. We will be able to address questions essential to mitigation, restoration, and preservation of oaks in our county such as: is there a size or age at which seedlings or saplings have a very high likelihood of long-term survival?, and what are the growth and survival rates of young oaks at different life stages and under

different conditions? Thus, future work will emphasize the seedling to sapling transition, to determine the factors affecting growth and survival of seedlings planted in 1996-2001 as they transition to this larger size and age class. Other research could include: experiments on watering enhancement to determine the optimal amount and timing of supplemental watering; experiments to determine the relative benefits of various weed control treatments such as mulching or application of weed cloth; research on factors limiting the seedling to sapling transition in natural oak recruits, with the goal of developing a prescription for nurturing natural seedlings; a study of long-term demographic trends in valley oak using tree-ring analyses; additional oak plantings at appropriate restoration sites on Sedgwick Reserve in years that acorns are available, using methods described in our "prescription".



Sedgwick has been and will continue to be an ideal location to conduct this work, for several reasons. First, all three species of oak impacted by the AAPL project – blue oak, valley oak, and coast live oak – co-occur and are common there. Second, the reserve's large size and diversity of terrain, soil type, and land-use history have provided the opportunity to examine survival and growth of oak plantings in a range of environmental conditions. Third, consistent with the reserve's dedication to research and outreach, their staff and docents have contributed countless hours toward infrastructure maintenance and toward educating the community about oaks and this restoration program. Such outreach and continued support from the Sedgwick Reserve is valuable component of the Santa Barbara Oak Restoration Program. Finally, the reserve's use and management policies provide the stability required for the establishment and protection of a long-term planting experiment and restoration program that can be maintained far into the future.

I. Introduction

A. Oaks in California and in Santa Barbara County

Oak woodlands and savannas make up nearly a quarter of California's forests and woodlands, and they define much of central California's natural landscapes. They are among the most diverse communities in North America, possessing more than 1400 species of flowering plants, over 300 species of vertebrates, and thousands of invertebrate species. In addition to their importance as "hotspots" of biodiversity, California's oak woodlands provide numerous important benefits and ecosystem services including watershed protection, wildlife habitat, grazing land, recreation, open-space and aesthetics.

In Santa Barbara County oak habitats form a major component of non-urban areas. The three dominant species of arborescent oaks are coast live oak, *Quercus agrifolia*, blue oak, *Q. douglasii*, and valley oak, *Q. lobata* (Figure 1). Coast live oak, an evergreen tree, is common and widely scattered in the coastal region of our county, especially on north slopes of hills inland to Bluff Camp, upper Sisquoc River to over 6400 ft, Montgomery Potrero and lower Cuyama Valley (Smith 1998). The deciduous blue oak is typically developed as woodland in the Lake Cachuma-Paradise County Park-Oso Canyon area, Mono Creek and Roblar Canyon; it is more common inland on west slopes of Figueroa Mountain, the lower Sisquoc River to Cuyama River Canyon, and in the northwestern part of county to north slopes of Sierra Madre (Smith 1998). Valley oak is also deciduous, and is among the largest and longest lived of the North American oaks. In our county it is commonly scattered in inland valleys from Santa Ynez to Los Alamos, the lower Cuyama valley and into foothills and mountains to ~ 4500 ft (Smith 1998).



Figure 1. Dominant oaks in Santa Barbara County. Photos are from Sedgwick Reserve. At top is *Quercus agrifolia*, coast live oak, in the middle is *Q. lobata*, valley oak, and at the bottom is *Q._douglasii*, blue oak.

Three other tree species of oaks that occur in the county - canyon oak, *Q. chrysolepis*, interior live oak, *Q. wislizeni*, and black oak, *Q. kellogii* - are found primarily at higher elevations in the eastern portion of the county.

In spite of their importance as natural resources, there have been significant losses of oak woodlands statewide. It has been estimated that the state's original 10-12 million acres of oak woodlands have been reduced to about 7 million, primarily by urban development, "rangeland improvement", and agricultural conversion. Approximately 1 million acres were lost just in the period 1945 – 1973 (Bolsinger 1988). Between 1973 and 1987 over 200,000 additional acres of oak woodland were converted, and future loss has been predicted to be a high as another quarter million acres by the year 2010 (Bolsinger 1988).

In Santa Barbara County the historical distribution and changes in oak woodland cover have not been fully documented. However, a pilot inventory and mapping program for Santa Barbara County of the Los Alamos Valley provides information on trends in vegetation change in the county (Davis et al. 2000). Comparing 1997 aerial photographs to data on oak cover recorded in the 1930's, polygonal areas were identified where oak species were mapped as present and a canopy dominant during the 1930's field survey, but were absent in 1997. Out of 1,900 total assessment units, or polygons, (average size per unit was 55 acres) Davis et al. (2000) found that in the Los Alamos Valley, valley oak was entirely lost from at least 99 polygons, coast live oak from at least 181 polygons, and blue oak from at least 43 polygons. Losses of oak woodlands in Santa Barbara County have occurred primarily in land that is currently rangeland, cropland, and vineyards (Davis et al 2000).

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Compounding the threat to these systems from the loss of adult trees is the same concern raised in other oak woodlands globally – that natural recruitment of oaks may be insufficient to maintain current densities within extant populations, producing a gradual but steady decline in total abundance under current climate and land use. As early as the beginning of the 20th century, researchers observed that California oaks did not appear to be regenerating well (Sudworth 1908; Jepson 1910). Because many oak populations are dominated by older individuals, with seedling and sapling size classes either unrepresented or underrepresented, there is concern that stands do not have enough sapling recruits to balance losses from adult mortality. However, quantitative assessments of existing oak stands in California have produced conflicting conclusions about the extent of the "regeneration problem", and regeneration status appears to be highly site- and species-specific (Tyler et al. in press, Appendix A).

B. The All American Pipeline Project

In December 1986 Santa Barbara County approved the pipeline development plan submitted by Celeron Pipeline Company (subsequently All American Pipeline, currently owned by Plains Pipeline L.P.), which required a program to restore oaks destroyed during implementation of the project. The original losses were projected to be 250 - 500 oak trees within Santa Barbara County. Actual losses far exceeded those projected – a total of approximately 2,300 oak trees.

Based on these actual losses, mitigation was amended in 1987 (Table 1). To mitigate for the removal of 878 blue oaks, there was to be a one-time planting of 8,000 -10,000 blue oak acorns, and a provision of funding to the US Forest Service for oak related research. To mitigate for the loss of 82 mature valley oaks, establishment of 400 6-ft high saplings was required. Mature coast live oaks were to be replaced at a 1:1 ratio, requiring the establishment of 1303 coast live oaks. Mitigation efforts proceeded based on these revised requirements.

In 1992, the following results were reported (Table 1). The planting of blue oak acorns resulted in no seedlings or saplings. Valley oak planting efforts in the Santa Ynez Valley produced 400 seedlings that in 1992 had not yet attained a release height of 6 ft. Two attempts to plant coast live oaks at Vandenberg Air Force Base failed; coast live oak plantings at Gaviota produced 69 seedlings that were 10 - 14" in 1992.

<u>Species</u>	<u>Removed</u>	<u>Required</u> mitigation	<u>Surviving in</u> <u>1992</u>	<u>Outstanding</u> requirements
Blue oak	878	10,000 acorns + research funding USFS	none	-
Valley oak	82	400	400	Waiting for 6 ft release height
Coast live oak	1303	1303	69	1234
totals	2263	1703	469	1234

Table 1. All American Pipeline project oak removal, original required mitigation, and requirements outstanding in 1992.

C. Alternative Oak Mitigation Program

In December 1992 the Santa Barbara Planning Commission determined that efforts to mitigate were unsuccessful and that All American Pipeline (AAPL) would instead be required to fund an alternative program. A Request for Proposals (RFP) was announced in September 1993 for an Alternative Oak Mitigation Program. This alternative program was intended to promote the "natural" regeneration of oak habitats within Santa Barbara County through fencing and cattle grazing management in order to increase the survivorship and recruitment of oaks.

The Request for Proposals described the following project assumptions:

The Oak Restoration Program is based on the assumption that cattle grazing in oak forest, woodland, and savanna habitats can be controlled and managed so as to enhance the natural regeneration of oaks. This assumption is based on two lines of evidence:

(1) Cattle grazing causes the loss of oak seedlings and the detrimental alteration of oak habitats through mechanisms such as grazing, trampling, soil compaction, defecation, and facilitation of the spread and dominance of weeds.

(2) Oak regeneration is negatively affected by the competitive presence of exotic weeds, especially winter-growing annual grasses of Mediterranean origin, which inhibit acorn germination and reduce the survival of oak seedlings.

A working hypothesis of this program is that cattle grazing early during the winter-spring growing season will inhibit weedy grasses, without adversely affecting oak seedlings. Subsequent curtailment of grazing, in combination with the reduced abundance and competitive effects of annual grasses, should optimize conditions for oak seedling establishment. The program should address predation by vertebrates other than cattle (e.g., birds, gophers, squirrels, deer, pigs), but the primary focus is to be on carefully managed cattle grazing.

D. Santa Barbara County Oak Restoration Program – UC Santa Barbara

In November 1993, the proposal submitted by the University of California Santa Barbara was selected to fulfill requirements for a Santa Barbara County Oak Restoration Program. Principal investigators Bruce Mahall and Frank Davis designed the restoration program as a long-term ecological investigation that would improve our understanding of the role of cattle and other ecological factors in limiting or promoting recruitment by valley oak (*Quercus lobata*), blue oak (*Q. douglasii*), and coast live oak (*Q. agrifolia*) in large-scale, landscape-level environments. The program represents a long-term commitment by the principal investigators, the University of California at Santa Barbara, and the UC's Natural Reserve System to: 1) restore several hundred acres of valley oak savanna and blue oak woodlands on Sedgwick Reserve, a 5896-acre ranch at the base of Figueroa Mountain; 2) conduct large-scale grazing and related experiments that will give practical guidance to resource managers and land owners in Santa Barbara County who are concerned with management and restoration of local oak woodlands; 3) disseminate findings in the form of presentations, onsite demonstration projects, and literature that is directed towards locals landowners and resource managers.

Funding and research were initiated in winter 1995. This report provides a summary of the work completed and research findings to date.

II. Site description

A. Sedgwick Reserve

Research and restoration are being conducted on the Sedgwick Reserve, a 5860acre (2372-ha) ranch located at the base of Figueroa Mountain in the Santa Ynez Valley in central Santa Barbara County (Figure 2). The reserve spans an elevation gradient from 950 to 2,600 ft (290 – 790 m) and is noted for both its large size and environmental heterogeneity. It contains a major geologic fault system and two distinctive geologic

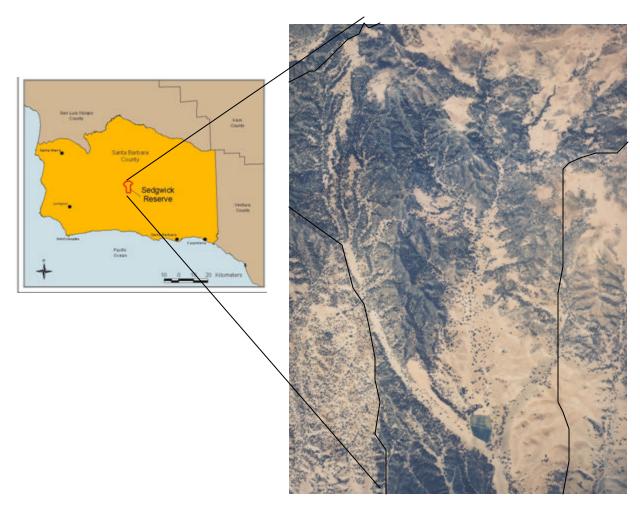


Figure 2. Sedgwick Reserve, Santa Barbara County, CA

formations: relatively young Paso Robles alluvium and much older Franciscan metamorphosed seafloor, including large areas of serpentine. The site contains major portions of two watersheds – Figueroa and Lisque. Diverse vegetation types include coast live oak forest, blue oak woodland, valley oak savannah, buckbrush chaparral, coastal sage scrub, grassland, willow riparian forest, and agricultural lands. Sedgwick Reserve is managed by the University of California Natural Reserve System (http://nrs.ucop.edu/) whose mission is to "contribute to the understanding and wise management of the Earth and its natural systems by supporting university-level teaching, research, and public service at protected natural areas throughout California."

Sedgwick has been an ideal location for this work for several reasons. First, all three species of oak impacted by the AAPL project – blue oak, valley oak, and coast live oak – co-occur and are common there. Second, the reserve's large size and diversity of terrain, soil type, and land-use history have provided the opportunity to examine survival and growth of oak plantings in a range of environmental conditions. Third, the reserve's use and management provide the stability required for the establishment and protection of a long-term planting experiment and restoration program that can be maintained far into the future. Finally, consistent with the reserve's dedication to research and outreach, their staff and docents have contributed countless hours toward infrastructure maintenance and toward educating the community about oaks and this restoration program.

B. Grazing regime and management

Under a cooperative grazing agreement with the College of Agriculture at California Polytechnic University, San Luis Obispo, and under the direction of faculty Mike Hall, students from Cal Poly maintained and cared for the cattle herd at Sedgwick, and assisted with the application of grazing treatments in our experiments, from 1995 to 2002. They also installed the majority of electric fencing and water pipe at the initiation of the project. From 2002 to 2004, cattle grazing was managed by John Solem of Wise Acres Ranch, adjacent to Sedgwick Reserve.

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The total area of grazed land on Sedgwick is 1060 acres (429 ha), and approximately half of this area (525 acres / 212 ha) includes the experimental pastures where planting and vegetation monitoring is being conducted for the Oak Restoration Program. Within the experimental areas, grazing pastures (paddocks) range from 1 to 52 acres, with an average size of 23 acres (9 ha). The timing and duration of grazing has varied from year to year, dependent on grass availability, but has been conducted each year in winter/spring between the period November – June. Herd size has also varied annually based on forage availability, but has averaged 124 heifers or cow/calf pairs.

In accordance with the Institutional Animal Care and Use Committee (IACUC) at UCSB, our research protocol, animal use records, and training sessions on handling and care of cattle at Sedgwick Reserve were overseen by UCSB's veterinarian and IACUC representative, Dr. Diane McClure.

C. Infrastructure

Infrastructure present at Sedgwick Reserve prior to initiation of this study included roads, over 20 miles of barbed wire perimeter and pasture fencing, cattle troughs and corrals. The Sedgwick Reserve purchased and installed high voltage energizers to charge the electric fence, and has contributed over a thousand person-hours toward maintenance of infrastructure for this project (fencing, gates, water lines, tanks). Using funds from the SBCORP, and hundreds of hours of volunteer assistance from Cal Poly San Luis Obispo students and others, we have installed and maintained more than 15 miles of electric fencing for experimental plots, grazing paddocks, and riparian habitat protection; 4.5 miles of water pipe; two 10,000 gallon water storage tanks; and six additional water troughs.

III. Results

A. Restoring oak habitats: numbers of established seedlings/saplings

The emphasis of planting activities has been on conducting large-scale, replicated experiments to determine the relative importance of factors influencing growth and survival of oaks. Thus, not all treatments necessarily promote establishment of oaks (e.g., planting in dry years, or without protection from grazers) but are critical to the study design. These activities differ from those carried out in a strictly restoration-oriented program, in that the ratio of successfully established seedlings to planted acorns is less than it would be if the goal were solely to plant oaks and protect them with any means available. However, one of the goals of UCSB's program is to restore oak woodland and savanna, and therefore all planting activities have been carried out in areas that are appropriate (i.e., suitable for establishment of oak, and in areas that will be protected from future development) and that will benefit from establishment of young oaks. The total area within which planting is being conducted for the Oak Restoration Program is 525 acres (212 ha). As a result of our planting experiments to date there are currently valley and coast live oaks of five age classes (Table 2), most of which are still under 1 meter high (Figure 3). There are a total of 220 coast live oaks, within 146 individual planting locations, ranging in size from 3 - 214 cm; the average height for all age classes combined is 55 cm. There are a total of 573 valley oaks, within 406 planting locations,

ranging in size from 2 - 192 cm; average seedling height for all age classes combined is 31 cm.

			planting year			
• • • •	<u>1996-97</u>	<u>1997-98</u>	<u>1999-2000</u>	<u>2000 - 2001</u>	<u>2002 - 2003</u>	Sum
Quercus lobata	11	175	105	90	192	573
Quercus agrifolia	<u>6</u>	<u>120</u>	<u>21</u>	<u>36</u>	<u>37</u>	<u>220</u>
sum	17	295	126	126	229	793

Table 2. Total number of seedlings of each species in each age class surviving to May 2004.

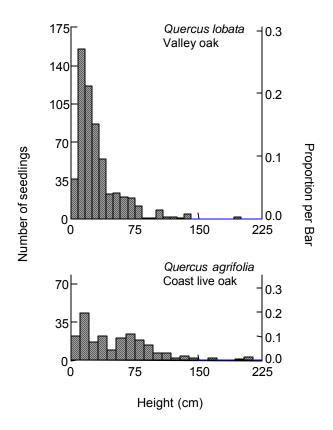


Figure 3. Size distribution of valley oak and coast live oak seedlings and saplings resulting from planting experiments conducted 1996 – 2003. Data are heights measured in June 2004 and include all five age classes.

B. Literature review – factors limiting recruitment of oaks

Funded primarily by the Packard Foundation, we (with Bill Kuhn from UCSB) prepared a comprehensive review of the scientific literature on factors limiting recruitment in valley, blue and coast live oaks (see Appendix A). We provide here a summary of those findings.

We reviewed over 150 published articles that focused on some aspect of oak population size- or age-structure, changes in populations over time, and stage-specific mortality and recruitment. Blue oaks are the species that have been most studied, followed by valley and coast live oak; other California oak species were the focus of fewer than 20% of all studies. The majority of studies have focused on acorns and seedlings; there is a conspicuous lack of information about the factors affecting the transition from seedlings to saplings, and from saplings to adults, mainly because saplings are uncommon and because long-term study is required. Most research has been of short duration (one to two years), and thus little is known about how recruitment, survival and growth vary over time at a site.

Considerable research has been conducted on the biological and physical factors that limit natural seedling recruitment of oaks. There is consistent evidence that acorn predation, herbivory of established seedlings and saplings, and low rainfall in some years can significantly limit seedling recruitment in the field; competition between oak seedlings and non-native annual grasses for water has also been shown to reduce establishment rates. Other factors cited as limiting establishment include acorn diseases, soil compaction by cattle, lack of fire, and low tree population density. Successful oak recruitment appears to require a combination of events including abundant acorn production, sufficient rainfall, limited competition for light and water from neighbors, and protection from seed predators, herbivores, and browsers. Any one of these may act as a limiting factor in preventing the recruitment of seedlings and the subsequent transition to sapling and tree.

Although research has demonstrated what treatments or interventions are necessary to ensure high rates of initial oak seedling establishment, far less is known about factors limiting establishment of saplings. The most significant gaps in our knowledge of seedling and sapling establishment are data on survival rates among size/age classes, and how various treatments or locations influence those rates. Such information will require bng-term study, including historical aerial photography, ringbased age structure analysis, and monitoring of permanent plots, to determine spatial and temporal variation and trends in oak demography, and in particular causes and rates of mortality within the sapling and adult life stages.

C. Tree cover dynamics in foothill woodland of Sedgwick Ranch, Santa Barbara County, 1943-1989

Mapping the modern and historical distribution of oak woodlands at the Sedgwick Reserve was an important first step in designing the restoration experiment. This information was used to measure trends in oak cover and density, to identify areas of historic oak removal that would be prime candidates for restoration, and to lay out experimental plots across a range of environments with varying oak density and population trends.

1. <u>Methods</u>

We used archival air photos to measure changes in oak density between 1943 and 1989. First, twenty monitoring areas totaling 962 acres were mapped using 1989 photography. We mapped areas of relatively uniform topography and soil conditions that currently supported or historically supported oak woodland or savanna. We did not attempt to map and monitor oak density in dense oak woodland and forest because it was not possible to identify individual trees. The map polygons were drawn onto mylar sleeves covering the photos, and the lines were then transferred to a 1977 orthophotoquad before being digitized and stored in a Geographic Information System (GIS) (Figure 4).

After a search of archival aerial photography at the UCSB Map and Imagery

Laboratory we selected four dates for oak monitoring (Table 3) based on criteria of image

quality, scale (1:20,000 - 1:24,000), and time of year (summer, the season of minimum

shadowing). The years of observation were 1943, 1954, 1967 and 1989. Examples of the

1943 and 1967 imagery, and a more recent 1993 orthophoto, are shown in Figure 5.

Table 3. Aerial photography used to measure changes in oak density at Sedgwick Reserve for the period 1943-1989.

Flight Symbol BTM, USDA 2609-41B, frames dated September 19, 1943, 1:20,000 black & white paper prints, flown by Aero Service Corp., Philadelphia, PA for US Dept. of Agriculture, Agriculture Adjustment Administration. Frames used: 1B-81 to 1B-85, 1B-103 to 1B-108.

Flight Symbol BTM-PMA-6-53-DC, Item No. 3, frames dated June 6, 1954, 1:20,000 black & white paper prints, flown by Pacific Air Industries, Long Beach, CA for US Dept. of Agriculture, Production and Marketing Administration. Frames used: 12K-86 to 12K-90.

Flight Symbol BTM, Invitation No. ASCS 9-67 DC, Item 6, frames dated May 14, 1967, 1:20,000 black & white paper prints, flown by Western Aerial Contractors, Inc., Eugene, OR for US Dept. of Agriculture, Agricultural Stabilization and Conservation Service. Frames used: 2HH-9 to 2HH-11, 2HH-70 to 2HH-73, 2HH-86 to 2HH-90.

Flight PW-SB 7, frames dated July 31, 1989, 1:24,000 color paper prints, flown by IK Curtis Services, Inc., Burbank, CA for Pacific Western Aerial Surveys, Santa Barbara, CA. Frames used: 234, 235, 255, 256.

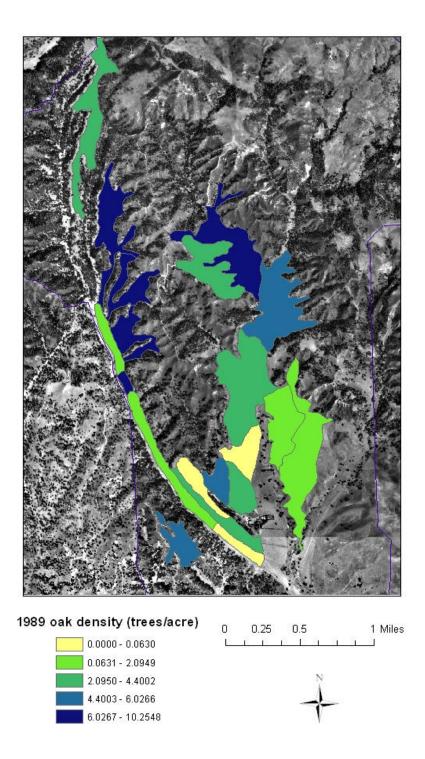


Figure 4. Map of 20 oak woodland and savanna areas on Sedgwick Reserve that were monitored for changes in oak density during the period 1943-1989. Colors indicate oak density in 1989. Map polygons are displayed on a 1993 orthophoto of the Sedgwick Reserve. The reserve boundary is indicated by the blue line.

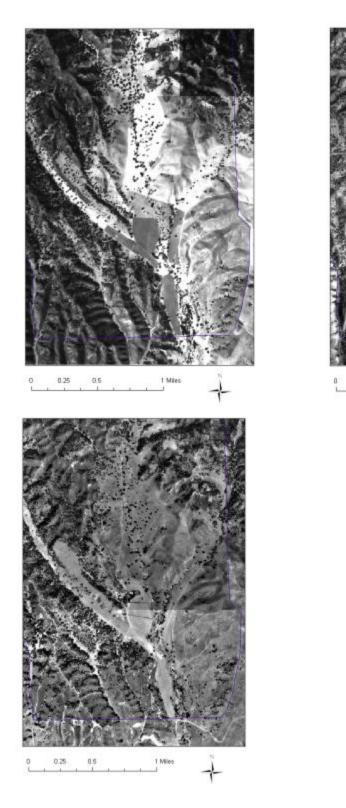


Figure 5. Sample historical air photos of the southern portion of Sedgwick Reserve from 1943 (upper left), 1967 (upper right) and 1993 (lower left). The blue line is the reserve boundary.

0.5

0.25

1 Miles

Interpretation was performed on all twenty polygons in each time period. Frames were viewed in stereo using an Aeroscope mirror stereoscope with 3X binocular lenses. Trees in each polygon were marked on a mylar sleeve covering the photo. Whenever possible, the size of the mark was made to reflect the relative size of the canopy being marked. We were not always able to tell whether a large crown was a single tree or a clump of two or more trees growing together. Instead we simply counted every distinct crown area as an individual. Thus our densities may underestimate the actual number of trees but still serve to show relative changes in tree density through time. Also, we could not always reliably discriminate blue oak, valley oak and coast live oak canopies in the summer imagery, so we cannot report species-specific trends.

Table 4. Summary of changes in oak density through time in oak woodlands and savannas of Sedgwick Reserve. Population growth rate is the annual rate of population growth, calculated as (number of trees in time 2 / number of trees in time 1) ^(1 / number of years between t1 and t2). Values of 1 indicate no change in population, greater than 1 indicate population increase, and less than 1 indicate declining population.

	Stand density (trees per acre)					Population growth rate			
Stand	1943	1954	1967	1989	43-54	54-67	67-89	43-89	
1	3.99	3.85	3.78	3.66	0.997	0.998	0.999	0.998	
2	9.67	9.62	7.79	7.78	1.000	0.984	1.000	0.995	
3	10.72	10.59	10.34	10.25	0.999	0.998	1.000	0.999	
4	4.46	4.38	4.31	4.23	0.998	0.999	0.999	0.999	
5	11.58	11.47	9.67	9.42	0.999	0.987	0.999	0.995	
6	6.22	5.07	4.91	4.84	0.981	0.998	0.999	0.994	
7	3.26	1.82	1.44	1.44	0.949	0.982	1.000	0.982	
8	11.83	11.83	9.12	8.76	1.000	0.980	0.998	0.993	
9	4.78	4.64	4.57	4.40	0.997	0.999	0.998	0.998	
10	2.30	2.21	2.11	2.09	0.996	0.997	1.000	0.998	
11	9.66	9.48	9.13	9.13	0.998	0.997	1.000	0.999	
12	4.77	2.37	2.33	2.03	0.939	0.999	0.994	0.981	
13	2.54	2.47	2.33	2.03	0.997	0.996	0.994	0.995	
14	0.06	0.03	0.03	0.03	0.939	1.000	1.000	0.985	
15	4.01	0.00	0.00	0.00	0.000	0.000	0.000	0.000	
16	5.48	5.48	5.48	5.48	1.000	1.000	1.000	1.000	
17	3.97	3.67	3.44	3.44	0.993	0.995	1.000	0.997	
18	4.17	3.60	3.10	2.93	0.987	0.988	0.997	0.992	
19	6.19	6.19	6.19	6.03	1.000	1.000	0.999	0.999	
20	0.13	0.06	0.06	0.06	0.939	1.000	1.000	0.985	
Average	5.49	4.94	4.51	4.40					

2. <u>Results</u>

For 1943 we counted 5,343 oaks in the twenty stands at an average density of 5.49 trees per acre (Table 4). Over the 46-year survey period, 897 canopy trees disappeared, representing 16.7% of the starting sample and an average mortality of 37 trees/10,000 trees/year (Figure 6). Average stand densities declined from 5.49 trees per acre to 4.40 trees per acre. No recruitment of new canopy oaks was observed in the 962-acre study area during the time period 1943-1989.

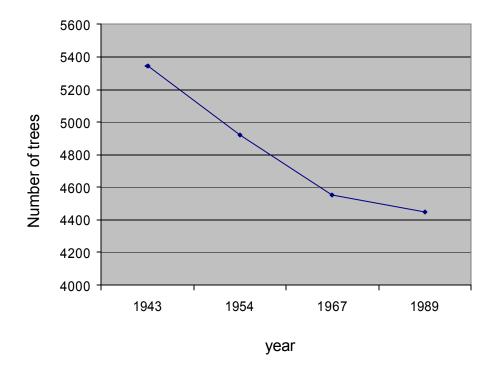


Figure 6. Changes in total oak population size in 20 sample stands (962 acres) on Sedgwick Reserve, 1943 – 1989.

One stand was cleared between 1943 and 1954 for an airplane landing strip (Figure 7; Table 4, stand #15). Except for a stand that showed no change in tree density, the remaining stands all exhibited a gradual decline in oak population sizes; annual population growth rates were less than one, indicating declining population growth (Table 4). On average, the annual rate of population decline was slightly higher during the period 1943-1954 than in the other periods, even ignoring the one stand that was cleared. Annual rates of decline were highest in Lisque Canyon in the part of the valley floor that was cultivated historically but, like the other stands, was grazed during the period of observation.

3. Discussion

Observed oak densities and population trends were comparable to those measured in other areas of Santa Barbara County. Oak densities in the 20 stands observed ranged from less than one to nearly 12 trees per acre, spanning the range of values that were observed by Davis et al. (2000) in their inventory of oak woodlands and savannas in the Los Alamos Valley. Like previous studies of Santa Barbara County oak savannas and woodlands with grass understories, we observed a gradual but steady decline in oak populations. In the Santa Ynez Valley, Brown and Davis (1991) documented a 21% decline in the number of overstory valley oaks between 1938 and 1989. No new trees established in the twelve surveyed populations during this time period. In a detailed mapping study of tree populations in lower Figueroa Creek Valley on Sedgwick Reserve, Sork et al. (2002) reported a 20.3% loss of valley oaks in a 325-acre study area between 1943 and 1999.

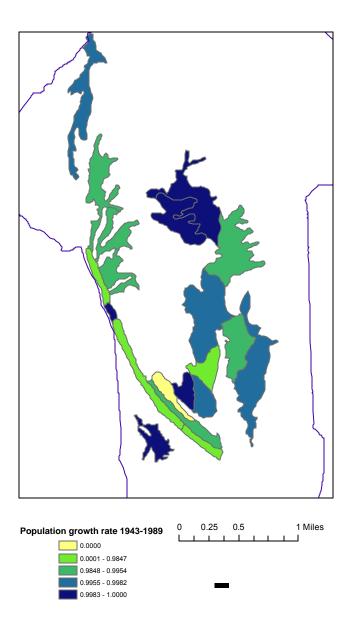


Figure 7. Average oak population growth rates for the period 1943 – 1989. Smaller numbers (lighter green) indicate faster rates of population decline. The yellow area was cleared between 1943 and 1954 and exhibited no regeneration between 1954 and 1989.

Because of their longevity and relatively low densities, oak populations must be surveyed over long time periods and large study areas to measure population trends. Our historical analysis of oaks on the Sedgwick Reserve clearly indicates that large areas of the reserve have supported higher oak densities in the recent past and would thus be good candidates for oak restoration. Oak woodlands on the reserve have experienced a range of land use histories providing an opportunity to study oak restoration methods in areas that have undergone complete tree removal to mechanical tillage under the tree canopies to grazing. With this background information we were able to locate the experimental plots for the grazing experiment to sample these variations in land use history.

D. Large-scale planting experiments

The major work effort of The Santa Barbara County Oak Restoration Program has been to conduct replicated large-scale planting experiments in four different years to determine the effects of cattle and other ecological factors on oak seedling establishment in oak savannas and woodlands. At the site of this research, the Sedgwick Reserve in the Santa Ynez Valley, the climate is Mediterranean, with hot dry summers and cool wet winters. Mean annual rainfall (calculated for a 55-year period) is 400 mm (15.8 inches). Total precipitation (as recorded at the nearest National Weather Service recording station) for the rain-years including 1996 – 2001, when planting was conducted, ranged from 300 mm in 1996-1997 to 830 mm in 1997 – 1998 (Figure 8). As described previously, cattle grazing at Sedgwick Reserve during this period was conducted under a cooperative grazing agreement with the College of Agriculture at California Polytechnic University, San Luis Obispo.

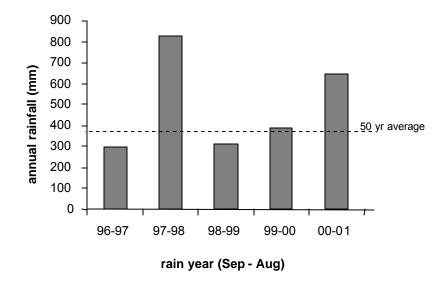


Figure 8. Annual rainfall from fall 1996 through summer 2001 at Sedgwick Reserve. Data are from the Santa Ynez fire station, ~9 km from the reserve.

In September - October of 1996, 1997, 1999, and 2000, we collected acorns with assistance from students and other volunteers from the community. With each collection group, we conducted a short tour of Sedgwick Reserve, discussed the goals of the Oak Restoration Program, and taught volunteers to identify the three species of oaks that occur on the Reserve. Each year, we collected between 1500 – 4000 acorns of coast live oak and valley oak. We mapped the location of each tree from which acorns were collected, and labeled bags with the identity of each parent tree. In the laboratory damaged or insect infested acorns were discarded, and the remaining acorns were placed in a bucket filled with water and bleach (1/2 cup bleach to 1 gallon water). Floating acorns were discarded. Intact ("good") acorns were air dried, counted, placed in plastic

bags with vermiculite, and stored in refrigerated coolers (temperature = 5° C) prior to planting.

Our large experimental plots were 50 x 50 m. Fifteen of these large plots were controls, open to cattle grazing, and fifteen excluded cattle with the use of electric fence. In savanna areas, we centered each plot on an adult oak tree, the canopy of which covered an average of 10% of the total plot area. A total of eight plots were located in an area where all trees had been cut in ~1950 (the "Airstrip"), and thus these had no oak canopy cover. Plots were chosen in pairs, with one plot randomly selected to be fenced to exclude cattle. These plots were established in 1995. In addition, 3 single 50 x 50 m plots were established in 1996 in three large ungrazed areas.

Within the plots, experimental treatments included: 1) no protection from mammalian grazers (Fig. 9a), 2) protection from large animals such as cattle, deer, and pigs (Fig. 9b), and 3) protection from small mammals such as gophers and ground squirrels, birds, and large animals (Fig. 9c). The characteristics, or conditions, of these treatments varied depending on whether they were within large plots grazed by cattle or plots fenced to exclude cattle (Table 5). Most notably, within grazed plots grass and herbaceous cover was reduced on average for all treatments, while ungrazed plots generally had abundant cover and biomass of grasses and other vegetation. Also, the "open" treatment was not accessible to cattle in the ungrazed plots.

Large cages that protected from deer, pigs, and cattle (Fig. 9b) within the plots were constructed of 4' high, 2" x 4" mesh galvanized wire (12 gauge); the y were vertical cylinders (diameter = 18") and supported at one side with a 5' t-post, and at the other side with a 4' rebar; this design was based on the "Vaca cage" described in Swiecki and Bernhardt (1991). Smaller cages to exclude both small and large mammals (Fig. 9c) were vertical cylinders constructed of 3' high hardware cloth (mesh size = 0.5"); they were sealed at both ends with aviary wire. In positions with cages (small mammal exclusion), the cages were set 12" into the ground. Each of these treatments was replicated 5 times within each plot for each species. We included several additional treatments, which varied among years. In 1996-1997, and 1997-1998, we also planted in cage controls, one per species per plot, to test for artifacts of our caging treatment (Fig 9d); this treatment allowed access to small mammals but mimicked some of the potential "side-effects" of caging such as shading, and increased moisture deposition.

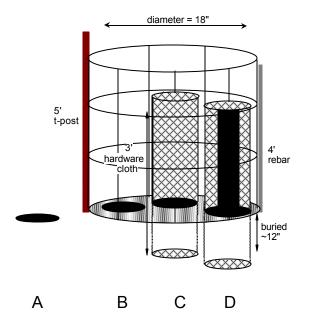


Figure 9. Treatments used for acorn plantings. A: open. B: fenced to prevent grazing by large animals. C: caged and fenced to prevent grazing and herbivory by both large and small mammals and birds. D: cage control to test for caging artifacts (small cage open at one side). These treatments are replicated in both 1) plots that are grazed by cattle and 2) plots that are fenced to exclude cattle.

	-	RAZED azed by cattle		GRAZED cluding cattle		
	plantings	accessible to:		plantings	accessible to:	
<u>Treatment</u>	<u>small mammals</u>	deer & pigs	<u>cattle</u>	<u>small mammals</u>	<u>deer & pigs</u>	<u>cattle</u>
"open"	Yes	Yes	Yes	Yes	Yes	No
"no lg mammals"	Yes	No	No	Yes	No	No
"no sm or lg mammals"	No	No	No	No	No	No
		herb cover: duced			<u>herb cover:</u> undant	

Table 5. Characteristics of treatments within large plots grazed by cattle vs. those excluding cattle.

In 1997-1998, we re-used planting locations dug in the previous year, and therefore included an additional treatment (repetition of treatment illustrated in Fig 9a) to determine whether seedling establishment was affected by re-using planting positions. In 1999-2000, and 2000-2001 we included an additional treatment (similar to treatment illustrated in Fig 9c, but with no bottom on the mesh cylinders), one per species per plot, to test an alternative to our small mammal exclosure; this cage was similar to the small cage – 3' high hardware cloth, sealed at the top with aviary wire, and set 12" into the soil - but the bottom was open to allow roots to grow unrestricted.

We employed a stratified random design to designate positions for planting within the large 50 x 50 m plots (Figure 10). We added an additional complete set of planting positions to the plots each year, with the exception of 1997 - 1998, when we re-used positions established in the previous year because survival had been so poor, and thus nearly all positions were empty (i.e., devoid of seedlings).

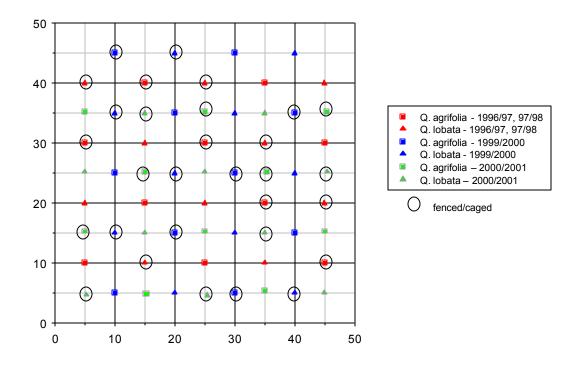


Figure 10. Design for the designation of planting positions within large 50 x 50m plot. Squares indicate positions where *Quercus agrifolia*, coast live oak, are planted; triangles are *Q. lobata*, valley oak. Uncircled figures represent locations for open treatments. All circled figures represent locations that include 2 treatments: fenced to prevent large mammal grazing, and fenced & caged to prevent large and small mammal grazing. At two of the circled locations per plot, one per species, there is one additional treatment in each planting year: cage controls.

Following the onset of consistent seasonal rains (generally December or January), at each planting location holes were augured to a depth of 12", soil replaced and two viable acorns planted 1-2" below the soil surface. We planted acorns collected from valley oak and coast live oak on the site in the fall of the same year. Prior to planting, acorns were placed into buckets of water. Acorns that floated were discarded; we planted only acorns that sank and appeared viable. Acorns and seedlings did not receive supplemental watering.

In winters of four years, 1996 - 1997, 1997 - 1998, 1999 - 2000, and 2000 - 2001, we planted approximately 1000 acorns of each species (see Table 6), thereby establishing four cohorts, or age classes. (A **cohort** is defined as a group of individuals of the same age, recruited into a population at the same time.) Acorns were extremely rare in fall 1998, so no planting occurred in 1998-1999. In 1996-1997, and 1997-1998, we planted in all 33 plots. In January 1998 (El Niño year), the trees in the middle of 2 of these plots were blown over. The broken trunks and downed large limbs made future planting in these plots unfeasible. Because the plots are paired, we removed the two sets of plots (total of 4) from additional planting experiments, reducing the number of plots in 1999-2000, and 2000-2001 to 29: 13 fenced, 13, unfenced, and 3 in large ungrazed pastures.

<u>Treatment</u> open	<u>1996-1997</u> 5	# locations plan <u>1997-1998</u> 5	nted per plot <u>1999-2000</u> 5	<u>2000-2001</u> 5
large mammal exclosure	5	5	5	5
small mammal exclosure	5	5	5	5
cage control	1	1	-	-
additional open	-	5	-	-
cage alternative (no bottom)	-	-	1	1
total locations per plot	16	21	16	16
number acorns planted per location	2	2	2	2
number of large plots (50 x 50m) planted	33	33	29	29
total acorns planted per species per year	1056	1386	928	928
total acorns planted	2112	2772	1856	1856

Table 6. Number of locations and total number of acorns planted each year.

To achieve adequate replication in all treatments, we were able to include two species of oak in these experiments. We considered a number of factors in deciding to plant valley and coast live oak, and not blue oak. Valley oak was selected because it is the oak species of greatest concern in California, in large part because its reported recruitment is the lowest among all eight oak tree species in the state (Griffin 1971, Muick and Bartolome 1987, Bolsinger 1988). This species has also been heavily impacted through various forms of development as its distribution coincides with areas of intense land use and land development, contributing to its perceived critical status. Coast live oak provides an excellent comparison to valley oak because: 1) it commonly occupies the same type of savanna and open woodland habitat, 2) it is every even in contrast to the fully deciduous valley oak, and 3) it is reported to have much higher levels of natural seedling establishment. Although there is overlap in distribution, blue oak generally occupies drier slopes rather than the alluvial valleys and terraces where valley oak and coast live oak co-occur. Of the three oak species dominant in Santa Barbara county, coast live oak has been the least studied, while blue oak has received the majority of prior scientific study on oaks. Thus, a comparative study of valley and coast live oak presented the best opportunity to make a significant contribution toward understanding factors limiting establishment of oaks in Santa Barbara County and California.

1. Cohort planted in 1996-1997: survivorship and growth

Emergence and survivorship were both very low for this first planting effort. Rainfall in 1996-1997 was well below average, with the last rainfall of the season occurring in mid-January 1997, only weeks after planting was completed. Only a total of 17 seven-year-old seedlings have survived to date. There are presently 11 seven-year-old valley oak and 6 seven-year-old coast live oak seedlings surviving from this cohort, or age class. The treatment that was most successful was that which excluded small and large mammals (Figure 11, see "no sm or lg mammals"). There is one valley oak seedling surviving from the 1996 - 1997 planting that is in the open. There are more seedlings present in areas that are grazed by cattle than in ungrazed areas (11 vs. 6).

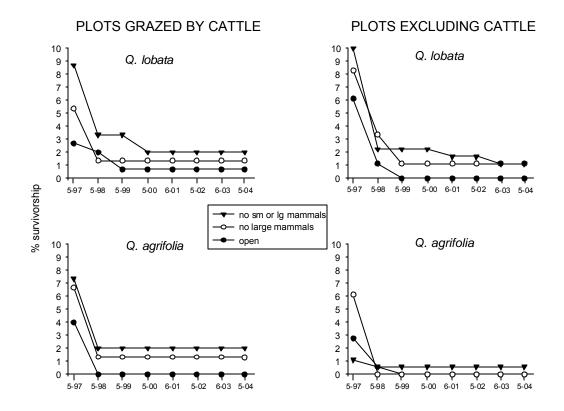


Figure 11. Percent survivorship of 7-yr old seedlings (planted in 1996-97) in large plots grazed by cattle, vs. those fenced to exclude cattle. Data are totals [100 * (# seedlings/#acorns planted)] for three experimental treatments for eight sampling dates. Note scale of y-axis: maximum value=10.

Seven-year-old valley oak seedlings range in height from 10 to 116 cm (4 to 46"), with a mean of 55 cm (22"). Seven-year-old coast live oak seedlings range from 14 to 110 cm (5 to 43") with a mean of 73 cm (29").

2. Cohort planted in 1997-1998: survivorship and growth

In contrast to the previous year, this planting year was accompanied by an El Niño weather pattern and above-average rainfall. The cohort of seedlings established in this year, is the largest of all four planting efforts (Figure 12). Including all treatments and both species, 11% of the acorns planted in 1997-98, are now seedlings/saplings. There are currently 295 six-year-old seedlings (175 valley oak, and 120 coast live oak).



Figure 12. Saplings planted in 1997-1998 protected from both small and large mammals. On the left is *Q. agrifolia* and on the right is *Q. lobata*. Both individuals are over 2 m tall.

There were no significant differences between cage controls and fenced "open" locations in seedling establishment, or numbers of individuals surviving in 2004, for either species (logit regression: p > 0.1). We also found no significant differences between these two treatments in seedling height for any date, or growth rates for either species (ANOVA: p > 0.1). Thus we conclude that the cages that exclude small animals do not have unknown secondary effects or "caging artifacts" beyond the exclusion of small mammals.

We compared open locations re-used from the 1996-1997 experiments to open locations freshly dug in 1997-1998. There were no significant differences between these two treatments in seedling establishment, or numbers of individuals surviving in 2004, for either species (logit regression: p > 0.1), nor were there any significant differences between these two treatments in seedling height for any date, or growth rates for either species (ANOVA: p > 0.1). Thus we conclude that using freshly dug holes vs. holes dug in the previous year did not impact success rate, and we combined these two treatments in following analyses.

The highest seedling/sapling emergence and establishment rates are for those protected from small mammals (Figure 13). Seedling establishment was greater in this treatment than in the open controls, locations protected from large mammals only and in both grazing treatments for all dates for both species (logit regression p<.05). One surprising result was that protection from large animals was only different from unprotected, open controls in both grazed and ungrazed plots for a few dates (1998 for valley oak, and 1998 – 2000 for coast live oak), indicating that small mammals severely limit oak seedling recruitment even when acorns and seedlings are protected from cattle and deer. Highest average mortality rates have been for seedlings planted in the open (~28% per year for valley oak, and ~43% per year for coast live oak) (Table 7).

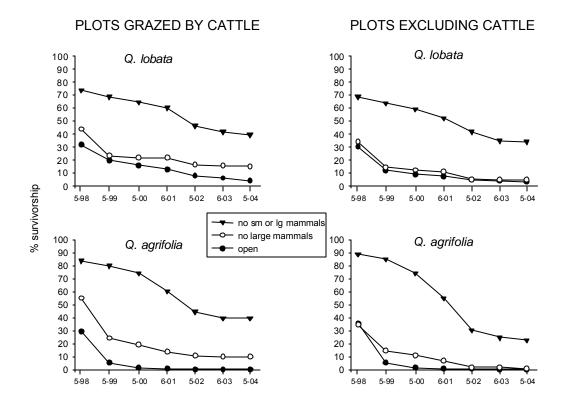


Figure 13. Percent survivorship of 6-yr old seedlings (planted in 1997-98) in large plots grazed by cattle, vs. those fenced to exclude cattle. Data are totals [100 * (#seedlings/#acorns planted) for three experimental treatments for seven sampling dates.

Mortality has been slightly higher in fenced/ungrazed plots than in plots grazed by cattle (Table 7). In addition, fenced plots (all treatments combined) have had fewer surviving seedlings than grazed plots for both species most years (statistically significant in 1999- 2004 for valley oak, and in 2002 – 2004 for coast live oak; logit regression p<.05). This suggests a positive effect of cattle grazing on oak seedling recruitment, when individual seedlings are protected.

Table 7. Percent mortality for each year, annual mean, and standard error (SE), for each species and treatment for the cohort planted in 1997-1998. Treatments are: open, fenced to prevent grazing by large animals (no lg anim), and caged to exclude both large and small mammals (no sm or lg mamm). Mortality calculated as: 100*(number yr 2 – number yr 1)/(number yr 1).

				mortality	rate (%)				
	treatment	<u>98-99</u>	<u>99-00</u>	<u>00-01</u>	<u>01-02</u>	<u>02-03</u>	<u>03-04</u>	<u>mean</u>	<u>SE</u>
Valley oak	open	37.2	20.3	19.1	39.5	21.7	33.3	28.5	3.7
plots grazed by cattle	no lg anim	46.9	5.9	0.0	25.0	4.2	4.3	14.4	7.4
- 	no sm or Ig mamm	6.6	6.1	6.5	23.0	10.4	5.0	9.6	2.8
	open	60.2	25.6	15.6	37.0	17.6	14.3	28.4	7.2
plots excluding cattle	no lg anim	56.9	16.0	9.5	52.6	11.1	0.0	24.4	9.9
	no sm or Ig mamm	7.6	7.3	11.8	20.0	16.7	1.7	10.8	2.7
Coast live oak	open	81.8	75.0	50.0	50.0	0.0	0.0	42.8	14.5
plots grazed by cattle	no lg anim	55.8	20.6	29.6	21.1	6.7	0.0	22.3	8.0
	no sm or Ig mamm	4.1	7.7	18.5	26.1	10.8	0.0	11.2	3.9
	open	85.0	73.7	40.0	0.0	66.7	0.0	44.2	15.2
plots excluding cattle	no lg anim	58.1	23.1	40.0	75.0	0.0	66.7	43.8	11.6
	no sm or Ig mamm	4.4	12.6	25.8	44.9	18.5	9.1	19.2	6.0

Contrary to our expectations, mortality rates have been higher for coast live oak than for valley oak nearly every year, in every treatment. This result suggests that observed patterns of high natural recruitment in coast live oak (e.g., Bolsinger 1988), are not due to higher seedling survivorship rates in this species, but may be a result of other factors such as differences in acorn production or seed predation rates.

Surviving six-year-old valley oak seedlings range greatly in height, from 4 to 192 cm (2 to 76") with a mean of 45 cm (18"). Heights of surviving six-year-old coast live

oak seedlings also range greatly, from 7 to 214 cm (3 - 84") with a mean of 72 cm (28"). The tallest seedlings present in our experiments are those planted in this cohort. Seedling height has been significantly higher in the "no rodent" treatment compared to controls in all years, for both species (ANOVA: p < .05). From 1999 – 2001, seedling of both species in the "no rodent" treatment were taller than those in locations protected from large grazers only, but since 2004 these differences were no longer significant, suggesting that exposure to small mammals may not limit growth once seedlings have reached a certain size or age class.

3. Cohort planted in 1999-2000: survivorship and growth

Acorn production in the fall of 1998 was extremely low, so the next planting was conducted the following year in fall 1999/winter 2000, a year of average rainfall. Including all treatments and both species, 7% of the acorns planted in 1999-2000, are now seedlings. There are currently 126 four-year-old seedlings (105 valley oaks, and 21 coast live oaks). Seventy percent of these seedlings are in the treatments protected from small mammals.

As above, the highest seedling/sapling emergence and establishment rates for both species are for those protected from small mammals (Figure 14). Seedling establishment was greater in this treatment than in open controls, the locations protected from large mammals only and in both grazing treatments for all dates for valley oak (logit regression p<.01). Protection from large animals was only different from unprotected, open controls for initial emergence in May 2000 for valley oak, indicating that small mammals limited oak seedling recruitment even when seedlings were protected from cattle and deer.

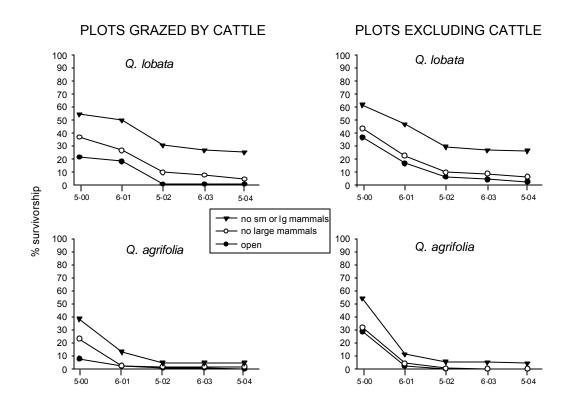


Figure 14. Percent survivorship of 4-yr old seedlings (planted in 1999-2000) in large plots grazed by cattle, vs. those fenced to exclude cattle. Data are totals [100 * (#seedlings/#acorns planted) for three experimental treatments for five sampling dates.

Establishment of coast live oaks was low in all treatments, and locations protected from small mammals had significantly higher establishment rates only in the first year, 2000. Both species had significantly higher seedling emergence in fenced/ungrazed plots (May 2000), but subsequent numbers of seedlings surviving has not differed in grazed and ungrazed areas.

Highest average mortality rates have been for seedlings planted in the open, followed by those protected from large grazers only (Table 8). Mortality has also been slightly higher overall in fenced/ungrazed plots compared to plots grazed by cattle(Table 8). As we observed with the cohort planted in 1997-98, mortality rates have also been higher for coast live oak than for valley oak every year, in every treatment for this cohort. **Table 8.** Percent mortality for each year, annual mean, and standard error (SE), for each species and treatment for the cohort planted in 1999-2000. Treatments are: open, fenced to prevent grazing by large animals (no Ig anim), and caged to exclude both large and small mammals (no sm or Ig mamm). Mortality calculated as: 100*(number yr 1 – number yr 2)/(number yr 1).

	1	00.04		y rate (%)			05
	treatment	<u>00-01</u>	<u>01-02</u>	<u>02-03</u>	<u>03-04</u>	<u>mean</u>	<u>SE</u>
Valley oak	open	14.3	95.8	0.0	0.0	27.5	23.0
plots grazed by cattle	no lg anim	27.1	62.9	23.1	40.0	38.3	9.0
	no sm or Ig mamm	8.5	38.5	12.5	5.7	16.3	7.5
	open	54.2	63.0	30.0	42.9	47.5	7.1
plots excluding cattle	no lg anim	48.6	55.6	12.5	28.6	36.3	9.8
	no sm or Ig mamm	24.2	37.3	8.5	2.3	18.1	7.9
Coast live oak	open	70.0	100.0			85.0	10.6
plots grazed by cattle	no lg anim	90.0	33.3	0.0	0.0	30.8	21.2
	no sm or Ig mamm	66.0	64.7	0.0	0.0	32.7	18.9
	open	91.3	100.0	•		95.7	3.1
plots excluding cattle	no lg anim	86.3	85.7	100.0		90.7	4.0
	no sm or Ig mamm	79.3	50.0	11.1	12.5	38.2	16.4

Surviving four-year-old valley oak seedlings range in height from 3 to 72 cm (1 to 28") with a mean of 24 cm (9"). Heights of surviving four-year-old coast live oak seedlings range from 10 to 63 cm (4 - 25") with a mean of 35 cm (14"). Seedling height was significantly higher in the "no rodent" treatment (mean 29.0 cm, se 1.6) compared to controls (mean 10.0 cm, se 1.9) and locations protected from large grazers (mean 20.4 cm, se 2.6) in 2004, for valley oak (ANOVA: p<.01). There were no significant differences between treatments for coast live oak heights.

Establishment and growth of seedlings was not significantly different between full cages and "alternative" cages with no bottoms for either species (logit regression on establishment data: p > 0.1; ANOVA on height and growth of seedlings: p > 0.1). We conclude that cages do not require bottoms to effectively exclude small mammals and reduce initial mortality from underground herbivores.

4. <u>Cohort planted in 2000-2001: survivorship and growth</u>

Establishment rates for this cohort were similar to previous years, but less than might have been predicted based on rainfall, which was well above average for the rain year 2000-2001 (Figure 8). A significant source of mortality this year was herbivory by insects that affected seedlings in all treatments; there was an outbreak of grasshoppers in the Santa Ynez Valley, and many newly emerged seedlings were completely defoliated.

As in the previous years' plantings, the highest establishment rates for both species have been for seedlings that are protected from small mammals (Figure 15). Including all treatments and both species, 7% of the acorns planted in 2000-2001, are now established seedlings. There are currently 126 established three-year-old seedlings (90 valley oaks, and 36 coast live oaks). Ninety-one percent of these seedlings are in the treatments protected from rodents (i.e., "no rodent" and "alternative cage" treatments). For both species and on all dates, seedling establishment was significantly higher in locations protected from small mammals than in either those protected from large animals or in open controls (logit regression, p < .01). Protection from large animals did not improve survivorship over open controls. There also were no differences in

establishment in grazed versus ungrazed plots, indicating that cattle grazing did not limit or promote oak seedling recruitment in this cohort.

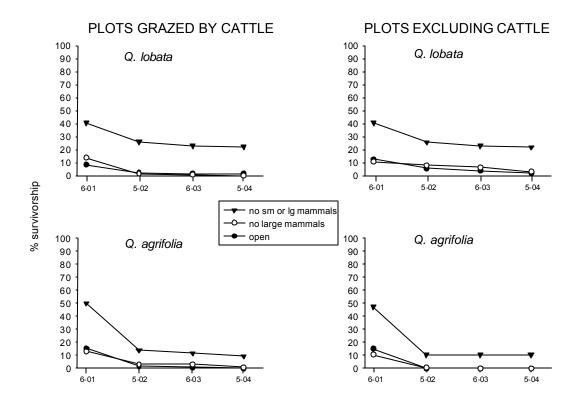


Figure 15. Percent survivorship of 3-yr old seedlings (planted in 2000-2001) in large plots grazed by cattle, vs. those fenced to exclude cattle. Data are totals [100 * (#seedlings/#acorns planted)] for three experimental treatments for four sampling dates.

The lowest mortality rates have been for those seedlings protected from small mammals ("no sm or lg mamm", Table 9), and for valley oak, consistent with previous years' findings.

Table 9. Percent mortality for each year, annual mean, and standard error (SE), for each species and treatment for the cohort planted in 2000-2001. Mortality calculated as: 100^{*} (number yr 2 – number yr 1)/(number yr 1).

	,	mo <u>01-02</u>	rtality rate <u>02-03</u>	(%) <u>03-04</u>	<u>mean</u>	<u>SE</u>
Valley oak	open	72.7	33.3	0.0	35.4	21.0
plots grazed by cattle	no lg anim	88.9	50.0	100.0	79.6	15.2
	no sm or Ig mamm	35.8	11.8	3.3	17.0	9.7
	open	55.0	33.3	50.0	46.1	6.5
plots excluding cattle	no lg anim	23.5	23.1	50.0	32.2	8.9
	no sm or Ig mamm	36.9	9.8	5.4	17.4	9.9
Coast live oak	open	90.0	50.0	100.0	80.0	15.3
plots grazed by cattle	no lg anim	76.5	0.0	75.0	50.5	25.2
- 	no sm or Ig mamm	72.3	16.7	20.0	36.3	18.0
	open	100.0			100.0	
plots excluding cattle	no lg anim	94.1	100.0		97.1	2.4
	no sm or Ig mamm	77.6	0.0	0.0	25.9	25.9

A significant source of mortality for this cohort was herbivory by grasshoppers following emergence, reflected in the high mortality rates from 2001 to 2002 (Table 9) across all treatments. Seedlings in the other, older cohorts were also defoliated to some extent and also suffered an increase in mortality in this time period. However the newly emerged seedlings in this cohort apparently were more vulnerable to this attack, especially coast live oak seedlings that suffered mortality rates over 70% even for those individuals protected from both small and large mammals.

Surviving three-year-old valley oak seedlings range in height from 6 to 44 cm (2 to 17") with a mean of 24 cm (9"). Valley oak seedlings were significantly taller in 2004

in locations protected from small mammals compared to open controls (ANOVA p = .004). Heights of surviving three-year-old coast live oak seedlings range from 10 to 44 cm (4 to 17") with a mean of 22 cm (9"); coast live oak seedling height did not vary significantly among treatments.

Comparing survivorship of seedlings in full cages vs. "alternative" cages with no bottoms, we found no significant differences between these two treatments for either species for any date (logit regression: p > .5). From planting in 2001 through May 2004, valley oak seedling survivorship was 24% in full cages vs 28% in cages with no bottoms. coast live oak seedling survivorship in full cages was 9%, vs 10% in cages with no bottoms. There were also no significant differences in seedling height or growth between these two treatments for either species (t-tests: p>.50). These results corroborate findings from the cohort planted in 2000 and thus we are confident that below-ground cages do not require bottoms to effectively exclude small mammals and reduce initial mortality from underground herbivores.

5. Summary and implications for oak restoration plantings

Results from our four large-scale planting experiments (1996 - 1997, 1997 – 1998, 1999 – 2000, and 2000 - 2001) indicate that several factors play a role in limiting or promoting seedling recruitment of oaks. First, abundant rainfall in late winter and spring, as seen in the El Niño year 1998, can significantly enhance emergence and survivorship; the cohort established in that year remains the most numerous and tallest. In addition, very low rainfall, particularly during late winter and spring, results in low seedling emergence, as seen in the 1996 – 1997 cohort, and in increased seedling mortality as observed in 2002. Second, as observed in all four planting years, at all

planting sites, and in both grazed and ungrazed plots, seed predation and herbivory by small mammals (most likely gophers and ground squirrels) significantly reduces oak seedling recruitment. While overall seedling establishment rate from all acorns planted is presently 6.6% (8.9% for valley oak, 4.3% for coast live oak), plantings that were protected from small mammals currently have rates as high as 40% ('97-'98 valley oak and coast live oak). Third, herbivory by insects such as grasshoppers may reduce seedling survivorship across all treatments in some years, as observed in 2000 - 2001. Fourth, acorn and seedling survivorship is not strongly negatively impacted by winter/spring livestock grazing. In fact survivorship of protected seedlings was slightly higher in areas grazed by cattle than in ungrazed areas. This result may not hold at higher stocking densities or if grazing is continued into the summer months when seedlings are more likely to be browsed.

The results of these experiments also provide some guidance for those planting oaks in similar conditions by indicating the range of survival and growth one might expect if acorns are planted using these treatments. Table 10 summarizes these results for seedlings planted 1998 through 2001 in both grazed and ungrazed plots (we have not included data from 1996-97 because emergence was so low in all treatments.) As discussed previous ly survival and growth rates have varied considerably among years, planting cohorts, and species.

	<u>yr planted</u> 1998	<u>sdling age</u> 6 yr-old	<u>treatment</u> open	<u>% surviving to 2004</u> 3.7	<u>mean ht (cm)</u> 13
			no lrg anim	9.5	46
			no sm or lg mammals	36.6	58
Valley oak	2000	4 yr-old	open	1.7	10
			no Irg anim	5.5	20
			no sm or lg mammals	25.9	29
	2001	3 yr-old	open	1.7	7
			no Irg anim	1.7	20
			no sm or lg mammals	22.1	26
	1998	6 yr-old	open	0.3	8
			no Irg anim	4.6	67
			no sm or lg mammals	30.2	82
Coast live oak	2000	4 yr-old	open	0.0	-
			no lrg anim	0.7	46*
			no sm or lg mammals	4.5	36
	2001	3 yr-old	open	0.0	-
			no lrg anim	0.3	16
			no sm or lg mammals	10.0	23

Table 10. Summary of survival rates and average height (in cm) for valley oak and coast live oak seedlings planted 1998 – 2001. Data are combined for plots grazed by cattle and plots excluding cattle. * note, n = 2

For valley oaks, survival of seedlings protected from both small and large mammals has been at least 22% up to age 3, and for those in the open at least 2% up to age 3. This means that if 1000 acorns were planted in a year with average or above-average rainfall, one might reasonably expect to find at least 220 seedlings surviving to age three if these were caged to exclude small mammals. If those acorns were planted without any protection, there should be at least 20 valley oak seedlings reaching age 3. Thus one could choose to establish valley oaks by planting without protection from animals, by greatly increasing the number of acorns planted, and planting over multiple years. It must be noted that if acorns were planted in an exceptionally dry winter/spring (such as 1996-97), there may be no seedlings produced in any treatment. It is interesting to note that protecting from large grazers only does not always improve survival rates over no protection at all (e.g., those planted in 2001). However, in all cohorts, protecting the seedlings from large grazers only has significantly improved growth rates, and in some years tripled survival rate over unprotected seedlings. Thus, even providing a minimum of caging or fencing to reduce herbivory by large animals would improve long-term planting success rates for valley oaks.

For coast live oaks, 1000 acorns planted with protection from small mammals (in a good rain year) should yield at least 45 seedlings after 4 years. Survival rates of unprotected coast live oak acorns and seedlings have been consistently so low, that planting without protection from animals would probably be entirely unproductive. As with valley oak, although protecting from large grazers only does not always improve survival rates over no protection at all, coast live oak seedlings protected from large grazers have better growth rates than unprotected seedlings. Thus, even a minimum of caging or fencing to reduce herbivory by large animals is warranted when planting coast live oaks.

E. Summer drought physiology of adult oaks and planted seedlings

1. Preliminary study of tree and seedling water availability

In the fall of 1997, before any significant rains had fallen, we measured the water availability to valley oak and coast live oak, to test ideas about drought stress on adult oaks. We assessed water availability by measuring the pre-dawn xylem pressure potentials (PDXPPs) of water in live twigs. During night, water potentials of the plants become equilibrated to those of the soil, so predawn measurements of xylem pressure potentials in twigs are useful indicators of the availability of soil water to the plants' roots. We hypothesized that the trees would be under great water stress due to the long interval since rainfall (January - November 1997), and that there might be differences among locations and between the two species.

We sampled 4 pairs of trees (valley oak paired with coast live oak) in open savanna habitats in three different geomorphic settings on the ranch: 1) "the Mesa," which is an elevated Quaternary terrace whose soil is mapped as Positas sandy loam, a fine sandy loam with a heavy clay subsoil; 2) the valley floor of lower Lisque Creek Valley, which is recent Quaternary fill mapped as clay loam with a silty clay-loam subsoil; and 3) the valley floor of Figueroa Creek below the Little Pine Fault, which is nearly level alluvial fan material mapped as Salinas silty clay loam. Based on topographic position, we would expect the water table to be much closer to the soil surface at the latter two sites than at the Mesa, whose surface is roughly 100 ft. above the valley floor. These three locations are within approximately four miles of each other. From each tree we collected and measured the PDXPPs of three to four live twigs. In addition, at Figueroa, where there were abundant live oak seedlings, we collected and measured the PDXPPs of three seedlings. Results are summarized in Table 11.

Contrary to our expectations, we found that the two species had very similar water potentials, and that the values were not very low (the lower the value, the more "waterstressed" a plant is). This suggests that mature trees of both species may be using the same, deep water sources. In addition, we found no differences among locations. Both species of trees had similar amounts of water available to them, at the different sites on the ranch.

Table 11. Water availability of adult valley oaks, *Q. lobata*, and coast live oaks, *Q. agrifolia* on Sedgwick Ranch, November 7, 1997. Pre-dawn xylem pressure potentials measured in Mega Pascals (MPa) (0.1 MPa = 1bar = 14.51 lbs per sq inch \cong 0.987 atmospheres.) Data are means of four trees. Also shown is the mean PDXPP for 3 coast live oak seedlings.

		measurements in MF	'a
location	<u>species</u>	mean	<u>se</u>
MESA	Valley oak	-1.03	.09
	Coast live oak	-1.06	.07
LISQUE	Valley oak	-1.04	.10
	Coast live oak	-1.05	.06
FIGUEROA	Valley oak	-1.13	.04
	Coast live oak	-1.04	.07
seedlings FIGUEROA	Coast live oak	-4.20	.23

Also interesting was the finding that seedlings had significantly less water available to them. The average of -4.2 MPa suggests a considerable water stress for seedlings relative to the adult trees found in the same location (compare to -1.0 MPa). These measurements support our hypothesis that water stress was a dominant cause of mortality for seedlings establishing in 1996 - 1997. They also suggested that further study of plant water relations could provide information about factors limiting natural regeneration of oaks.

2. Effects of summer drought on oak seedling physiology

Since environmental stresses, particularly those related to resource acquisition, are often inversely related to size, summer drought poses a formidable barrier to the survival of oak seedlings. The availability of seedlings, established from acorns planted as described above, provided an opportunity to determine how various aspects of physiology of coast live oak, *Quercus agrifolia*, and valley oak, *Q. lobata*, seedlings are affected by the Mediterranean climate's annual summer drought and to elucidate the possible role such effects might have on seedling survival and transition to the sapling stage here in Santa Barbara County. We asked the following specific questions: (1) What are the water relations and gas exchange characteristics of established oak seedlings during summer drought? (2) How do these characteristics vary between an evergreen and a fully deciduous oak species? (3) How do these characteristics tell us about growth and the likelihood of survival of these seedlings?

a) Study plants

To address these questions we chose seedlings from the cohort, or age class, planted as acorns in January 1998, which emerged later that spring (by May 1998). For each species, we selected 14 seedlings that were within 1 km of each other in the same savanna area, and that were in the open at least 5 meters from the canopy of an adult tree. Seedlings were chosen to represent the range of sizes observed in their entire cohorts. Adults chosen (2 coast live oaks, 4 valley oaks) were those nearest the sampled seedlings. The following measurements were done on these plants during summers of 2002, 2003 and 2004.

b) Physiological measurements

For an index of water availability we measured pre-dawn xylem pressure potentials (PDXPPs) of the seedlings and trees between 2-5 AM using standard methods (Scholander et al. 1965) and a PMS, Inc., pressure chamber. These measurements provide an estimate of the force or tension with which water is held in the soil where the plant's roots are. More negative numbers indicate greater forces or tensions holding the water to the soil and therefore making it less available to the plant, and suggesting greater water "stress".

To assess the effects of summer drought on the exchanges of carbon dioxide and water vapor between leaves and surrounding air, measurements were made using a Li-Cor 6400 (Li-Cor, Inc.) leaf gas exchange measuring system. For diurnal variations in leaf gas exhange, we used a subset of the study plants, and measured gas exchange rates of one leaf on each of four seedlings and on each of four adults of each species hourly during a clear day in August, 2004. To assess seasonal variations in leaf gas exchange during summer drought, measurements were performed on leaves of all the study plants during one clear-weather day selected from each of three periods spanning summer droughts (July, August-September, and November) of 2002 and 2003. During each of these chosen days measurements were made on one leaf of each study plant during three

sampling time periods: early morning (8:15 am), late morning (11:30 am) and afternoon (4:00 pm). These measurements were completed on all study plants within \pm 1.25 hrs of each other during each sampling time period. To assess seasonal rather than instantaneous environmental effects on photosynthesis, we utilized the same controlled chamber conditions for every sampling date. These conditions replicated average environmental conditions for the drought season, specific to time-of-day.

To further assess stress on the photosynthetic apparatus, we measured chlorophyll fluorescence characteristics (Bilger et al. 1995) of the same leaves used for gas exchange on all studied seedlings and adults using a portable Hansatech FMS 2 fluorimeter. These measurements tell us the degree to which the photosynthetic apparatus is down regulated (photoinhibited) due to limitations on gas exchange as a result of water stress and excessive light incident on the leaves (quantum efficiency of Photosystem II, PSII). They also tell us the degree to which the leaves' photosynthetic systems are capable of recovering from these stresses during dim light or darkness (dark adapted variable fluorescence as a proportion of maximum fluorescence, Fv/Fm). Here we report just the latter set of measurements. High Fv/Fm values (0.7-0.9) indicate nearly complete recovery.

c) Statistical analyses

For each parameter measured we used repeated measures analysis of variance, with all sampling dates included, to test for four overall differences between species and size/age classes: 1) coast live oak and valley oak seedlings, 2) coast live oak and valley oak adults, 3) coast live oak seedlings and adults, and 4) valley oak seedlings and adults. These analyses allow for the examination of differences between species or size classes over the study period without assuming that samples are independent from one time period to the next. In addition, we compared values of these parameters at each date using independent samples t-tests with pooled (seedlings) or separate (adults) variances.

To examine the relationships between parameters (e.g., water availability and seedling height) we used linear regressions. All statistical tests were performed on non-transformed data.

d) Results and discussion

(1) Effects of summer drought

While drought may play an important role in determining survival of oak seedlings during the first year or two of their lives, the 4-5 yr-old established seedlings we studied here showed no evidence of severe drought stress. Even during a year (2002) of half average rainfall and an extremely dry spring, average PDXPPs during summer drought did not get below -2.7MPa for either coast live oaks or valley oaks (Table 12). PDXPPs were higher for both species during the following summer (2003), following an above average winter rainfall, but it is not clear whether this difference between years was due to the difference in rainfall or growth of the seedlings producing more favorable water relations (Fig. 16). Size of the seedlings was significantly, positively related to water availability in valley oaks, but not at all in coast live oaks, suggesting that size is not likely to be the sole factor responsible for more favorable summer water relations. **Table 12.** Pre-dawn xylem pressure potentials (PDXPPs in Mega Pascals, MPa) of *Q. agrifolia*, coast live oak and *Q. lobata*, valley oak seedlings and adults.

r re-dawn xylem pressure potentials (wr a)								
date		Q. a seedlings	grifol	lia adults	Q seedling	. lobat S	a adults	
	n	14		2	14		4	
July 02	mean	-1.9	*	9	-2.7	*	-1.0	
Aug 02	mean	-2.0	*	9	-2.3	*	-1.0	
Nov 02	mean	-2.6	*	-1.3	-2.5	*	-1.6	
Jul 03	mean	-1.4	*	9	-1.8	*	-1.0	
Sep 03	mean	-1.7	*	9	-2.4	*	-1.2	
Nov 03	mean	-1.1		-1.1	-1.5		-1.2	

Pre-dawn xylem pressure potentials (MPa)

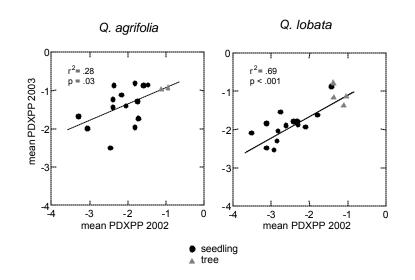


Figure 16. Relationship between mean PDXPP in 2002 and mean PDXPP in 2003 for both seedling and adult *Q. agrifolia*, coast live oak and *Q. lobata*, valley oak.

Data on chlorophyll fluorescence characteristics of the seedlings' leaves support the view that these seedlings were not under severe stress. Measurements during early mornings showed average dark adapted Fv/Fm values were 0.73 or higher for valley oak and 0.65 or higher for coast live oak (Table 13). These values indicate the leaves of both species fully or nearly fully recovered their photosynthetic capacity every day during summer months. However, in both species there was a trend for lower morning dark adapted Fv/Fm as the summer progressed, suggesting an accumulative, negative effect of photoinhibition due to high light and low water availability and/or an effect of leaf aging.

Table 13. Dark adapted chlorophyll fluorescence, Fv/Fm for *Q. agrifolia,* coast live oak and *Q. lobata,* valley oak, seedlings and adults.

Fv/Fm									
		Q. a		Q.	lobata	a			
date		seedlings		adults		seedlings		adults	
	n	14		2		14		4	
July 02	mean	.75				.80			
Aug 02	mean	.73		.81		.76	*	.83	
Nov 02	mean	.72		.78		.78	*	.83	
Jul 03	mean	.80		.85		.84		.84	
Sep 03	mean	.67	*	.80		.79	*	.83	
Nov 03	mean	.65	*	.78		.73	*	.79	

Fv/Fm

Photosynthetic rates for leaves of both species of seedlings were low during both summers (Table 14), but remarkably steady throughout the daylight periods (Fig. 17). During the low rainfall year of 2002 maximum photosynthetic rates (A_{max}) of both species were strongly and directly related to PDXPPs, but this relationship was not apparent during the higher than average rainfall year of 2003 (Fig. 18). These findings suggest photosynthetic rates per unit leaf area are limited by water availability during below average rainfall years, but this limitation is alleviated during average or above average rainfall years. Maximum photosynthetic rates were significantly related to size only for valley oak in 2002.

Mean Daily A _{max} (µmol / m² sec)								
	Q. agrifo	olia	Q. lobata					
date	seedlings	adults	seedlings	adults				
	n 14	2	14	4				
July 02	4.97		5.76					
Aug 02	4.88	5.80	7.82	12.45				
Nov 02	3.15 *	8.24	4.77 *	11.28				
Jul 03	5.01	5.80	6.67	8.13				
Sep 03	3.88 *	6.29	5.48 *	11.56				
Nov 03	4.51	4.76	6.36	9.84				

Table 14. Mean daily maximum rates of photosynthesis, A_{max} (umol CO₂ / m⁻² sec⁻¹) of *Q*. *agrifolia,* coast live oak, and *Q. lobata,* valley oak, seedlings and adults.

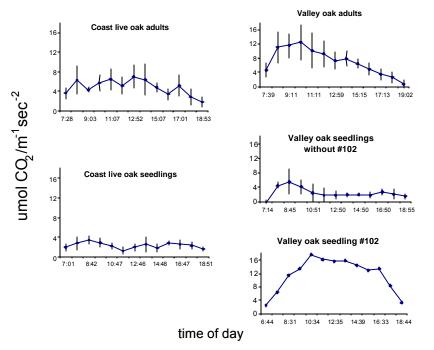


Figure 17. Diurnal photosynthesis curves. Data are rates of photosynthesis (umol $CO_2 / m^{-2} \sec^{-1}$) measured hourly from sunrise to sunset. Valley oak seedling data are presented separately for individual #102.

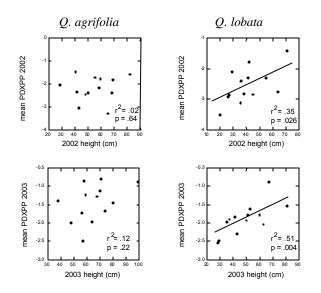


Figure 18. Relationship between water availability (PDXPP) and height of *Q. agrifolia*, coast live oak and *Q. lobata*, valley oak, seedlings for 2002 and 2003.

(2) <u>Evergreen coast live oak vs. deciduous valley oak</u>

There were similarities and important differences between the evergreen coast live oak and the deciduous valley oak. Seedlings of both species appeared similar in their PDXPP responses to annual rainfall totals (Table 12), with higher PDXPPs in the relatively wet year (2003) than in the dry year (2002). However, in three of the six PDXPP measurements of the seedlings, the two species differed, with the deciduous valley oak always having the lower water potentials; based on repeated measures analysis valley oak seedlings had significantly lower water potentials than coast live oak seedlings overall (P = .028). PDXPPs were not significantly related to size in either year in coast live oak, but there was a strong relationship between size and PDXPPs in both years in valley oak (Fig. 16). Assuming there is a relatively constant, positive relationship between the shoot sizes we measured and root sizes in each species, these differences between the two species in PDXPPs and the relationship of PDXPP to size suggest there may be an important difference between them in the ways their roots acquire soil water. In coast live oak seedlings, encounters with high-water-containing soil appear to be serendipitous and somewhat independent of root system size. Whereas in valley oak seedlings, encounters with high-water-containing soil appear to be more directly dependent on root system size and probably depth. Such differences between the two species could be due to differences in root architectures.

Seedlings of the two species also differed in their chlorophyll fluorescence characteristics and photosynthetic rates. The deciduous valley oak consistently (five out of six measurements) had higher dark adapted Fv/Fm than did coast live oak (Table 13); this difference was significant overall, based on repeated measures ANOVA. In addition, when there were significant differences between the species in mean daily A_{max} (three out of six measurements), valley oak always had the higher rates of CO₂ uptake; as above this difference was significant overall based on repeated measures ANOVA. Diurnal curves of photosynthetic rates differed slightly, but perhaps importantly, between the two species; those of coast live oak were quite flat throughout the day, while those of valley oak showed an early morning peak between 7:30am and 10am.

As adults, the two species differed in fewer ways than did the seedlings. We found no significant differences in PDXPPs between coast live oak and valley oak adults in either year (Table 12). There were also no apparent differences in dark adapted leaf chlorophyll Fv/Fm (Table 13). Leaves of adult valley oaks consistently had higher mean daily A_{max} than those of coast live oak, but these differences were not statistically significant, possibly due to the small sample sizes (Table 14). Diurnal curves of photosynthetic rates also differed between the species. As with the seedlings, photosynthetic rates of adult coast live oak leaves changed little during the day, while those of valley oak showed a strong peak throughout the morning and steadily declining in the afternoon (Fig. 17). Thus, interspecific differences in water relations and some leaf characteristics such as Fv/Fm and maximum photosynthetic rate (A_{max}) became less obvious with increasing size and age, but interspecific (i.e., between species) differences in other characteristics, such as diurnal patterns of photosynthesis, remained.

(3) Oak seedlings vs. adults

On average, in both species there were large intraspecific (i.e., within species) differences between seedlings and adults in PDXPPs, with seedlings often having PDXPPs two times lower than those of nearby adults (Table 12). The high PDXPPs of the adults and lack of variation in this measure between years indicate these trees utilize a supply of perennially available soil water. To the degree that PDXPPs may be interpreted as characteristics of water sources accessed by plants, plants with different PDXPPs are most likely accessing different water sources. Therefore, at four and five years old, most of the oak seedlings in this study had not yet attained access to a similar or the same source of water available to the adults.

There were also significant intraspecific differences between oak seedlings and adults in photosynthetic characteristics during summer drought. Average values of dark-adapted, variable chlorophyll fluorescence as a percentage of maximum chlorophyll fluorescence (Fv/Fm) values were consistently, and often significantly, lower in seedlings than in adults of the same species (Table 13). This difference may be due to the seedlings being under more stress and/or less capable of full recovery from this stress than the adults, or it could simply be a developmental difference. Rates of photosynthesis per unit leaf area as represented by mean daily A_{max} values (umol CO₂ m⁻²sec⁻¹) were also consistently and often significantly lower in seedlings than in adults of the same species (Table 14). These lower rates can also be interpreted as signs of stress in the seedlings or as developmental differences.

(4) Summer drought and oak seedling growth and survival

Since the interplay between stress and development is probably closely related to survival in oak seedlings, an examination of the variation among the seedlings in their physiological characteristics may provide some insight into and predictability regarding their growth and survival. Unlike in the adult trees, there was a lot of variability among the seedlings in their physiological characteristics. PDXPPs of the seedlings varied widely, while PDXPPs of the adults were closely clustered (coefficient of variations for mean PDXPP 2002 and 2003 for coast live oak seedlings = 0.27, for valley oak seedlings = 0.20, for coast live oak adults = 0.07, and for valley oak adults = 0.08). In summer of 2002 none of the coast live oak seedlings had PDXPPs as high as those of the adults, but by summer of 2003 three of the 13 coast live oak seedlings measured had achieved these high PDXPPs (Fig. 16). Only one of the 14 valley oak seedlings measured had PDXPPs as high as those of adults, but this seedling equaled the adults in both 2002 and 2003. Thus, while the root systems of most of these 5yr old seedlings had not attained access to the source of water available to the adults, three coast live oak and one valley oak seedlings may have, and, if so, this achievement could initiate a major surge in growth.

That such a surge in growth may be beginning in these few seedlings is suggested by a comparison of leaf photosynthetic rates (A_{max}) between seedlings and adults. In valley oak, again, there was more variability among seedlings than adults (coefficient of variations for mean A_{max} 2002 and 2003 for valley oak seedlings = 0.38, and for valley oak adults = 0.24); variability among seedlings and adults was similar for coast live oak. In the dry year of 2002, summer mean daily A_{max} rates of seedlings of both species were significantly, positively related to water availability as indicated by PDXPPs (Fig. 19). While this relationship vanished during the wet year of 2003, its presence in 2002 indicates water availability can control photosynthetic rates in these seedlings. Seedlings that achieve access to a large supply of perennially available soil water would be relieved of this control. Two of the three coast live oak seedlings with PDXPPs closest to those of the adults in 2003 also had the highest A_{max} rates among the coast live oak seedlings (Fig. 19). The one valley oak seedling in this category not only achieved Amax rates comparable to those of valley oak adults (Fig. 18), it also produced a daily photosynthetic curve as high or higher than any of the adults (Fig. 16).

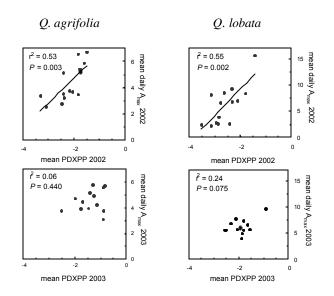


Figure 19. Relationship between the annual mean daily A_{max} (umol CO₂ / m^{-2} sec⁻¹) and annual mean PDXPP (MPa) in *Q. agrifolia* (coast live oak) and *Q. lobata* (valley oak).

The relationship between water availability during summer drought and rates of photosynthesis prompts the prediction that those seedlings achieving high PDXPPs should grow faster and achieve greater size than the others that have not yet acquired plentiful soil water sources. However, as mentioned above, the relationship between PDXPP and above ground size is significantly positive in valley oak seedlings only (Fig. 18), and A_{max} and size were significantly, positively related only in valley oak during summer, 2002, (Fig. 20). There was no significant relationship between either PDXPP or A_{max} and size in coast live oak seedlings. Thus, it appears that it may take a few more

seasons for the increased photosynthetic rates to be converted into increased growth and size.

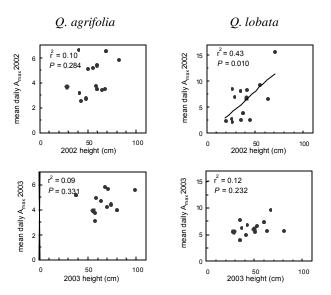


Figure 20. Relationship between the annual mean daily A_{max} (umol $CO_2 / m^{-2} \sec^{-1}$) and seedling height (cm) in 2002 and 2003 in *Q. agrifolia* (coast live oak) and *Q. lobata* (valley oak).

Thus, the population of oak seedlings in this study may be just on the verge of reaching the same water sources available to neighboring adults with consequent increases in rates of photosynthesis and growth, and it appears a few of these plants have actually begun this transition. We suspect this is the critical transition between seedling and sapling that is the most important bottleneck in the demographics of these oaks. Several more years of studying these plants should allow us to determine if this is what is happening, if the changes we have seen are permanent or ephemeral, and to further understand this transition process. Such study might also allow us to determine the consequences to oak seedlings of not undergoing this transition, and how long a seedling can survive before reaching the adult water source.

The acquisition of a large supply of perennially available water may be the crucial step in the seedling to sapling transition, and it is controlled by root growth and soil water distributions. From the results described above it appears that there are important differences between the root systems of coast live oak and valley oak that may affect this transition. The results described above plus some anecdotal observations suggest the hypothesis that the architecture of coast live oak root systems includes extensive lateral roots, that can serendipitously encounter patches of soil with high water contents, and potentially deep vertical roots capable of reaching perennially moist soil at depth, i.e. the water table. The relatively shallow lateral roots would allow some coast live oak seedlings to access soil patches with high water content without statures large enough to reach the water table. Once the plants are large enough, the deep roots could provide a more stable water supply from the water table. In contrast, valley oak root system architecture probably consists primarily of vertical roots that can grow very deep and reach perennial ground water at the water table. Without the extensive lateral roots, valley oak seedlings would have lower PDXPPs than coast live oak seedlings until they grew large enough to have long enough vertical roots to reach perennially available water at the water table. Thus, water availability would be strongly linked to seedling size in valley oak but not necessarily in coast live oak.

This hypothesized interspecific difference in root system architecture could play an important role in differences between these two species in landscape distributions. Valley oak may be confined to valley bottoms and special terraces because of its reliance on large stores of perennial water at depth. In contrast, coast live oak, with its extensive lateral and vertical root systems components, is much more versatile and capable of occupying a much wider variety of habitats including steep slopes, ravines, rock outcrops with scattered patches of high water content soil as well as terraces and valley bottoms with deep ground water.

F. Spatial and temporal patterns of natural seedling recruitment

In the summers of 1997, 1998, and 2004 we surveyed a sub-sample of our experimental plots in savannas to locate naturally established oak seedlings (n = 8 plots - 4 grazed, 4 ungrazed; total area = 2.0 hectares). The same plots were censused in all three years. Four of the plots had an adult valley oak in the center, and four (on the "Airstrip") had no trees within the plot.

The numbers of natural seedlings varied considerably among years (Table 15). For example in 1998, a year of high acorn production followed by a very wet winter (El Niño) resulted in relatively high rates of natural seedling establishment. However, most of these seedlings did not survive, as evidenced by the low numbers of seedlings present in 2004.

Table 15. Number of natural seedlings present in experimental plots surveyed in July 1997, 1998, and 2004. Data are total numbers of seedlings (natural recruits) for each species in 4 fenced plots and 4 unfenced/grazed plots. Total area surveyed was 2.0 ha (8 plots).

<u>year</u>		Valley oak	Blue oak	<u>Coast live oak</u>	total # seedlings
1997	fenced	1	2	1	4
	grazed	0	10	0	10
	<i>total</i>	1	12	1	14
1998	fenced	58	10	70	138
	grazed	49	32	116	197
	<i>total</i>	107	42	186	335
2004	fenced	2	19	11	32
	grazed	0	1	0	1
	<i>total</i>	2	20	11	33

Another interesting finding is that natural establishment of valley oak is the lowest of all three species, even though the only species of oak tree within the plots was valley oak.

In 1997, we conducted more extensive and detailed surveys. We located natural oak seedlings in a total of 18 of our experimental plots, 9 grazed and 9 fenced (total area = 4.5 ha), and mapped all 616 natural seedlings found using a total station transit. Canopy cover in the plots averaged 12% overall, and was predominately valley oak (Figure 21a). However, most seedlings were *Q. douglasii*, blue oak (Figure 21b). Thus, although we expected to find many valley oak seedlings (because many adult trees were present, and many acorns were produced the previous spring), we found that valley oak produced very few seedlings per meter square of conspecific canopy (0.02), compared to both coast live oak (0.20) and blue oak (1.37) (Figure 21c). The large number of blue oak seedlings found under the canopy of valley oak trees, is very likely a result of scatter-hoarding of acorns by scrub jays.

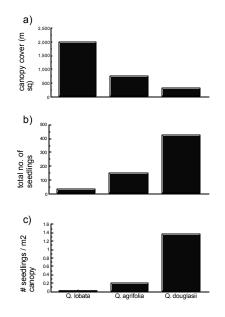


Figure 21. Results of natural recruit seedling survey, July 1997. a) total canopy cover of adult oaks in area surveyed; b) total number of seedlings present in all plots; c) number of seedlings per meter square of conspecific (i.e., same species) tree canopy.

Most seedlings were located in plots grazed by cattle (363 in grazed plots, 253 in fenced/ungrazed plots). Our data suggest that the relationship between cattle grazing and natural seedling establishment may vary among oak species (Figure 22); although there were more live oak seedlings (*Q. agrifolia*) found in ungrazed plots than in grazed plots, both valley oaks (*Q. lobata*) and blue oaks (*Q. douglasii*) were more abundant in grazed plots.

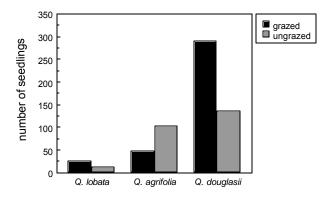


Figure 22. Effect of grazing on natural seedling establishment of *Quercus lobata*, *Q. agrifolia*, and *Q. douglasii*. Data are total numbers of seedlings in plots grazed by cattle (area = 2.25 hectares), and ungrazed/fenced plots (2.25 hectares), July 1997.

Another pattern we detected from our seedling maps was that seedlings were strongly aggregated under or near adult trees. In nearly all plots, there were significantly more seedlings found under tree canopy than expected (Table 16). Expected values were calculated based on the percent cover of canopy vs. open in each plot, and compared to observed values using chi-square goodness of fit tests. For example, in plot 2 tree canopy covered 9% of the plot and 91% of the plot was open; if seedlings were distributed randomly, we would expect to find 9% of the seedlings under tree canopy, and 91% in the open. However, in this plot we found 79% of the seedlings under the canopy (118 out of 150 seedlings), and 21% in the open (32 out of 150 seedlings).

	grazing	center			total	no. observed	no. expected	no. observed	no. expected	
<u>Plot no.</u>	treatment	<u>tree</u>	location	<u>% canopy</u>	<u>no. seedlings</u>	under canopy	under canopy	<u>in open</u>	<u>in open</u>	p
1a	fenced	valley oak	Lisque	18.6	13	5	2.4	8	10.6	0.063
2b	fenced	coast live	Lisque	9	150	118	13.5	32	136.5	<0.001
		oak								
3a	open	valley oak	Lisque	15.1	20	4	3	16	17	0.531
5b	open	coast live	Lisque	12.6	314	193	39.6	121	274.4	<0.001
		oak								
9c	fenced	valley oak	Lisque	9.6	4	1	0.4	3	3.6	0.317
10c	open	valley oak	Lisque	7.8	10	1	0.8	9	9.2	0.816
11d	open	valley oak	Lisque	10.5	6	5	0.6	1	5.4	<0.001
14d	fenced	valley oak	Lisque	12.3	0					
26e	fenced	coast live	Mesa	13.1	86	86	11.3	0	74.7	<0.001
		oak								
27e	open	coast live	Mesa	11.6	13	12	1.5	1	11.5	<0.001
		oak								

Table 16. Distribution of natural oak seedlings relative to adult tree canopy in savanna plots. Data from June-July 1997. Shown are only those plots with seedlings present

notes: Plot no: plots with the same letter are a pair grazing treatment: fenced plots were ungrazed by cattle, open plots were grazed p = significance based on chi-square test In the few plots where we found seedlings to be randomly distributed (plots 3, 9, 10), the seedlings were a different species than the adult tree in the plot, i.e., the acorns had clearly come from a source outside the plot. In plot 3 all seedlings were blue oak, *Q. douglasii*, and in plot 9 half were blue oak, but neither plot contained blue oak trees or canopy. Similarly all seedlings in plot 10 were blue oak but the plot contained only 2% of that species in total oak canopy cover.

G. Efforts to ameliorate factors that negatively affect oak recruitment

Results of our large-scale planting experiments, described above, indicate that two factors are associated with high rates of oak seedling recruitment: 1) above-average rainfall, and 2) protection from seed predation and herbivory by small mammals. We established two experiments in 2002-2003 to study potential means of influencing these factors in the field. Acorns were collected in Fall 2002 using collection, sorting and storage techniques described for previous planting experiments.

1. Use of raptor perches to reduce rodent activity

Our previous findings clearly demonstrate that small mammals significantly reduce seedling recruitment of oaks. We conducted a pilot study to investigate whether the addition of artificial raptor perches (large wood poles) leads to a reduction in small mammal activity and thus to a decrease in oak seedling mortality.

In January 2003 we established 5 pairs of circular plots (diameter = 20 m) in Lisque Canyon that were at least 70 m from a potential raptor perch, including natural perches such as trees or snags, and artificial perches such as phone poles. Plots were also at least 70 m away from each other. For each pair of plots, one was randomly selected to receive an artificial perch/raptor post. In the center of these plots we erected a large wood pole (~5 m high), with a 17 cm x 17 cm wooden platform nailed on the top, to serve as additional raptor perches. The other plot within each pair served as a control (i.e., ambient raptor use.)

Within all pairs of plots, we designated positions for planting with 10 replicates of three treatments: 1) protection from small mammals such as gophers and ground squirrels, 2) protection from large animals such as cattle, deer, and pigs, and 3) no protection from mammalian grazers. Large and small cages were of similar construction to those established in our previous large scale planting experiments.

Large cages/fences were constructed of 4' high, 2" x 4" mesh galvanized wire (12 gauge); they were cylinders (diameter = 18") and supported at one side with a 5' t-post, and at the other side with a 4' rebar. Smaller cages to exclude small mammals were cylinders constructed of 3' high hardware cloth (mesh size = 0.5"); they were open at the bottom and sealed at the top with aviary wire. We also treated these cages with an acid wash to remove the galvanization on the lower 6"; this treatment will allow the portion of the cage that is underground to rust and disintegrate more quickly. In positions with cages (small mammal exclusion), the cages were set 12" into the ground. Two viable valley oak acorns were planted 1-2" below the soil surface, at each planting location. Prior to planting, acorns were placed into buckets of water. Acorns that floated were discarded; we planted only acorns that sank and appeared viable. Treatments were replicated 10 times per plot in each of 5 pairs of plots. Thus, there were a total of 100

acorns planted per treatment or 600 overall. All plots are within rangeland grazed by cattle. Planting was completed February 28, 2003.

We monitored all planting locations in May 2003 and April 2004. Seedling emergence and survival rates were significantly higher in locations protected from small mammals (Fig. 23) (logit regression: treatment, p < .001); we found no significant difference between open planting locations, and those protected from large mammals.

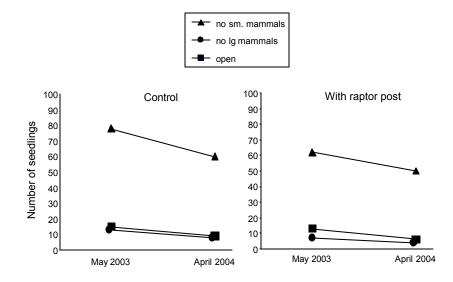


Figure 23. Effects of experimental raptor perches on establishment of valley oak seedlings planted with varying protection from seed predators and grazers. Shown are total numbers of seedlings emerged and surviving out of 100 acorns planted. Acorns planted in February 2003. Data from May 2003 (emergence) and April 2004.

Soon after planting in February 2003 we observed that many of the locations open to small mammals were disturbed; the acorns had been excavated and eaten, with the acorn

shell deposited at the soil surface. We hypothesize that ground squirrels were responsible for most acorn removal.

Contrary to our expectations, we found no significant effect of the raptor perches on either emergence or numbers of seedlings present in April 2004 (Fig. 23) (logit regression: post, p > .20).

The results of this pilot study support our findings from the large-scale planting experiments: small mammals significantly reduce emergence and establishment. The addition of artificial perches to attract predators did not reduce small mammal activity however. We propose several possible explanations for the lack of an effect of the raptor perches. First, raptors may not have been attracted to the posts. The perches may not have been large enough, or it may require a period of time for raptors to get accustomed to and begin to use the posts. Second, the posts may have been used by raptors that do not reduce the "critical" small mammals. We made observations of small fakons, such as American Kestrels, using the perches during the day. These birds primarily eat very small prey. We collected an owl pellet from below one of the posts; owls are nocturnal predators. Although Valley Pocket Gophers may be active day or night, California Ground Squirrels, one of the abundant small mammals at Sedgwick, is active/aboveground only during the day, and therefore not likely to be affected by nocturnal predators.

2. <u>Watering experiment</u>

We designed and established a pilot study to investigate the effects of supplemental water on valley oak and coast live oak seedling establishment. Within one large 40 x 45 m plot, in a portion of Figueroa Valley that is ungrazed by cattle, we planted valley oak and coast live oak acorns in winter 2003. For each species, we had 10 replicates of 3 treatments: 1) control, which received no supplemental water; 2) watered via disc with each rainfall event; and 3) watered once in early summer. The disc was a modified 63 cm diameter "snow saucer", attached to drip irrigation hose arranged in a 35 cm diameter circle around the seedling (Fig. 24). When installed, the device captured rainfall and directed the additional water to the oak seedling, approximately doubling the amount of water around the seedling with each rainfall event. The area of the disc was 3077 cm², so with a rainfall of 25 mm (1 inch) the disc would deliver ~ 7.7 liters (2 gallons) of water to the seedling. The last treatment ("watered once") was a "one-time" watering applied in the early summer, using the total amount of supplemental water received in the disc treatment.



Figure 24. Water addition treatment. The modified disc collects and redirects additional water to oak seedlings with each rainfall event.

All plantings were protected with cages to exclude small mammals. Cages were cylinders constructed of 3' high hardware cloth (mesh size = 0.5"); they were open at the bottom and sealed at the top with aviary wire (mesh size = 2.5"). We treated all cages with an acid wash to remove the galvanization on the lower 6"; this treatment will allow the portion of the cage that is underground to rust and disintegrate more quickly. Cages were set 12" into the ground. Two viable acorns were planted 1-2" below the soil surface, at each planting location. Prior to planting, acorns were placed into buckets of water. Acorns that floated were discarded; we planted only acorns that sank and appeared viable. Planting was completed February 6, 2003. Total rainfall for the season was above-average. A rain gauge placed ~100m from the plot recorded total rainfall for that season, September 5, 2002 to May 4, 2003 as 472 mm (18.4"), and cumulative precipitation from planting (February 6 to May 4) as 206 mm (8.1"). We estimated that the total amount of supplemental water received in the disc treatment was 60 liters (16 gallons). Thus, this was the volume of water applied on July 2^{nd} and 3^{rd} , 2003, to the "one-time" watering treatment; seedlings in this treatment were hand watered at a rate slow enough to avoid runoff.

We monitored all planting locations in 2003 and in May 2004. Seedling emergence rates were very high - 90% for both species and all treatments combined. Survival rates have also been high, ranging from 60 - 100% (Table 17). We have not detected any significant differences in establishment rates among treatments (Table 17). Consistent with previous planting experiments, establishment was slightly higher for valley oak than for coast live oak. This difference between species was statistically significant (logit regression, species: p = .048). **Table 17.** One-year-old seedlings established in watering experiment. Given for each treatment and each species are: number of locations (out of 10) with at least one seedling, total number of seedlings (out of 20 acorns planted), and mean height of seedlings in cm (with one standard error). Data from May 2004. Acorns planted in February 2003.

		<u>control</u>	treatment watered once	<u>disk – water each</u> rainfall
Valley oak	# locations	10	9	10
	total # seedlings	17	18	20
	mean ht., cm (s.e.)	16.0 (1.3)	16.7 (1.0)	16.3 (0.8)
Coast live oak	# locations	7	7	9
	total # seedlings	12	13	15
	mean ht. (cm)	5.9 (1.1)	11.9 (1.2)	11.2 (1.5)

Valley oak seedlings have established in nearly all 30 locations planted (29 out of 30), while coast live oak seedlings have established in 23 out of 30 planting locations.

Seedling heights vary between the two species and among treatments (Fig. 25). Valley oak seedlings are significantly taller than coast live oak seedlings, and for coast live oak we found significant effects of treatment on seedling height; seedlings that received water, either via one-time watering or disk, were significantly taller than controls (2-way ANOVA: species: p < .001; treatment: p = .02; species*treatment: p = .06).

The results of any supplemental watering experiment are likely to vary depending on the amount of rainfall occurring in the year of the study. In 2003 – 2004, rainfall was above average at 472mm (18.4"). Our finding that watering treatments did not improve emergence may have been due to the fact that there was enough natural precipitation to ensure germination; even emergence in the control treatment was very high. We suggest that supplemental watering could yield very different results in a year with below-average rainfall.

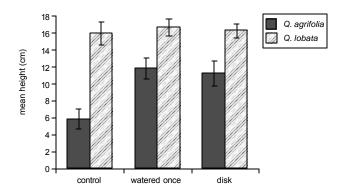


Figure 25. Effects of watering treatments on 1-year-old seedling height, May 2004. Data are means plus 1 standard error, for *Q. agrifolia* (coast live oak) and *Q. lobata* (valley oak).

One of the interesting findings from this pilot study is that the two species have responded differently. *Q. lobata*, valley oak, has not been affected by the watering treatment, but *Q. agrifolia*, coast live oak, has had higher growth rates with either method of adding supplemental water. Our previous work has shown that growth rates are often correlated with survivorship; the seedlings that die in a given year are, on average, the smallest individuals in the cohort. Thus, it is possible that we will observe higher mortality over time in the unwatered treatment for coast live oak, even though the watered treatments will not be receiving any additional water in the future. We hope to continue to monitor this experiment and determine whether the "boost" provided to the watered seedlings in their first year, results in higher survivorship and growth in the long-term.

H. Long-term effects of cattle grazing on grassland community composition

1. <u>Biomass sampling</u>

In order to determine the productivity of the pastures, as well as to compare understory plant biomass among plots where we have planted oaks, we collected samples of herbaceous vegetation from our large experimental plots in 1999 in two savanna sites. Within each of our large 50 x 50 m plots in Lisque Canyon (n = 14) and on the Mesa (n =8), we established three permanent quadrats. The rectangular quadrats were 2m x 12.5 cm. All quadrats were in areas that were in open grassland, away from tree canopy.

Sampling quadrats were established in both grazed and ungrazed plots. For those in grazed plots, we clipped and collected all vegetation to ground level, a day before cattle entered the pastures. Since cattle grazed all pastures over three rotations during 1999, this sampling was conducted three times (early January, April, and May). The sum of these collections provides an estimate of the total herbaceous biomass produced in each plot. The dead vegetation collected prior to any grazing in early January provides an estimate of residual dry matter (RDM). For comparison, we also clipped and collected samples from ungrazed plots in May at the end of the growing season. This comparison provides information on the effect of rotational grazing on annual herbaceous productivity. All samples were stored in the laboratory where they were sorted (live grass, dead grass, live forb, dead forb), dried, and weighed.

In winter-spring 1999 annual production (total live biomass produced in one season) was significantly higher in ungrazed plots in both areas. This suggests that there is not compensatory growth (positive growth response to grazing) in these herbaceous

species, and that, not surprisingly, total production is reduced with grazing. Production varied between the two sites, and was significantly higher on the Mesa relative to Lisque. However, total annual production was relatively low in both these areas: from 96.4 to 238.4 g/m² in grazed pastures, and 298.4 to 409.6 g/m² in ungrazed areas. Rainfall was below average in this year, and thus production is also likely to have been below average. Mean residual dry matter (RDM) in grazed pastures was 55.6 g/m² in Lisque and 41.6 g/m² on the Mesa. These values represent RDM left at the end of the previous year's grazing in 1998.

We also examined the relationship between the maximum height of vegetation within a sampled quadrat and the biomass of the whole sample (Figure 26). We found a significant correlation between these two variables.

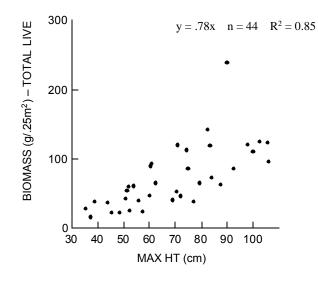


Figure 26. Correlation of maximum vegetation height and biomass. Data are from plant samples collected in open grassland in winter/spring 1999.

This is a useful finding, because we can easily measure maximum vegetation height when we conduct our vegetation monitoring each spring, and we now know that this value is representative of plant biomass. This allows us to compare relative biomass among plots, areas and years.

2. <u>Understory vegetation monitoring</u>

Cattle grazing is arguably the most pervasive anthropogenic disturbance in oak woodlands, savannas, and grasslands in California. It has been cited as a probable cause contributing to the invasion of non-native grasses, a lack of recruitment of oaks, and a decline in biodiversity. However, recent studies have shown that grazing may have positive effects on the herbaceous plant community depending on the substrate (Harrison et al. 2003). Diversity of annuals, both exotics and natives, was found to be higher in grazed vs. ungrazed grasslands (Hayes and Holl 2003), and the native perennial grass, *Nassella pulchra*, increased with spring grazing (Bartolome et al. 2004). In addition, exclusion of cattle from pastures that have long been grazed has not generally resulted in increased diversity or cover of natives. Stromberg & Griffin (1996) found that species composition and diversity in grasslands was more a function of land-use, i.e., historical cultivation, than of grazing.

In May 1996 we established permanent sampling quadrats within our large experimental plots to characterize the understory vegetation, and to examine effects of cattle grazing on the herbaceous vegetation of oak savannas and woodlands. Within each plot, using a stratified random design, we located 10 rectangular quadrats (100cm x 50cm), the corners of which were marked with metal spikes to facilitate resampling over the 10-year study period. For each quadrat, we recorded all plant species present, their percent cover, and the location of the quadrat relative to oak tree canopy. Ten quadrats for each of our 55 plots were sampled, for a total of 550 quadrats, almost every spring from 1996 to 2003. We used Detrended Correspondence Analysis (DCA) based on frequency data (rare species downweighted) to compare grassland composition in relation to grazing and site (vegetation, terrain, and historical land use). We used analysis of variance to examine differences among sites and between grazing treatments in species diversity, and % cover of natives and non-natives.

a) Species composition

Graphing the results of Detrended Correspondence Analysis (DCA) allows one to visually examine the relatedness in species composition among our large 50 x 50 m plots. The closer two points are located on the graph, the more similar they are. Figure 27 shows the results of DCA color-coded by grazing treatment. There are no clear groupings of plots based on presence or absence of cattle grazing in either 1996 or 2002. This indicates that similarities among plots based on species composition were not well explained by grazing (Figure 27). However, when the graph of DCA results are color-coded by over-story oak cover, terrain and land-use, groupings are evident, and thus patterns of species composition appear to be primarily a function of these factors (Figure 28). These patterns were consistent even after cattle were excluded for 7 years (2002), indicating the persistence of historical land use effects and robustness of local community assemblages (as described by Stromberg and Griffin, 1996).

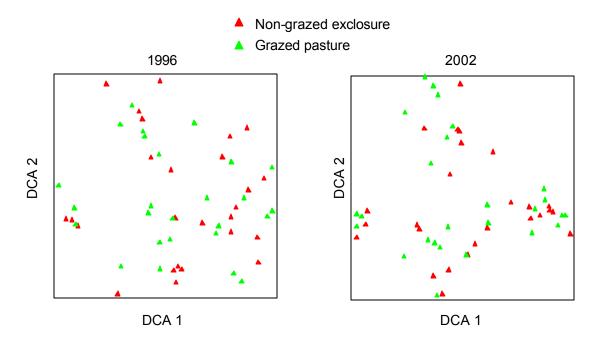


Figure 27. Results of detrended correspondence analysis, color coded by grazing treatment.

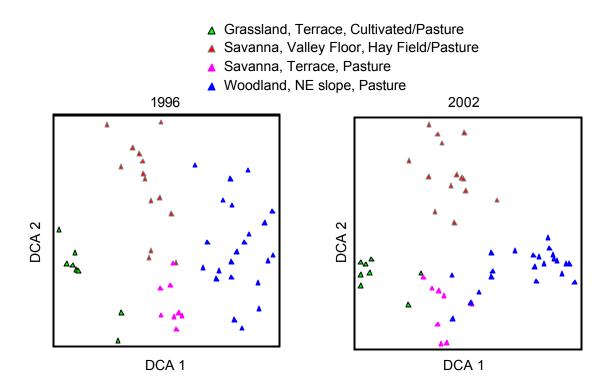


Figure 28. Results of detrended correspondence analysis, color coded by vegetation, terrain, and historical land use.

b) Plant species diversity

We examined two measures of diversity – species richness, which is the number of species present, and species evenness, which incorporates the relative abundance of all species present. Species richness was highest in the woodland site, and for all sites it was highest in the wettest year, 1998 (ANOVA, p < .001) (Table 18). Richness was not different in grazed vs. ungrazed plots, even after 7 years. Species evenness (Simpson's index D) was also highest in the wet year, but did not vary significantly among sites (Table 18). However, diversity (D) was significantly lower in ungrazed plots by 1998 (p = .020) and 2002 (p < .001) in all areas combined.

	Grassland n=8		Sa	Savanna, valley n=14		Savanna, terrace n=8		Woodland n=22		
	<u>year</u>	<u>grz</u>	<u>ungrz</u>	gr	<u>z</u>	<u>ungrz</u>	<u>grz</u>	<u>ungrz</u>	<u>grz</u>	<u>ungrz</u>
	1996	23	22	18	8	15	15	18	25	28
Species richness	1998	25	25	23	}	18	25	22	42	39
	2002	14	14	12	2	12	24	22	25	26
	1996	.65	.76	.6	9	.62	.59	.69	.68	.68
Simpson's D	1998	.74	.78	.6	9	.65	.84	.68	.87	.84
	2002	.73	.53	.6	1	.53	.77	.41	.67	.65

Table 18. Mean species richness and evenness (Simpson's index, D) in grazed vs. ungrazed plots in 4 sites. D was significantly lower in ungrazed plots in 1998 and 2002 in all areas combined.

In plots ungrazed by cattle, the proportion of native species present has declined significantly since the initiation of the experiment (paired t-test comparing 1996 to 2002, p = .04) (Figure 29). The percent cover of the non-native annual *Bromus diandrus*,

"ripgut brome", has decreased significantly in grazed plots (paired t-test p < .001) (Figure 29).

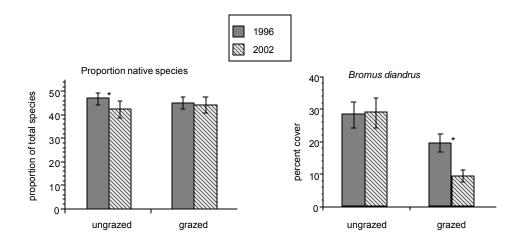


Figure 29. Mean proportion of native species, and percent cover of the non-native *B. diandrus* (rip-gut breome) in 1996 and 2002 (n = 26). Asterisks indicate a significant difference between the 2 years.

c) Conclusions

Our main findings related to the long-term vegetation monitoring are: 1) historical pattern of land use and physical terrain appear to be the dominant factors affecting species composition; 2) interannual variation in community diversity and composition is related to rainfall patterns; 3) moderate cattle grazing (winter/spring) may have positive effects on diversity and proportion of native species in the community; and 4) *Bromus diandrus*, ripgut brome, increased with removal of cattle.

IV. Prescription for planting oaks in Santa Barbara County's rangelands

Based on results of our field experiments to date, we recommend the following techniques for establishing oaks in large landscape or rangeland settings in Santa Barbara County. These methods can be adapted as appropriate to various planting environments; for example, if planting oaks in a residential setting, protection from large animals would be unnecessary, and watering would be feasible.

A. Site selection

Perhaps the most important criterion is that the plantings are done in sites that are suitable ecologically. Some factors to assess at a site include soil texture, fertility and moisture capacity. Valley oaks generally grow best on lower hillslopes, valley floors or alluvial deposits and on deep silty or shaly loam soils (Davis et al. 2000). Coast live oaks can grow in a wide range of settings but are positively associated with cooler moister sites (e.g., north facing slopes, shaded ravines and swales) and negatively associated with clay loam soils. Blue oak is mainly associated with interior foothill environments of the San Rafael Mountains, Sisquoc River Canyon and Cuyama River Canyons and the Sierra Madre range in northern Santa Barbara County. Blue oaks are positively associated with silty clay loams and shaly loams (Davis et al. 2000) and negatively associated with sandy or sandy loam soils.

Another criterion to consider is distance from the coast. *Q. lobata*, valley oak, is negatively affected by salt aerosols and does not occur naturally closer than 28 km from

the coast (Ogden 1975). A useful indicator of suitability for planting is if oaks are currently growing on the site or were there historically.

B. Acorns or seedlings?

In rangeland settings, we recommend planting acorns rather than seedlings when possible for several reasons. First, the primary root growth is rapid and vertical; for valley oaks, we have measured an average root length of 12" just 2 months after planting acorns in pot experiments, while the shoots were less than 4" tall. Thus, if an acorn is planted in a standard pot, the primary root will quickly hit the bottom of the pot and either curl around the bottom of the pot in a deformed morphology or the root tips will die. Since establishment of a well-developed root system is likely a critical factor in determining whether a seedling will survive summer drought, transplanted seedlings may start with a disadvantage in terms of root morphology and growth and may require supplemental watering. A second reason for planting acorns is that this method is easy and inexpensive. Anyone can collect acorns, storage requires only a refrigerator, and carrying acorns to the field for planting is far easier than transporting pots. Seedlings from acorns may appear to make slower starts than seedlings from pots, but over a period of a year or two in the field we believe seedlings from acorns will catch up and probably pass those from pots. If one desires to plant seedlings rather than acorns, we recommend growing the seedlings in tall pots and pruning the roots so that the tap root does not circle around the bottom of the pot. Pots and mesh containers designed to "air prune" the tap and lateral roots are commercially available. Potted seedlings that are transplanted to the field will almost certainly require irrigation for a minimum of a year.

C. Collection of acorns

Acorns are not produced in abundance every year and thus may be difficult to gather in some years. This failure of the acorn crop in some years occurs statewide. Factors responsible for the production of acorns in a given year are not well understood, but Koenig *et. al.* (1994), suggest that wet weather in the spring correlates well with low acorn production in the following fall. It has been speculated that heavy spring rain disrupts oak flower pollination. Thus, in any one year planting will be dependent on acorn production, since acorns generally remain viable for only up to one year.

We recommend collecting acorns from trees that are near the proposed planting sites in order to preserve existing genetic structure within a population, and because there is some evidence that oaks are genetically adapted very closely to conditions at a given location (e.g., acorns collected from the coast may not do as well if planted far inland). Thus, locally collected acorns probably provide the best chances for successful oak establishment. Acorns may not be available immediately adjacent to a proposed planting location, but in decreasing order a preference should be given to acorns collected: in the same canyon, the same ranch, an adjacent ranch, and so on.

Acorns should be collected in the fall, generally between late September and mid-October. They are ripe when they release easily from their caps. This timing generally corresponds to them turning from green to brown, or falling to the ground. Whether one collects acorns from the tree or from the ground will depend on accessibility; the lowest limbs on valley oaks are often out of reach. It is best to choose acorns that appear intact, have no holes, and don't rattle. Once collected, keep the acorns cool and out of direct sun.

D. Acorn sorting and storage

Damaged or insect infested acorns can be discarded, and the remaining acorns placed in a bucket filled with water and bleach (1/2 cup bleach to 1 gallon water). Floating acorns can be discarded. Intact ("good") acorns should be air dried on newspaper, and then placed in plastic bags with dry vermiculite and stored in a refrigerator (temperature ~ 5° C / 40° F) prior to planting. Storing the acorns in a refrigerator reduces the growth of fungi and slows germination until planting time

E. Planting times and conditions

Planting should be done in the late fall or early winter, as soon as possible after the first substantial rains (at least 1" cumulative for season); in Santa Barbara County this is generally between mid-November and early December. Planting too early (e.g., October) may increase the chances that the acorns will dry out before the first rains. Acorns planted too late in the season (e.g., March) may have already developed a long and/or twisted radical (primary root) making them difficult to plant; in addition they will have fewer months to grow a root system large or deep enough to survive the summer.

Prior to planting acorns should again be placed in a bucket with water, and the floating acorns should be discarded. To plant viable acorns, dig a hole ~12 inches deep and then fill it back in, packing gently to a couple inches below soil surface. Place one or two acorns per hole on its/their side. If the radical has emerged make an indentation in the soil and place the radical pointing down. Cover with 1-2" of loose soil. The loosened

soil in the hole below the acorn will allow the first roots to grow down quickly, and that above the acorn will protect it from the hot sun and acorn predators, and allow the new shoot to easily emerge.

In general we recommend that acorns be planted near each other in "neighborhoods" rather than widely spaced across the landscape. Adult trees that are too widely spaced may produce less fruit due to a lack of pollen (Knapp et al. 2001). We suggest separating planting sites within a neighborhood by at least 16-33 feet (5-10 meters) to provide ample space for individual tree canopies to develop.

F. Protection from herbivores

In rangeland settings where gophers or ground squirrels are present, belowground protection is strongly advised. Several options are available, some of which require placement prior to planting the acorn; these include commercially available aviary-wire "gopher baskets", short cylinders constructed of aviary wire, and plastic 1 qt yogurt or cottage cheese containers with the bottoms cut off.

We also recommend protecting acorns and seedlings from small mammals aboveground and some of these protection options include below-ground protection. Examples include hardware cloth cages (described in this report), similar cages constructed out of aviary wire and supported with rebar, or plastic tree shelters. We recommend sealing the tops with aviary wire. As shown by our work, bottoms on these cages are not necessary.

If cattle are present on the site, the cage must be sturdy enough to withstand rubbing by livestock. We highly recommend "vaca-style" cages (Swiecki and Bernhardt 1991). These cages can be constructed of 4' high, 2" x 4" mesh galvanized wire (12 gauge) in a cylinder (diameter ~ 18") and supported at one side with a 5' t-post, and at the other side with a 4' rebar. They can be installed around the smaller mesh cages, and may be left in place even after several years when the smaller cage is removed. The cost per cage is approximately \$10.

G. Supplemental water and weed control

If rainfall is below average, establishment, survival, and growth rates of seedlings will be improved by supplemental watering. Our work suggests that a single watering (by hand, hose, or water truck) at the end of spring will provide the same benefit as watering throughout the growing season. In a particularly dry year, two or three waterings through the winter and spring may be better than one end-of-the-season watering. A goal of supplemental watering might be to add enough water to each planting location so that the seedlings receive at least a total (natural rain plus supplemental water) of the seasonal average (~15") or perhaps a few inches above the average. Plantings should not be watered in the summer. Watering should not be necessary once the seedlings are 2-3 years old.

This prescription is designed for oak restoration in a large-scale rangeland setting where installation of permanent irrigation systems would be labor-intensive, extremely costly, or infeasible. If the goal is successful oak establishment and survival in the long term, the approach we suggest is to plant every year that acorns are available, knowing that some years' efforts will not be successful because of low rainfall or other factors. Once planting sites have been established and individual cages installed, these can be replanted in the following year if acorns fail to germinate or establish. The benefits of a regular irrigation system to oak seedling restoration in a large-scale rangeland setting are probably not worth the cost of materials and labor for installation and maintenance. Indeed, we believe that in most cases it would be much more cost-effective if additional costs were expended on planting more acorns to hedge against losses rather than to irrigate to increase survival.

Other studies have found a positive effect on seedling establishment and growth by applying some method of weed control, including mulching, weeding, or using weed cloth/mat.

H. Expected survival and growth rates

Survival and growth will depend on rainfall, supplemental watering, site conditions, and other factors and will probably vary considerably among sites. At Sedgwick Reserve we observed that survival of seedlings also varied between the two oak species. For seedlings that were protected from both large and small mammals and received no supplemental water, survival of valley oak seedlings has been at least 22% up to age three, and as high as 37% up to age six (see Table 10). Under the same conditions, coast live oak seedling survival has been at least 5% to age four, and as high as 30% to age six (Table 9).

Growth rates of unwatered seedlings protected from both large and small mammals averaged close to 10 cm per year for both species: an average of 9 cm per year for valley oak seedlings (ranging from 0 to 15 cm per year) and 13 cm per year for coast live oak seedlings (ranging from 0 to 18 cm per year). Six-year-old protected valley oak seedlings are an average of 58 cm high (range = 4 - 192 cm), and coast live oak seedlings are an average of 82 cm high (range = 18 - 207 cm).

I. Summary

- Locate a suitable planting site
- Collect acorns in the fall from oak trees close to the site
- Store acorns in a refrigerator
- Plant soon after the first substantial rainfall of the season (~December)
- Plant acorns 1-2" below the soil surface, protect below- and aboveground with small mesh caging or tree-tubes
- If cattle are present at the planting site, protect with additional caging
- Supplemental spring watering may be worthwhile in below-average rain years
- Plant every year acorns are available
- If seedlings are protected from both small and large mammals, but unwatered, survival rates for valley oak may be as high as 37% to six years old (i.e., out of 100 acorns planted, there are 37 surviving 6-yr-old seedlings), and for coast live oak as high as 30% to six years old. Growth of such seedlings may average ~10 cm per year, with a range of 0 to 18 cm per year.

V. Outreach

The outreach activities of the Santa Barbara Oak Restoration Program have been conducted since early in the project and on an ongoing basis to reach a diversity of people, including landowners, ranchers, school groups, policy-makers, restorationists, scientists, and other members of the community.

A. Site tours and public workshops

At the beginning of the project in 1996 and 1997, we held open house events at Sedgwick Ranch, co-led by Mike Hall, of Cal Poly San Luis Obispo. We invited local landowners, ranchers and other members of the public to tour the site, providing us with the opportunity to answer questions and receive feedback on our grazing program and experimental design.

We have been involved in several public workshops, most of which included a visit to the oak restoration plots at Sedgwick. In 1997-98 we participated in workshops sponsored by the UC Cooperative Extension, "Guidelines for Managing California's Hardwood Rangelands: a Workshop for Owners and Managers", and by the County of Santa Barbara, "Funding Sources and Techniques for the Preservation and Propagation of Santa Barbara County's Oaks: Practical Information for the Landowner". In 1998 we participated in a forum on oaks in the Santa Ynez Valley, sponsored by Women's Environmental Watch; we described the work of the Oak Restoration Program and, based on our research, what we currently know about recruitment of valley and live oaks.

In 2000 we hosted a 2-day program on valley oak regeneration and restoration. The evening lecture, given in Los Olivos, was presented by Dr. Frank Davis on "The Status and Distribution of Valley Oak in Santa Barbara County." The weekend workshop and field trip on "Techniques for Growing Oaks from Acorns" was led by Dr. Claudia Tyler and Dr. Douglas McCreary. Attendees included ranchers, landowners, land managers, planners, and other interested citizens. Events co-sponsors were Sedgwick Reserve, The Integrated Hardwood Range Management Program, and the Santa Ynez Natural History Society.

In 2003 we led a public workshop and fieldtrip at Sedgwick Reserve on growing oaks from acorns. This event was co-sponsored by the Santa Ynez Natural History Society, Women's Environmental Watch, Sedgwick Reserve, and the Santa Barbara County Oak Restoration Program.

Sedgwick Reserve's volunteer docents routinely include the oak restoration experiment in their tours for K-12 students and adult groups. We have given annual training workshops for Sedgwick docents to better familiarize them with the goals and findings of the project, and to teach about oak ecology and restoration. The workshops include classroom training and a tour of the project.

The Reserve's education and outreach programs have introduced thousands of people to the oak project. Especially noteworthy is the Kids in Nature program at Sedgwick, which brings over 1000 schoolchildren in grades 4 – 6, and accompanying parents and teachers to the Reserve each year (Figure 30). These students, many of whom are English learners from low performing schools, are involved in a year-long native plant botany, habitat restoration project. They learn to differentiate the three oaks before planting acorns in their habitat restoration/research plots. The volunteers teaching

them shared information about the oak project, learned from our previous docent training workshops.



Figure 30. Kids in Nature program at Sedgwick Reserve involves over 1000 schoolchildren from Santa Barbara County schools annually, and includes a component on oak ecology and restoration. School tours led by docents also educate students about oak habitats.

In addition, students in elementary and secondary schools (over 500 students plus parents and teachers per year) are taught about the ongoing oak research as they participated in docent-led tours at the Reserve. These visitors are also introduced to the oak research project, visit our experimental plots, and are told about the goals and present findings of this project.

Since the project's inception we have led tours of our project site for individual groups interested in learning about the Santa Barbara County Oak Restoration Project. In addition to the public workshops described above, we led tours for: classes from Antioch College; City College Adult Education; UCSB Graduate Courses in Restoration Ecology, Applied Ecology, and Landscape Ecology; UCSB Biogeography classes; UCSB Undergraduate courses in Plant Ecology, Physiological Plant Ecology, and Biogeography; local biology teachers from the Education Program at UCSB; the Summer Institute in Mathematics and Science (incoming UCSB freshmen); the Oak Symposium field trip (associated conference held at the Santa Barbara Natural History Museum); researchers from both U.S. and foreign universities; individuals from the press; the Integrated Hardwood and Range Management Program Task Force; National Science Foundation staff; the Land Trust for Santa Barbara County; and other interested members of the public.

B. Presentation for Board of Supervisors

In 1998-1999, we made a presentation to the Santa Barbara County Board of Supervisors and interested members of the public on the SB Co. Oak Restoration Project. We described the project, including goals, research approach, cooperative and volunteer efforts, current results, and work planned. All members of the board were present and gave their support to the project.

C. Roundtable discussions with Santa Barbara area specialists in oak restoration

In collaboration with County staff we coordinated two meetings (November 2002, June 2004) with consultants and other specialists involved with oak restoration projects in Santa Barbara County. The goals of this roundtable discussion were to provide information about the County's Oak Ordinance, and oak planting performance standards, and to provide a forum for discussion of problems and successes in oak restoration projects in the county. Although the types of projects discussed varied (e.g., whether watering was a viable option at the sites, what species of oaks were used, use of nurserygrown seedlings/saplings vs. acorns) there was general consensus that desiccation, and herbivory by mammals were substantial obstacles to restoration efforts. Most projects have not accumulated data over more than a few years and thus conclusions about longterm successes of various methods used in mitigation projects are still not yet available.

D. Lectures and presentations at scientific conferences

We have presented our research findings at several scientific meetings. In March 1996, we presented a talk entitled "Local tree cover dynamics in foothill woodland of Santa Barbara County, 1943 – 1989" at the Fourth Symposium on Oak Woodlands, held in San Luis Obispo, CA. The theme of this symposium was "Ecology, Management, and Urban Interface Issues."

In October 2001, we gave a talk at the Fifth Symposium on Oak Woodlands held in San Diego, CA. Sponsored by the UC Integrated Hardwood Range Management Program, and the UC Division of Agriculture and Natural Resources, the symposium's theme was "Oaks in California's Changing Landscape", and was designed to provide a forum for current research and case studies on oak woodland conservation and sustainability in California. The conference was aimed at natural resource managers, researchers, policy makers, and public and private interest groups. Our written paper was published in the conference proceedings, and is attached (Appendix B).

We participated in a symposium in June 1999 in Visalia, CA, sponsored by UC Integrated Hardwood Range Management Program and Center for Forestry. We presented a talk entitled "Status, Trends, and Impacts" at the symposium entitled "A Future for Valley Oaks: Developing Partnerships for the Next Century."

We participated in the Oak Conservation Workgroup Meetings in March 2000 and April 2003. The purpose of these meetings was to bring together academic and Cooperative Extension personnel of the University of California's Department of Agriculture and Natural Resources, along with other state-wide research and outreach partners, to share information, identify research and education needs, and address issues surrounding the state's oak woodlands. The meeting in 2000 was held in Santa Maria and included a site tour of Sedgwick Reserve and the Oak Restoration Program. In 2003 Dr. Claudia Tyler gave an oral presentation on our work at the meeting held in Morro Bay.

We have attended national meetings of the Ecological Society of America to present and discuss the findings of the Santa Barbara County Oak Restoration. In August 2002 we gave a talk in Tucson, Arizona on 'Factors Limiting Recruitment in Valley and Coast Live Oak''. In 2004 we presented a poster in Portland, Oregon on ''Effects of Cattle Grazing on Herbaceous Vegetation of Oak Savannas and Woodlands in Central California''.

E. Other media

We established a web-site to make information about the project goals and results available to those with access to the internet. We maintain this site at http://www.biogeog.ucsb.edu/projects/oak/oak.html. The Santa Barbara County Oak Restoration Program was highlighted on a short program about Sedgwick Reserve produced and aired by channel 18, the local government access television station. In addition, two video programs produced and aired by UCTV on local cable (channel 12) included interviews with the project researchers at Sedgwick describing the Oak Restoration Program. The first was a "State of Minds" program, and contains a six-minute overview of the Natural Reserve System. It is viewable online at http://www.uctv.tv/library-test.asp?showID=8138 (The NRS segment within this 28-minute "State of Minds" starts at about 12 minutes, 45 seconds into the program.) The second program focused entirely on Sedgwick Reserve. It is viewable online at http://www.uctv.tv/search-details.asp?showID=8385 (The segment on the oak project within this 29-minute program begins at about 22 minutes, 10 seconds.)

The Santa Barbara County Oak Restoration Program has been described in articles in the Santa Barbara News Press, Santa Barbara magazine, and the Los Angeles Times.

F. Other research on oaks following from the SBCORP

1. Gene flow in valley oak populations at Sedgwick Reserve

Co-PI Frank Davis carried out a three-year study of pollen dispersal and gene flow in valley oaks of Sedgwick Reserve with collaborators Victoria Sork (UCLA) and Peter Smouse (Rutgers University). The research, which was funded by the National Science Foundation, built from research performed for the Santa Barbara County Oak Restoration Project to examine how long-term declines in valley oaks might affect reproductive isolation of remaining trees. Using modern genetic analysis methods and computer mapping they found that acorns are produced by very local pollen pools (the average pollen grain travels only 50-150 m) and that decreasing local tree density can affect the diversity of the pollen pool reaching a mother tree. They also found that established adult trees have local patterns of genetic similarity.

VI. Future work: an emphasis on seedling to sapling transition

We have demonstrated the relative importance of factors that limit the establishment and survival of oak seedlings, or the transition from acorn to seedling. The next unknown in the life-stage of an oak is: what limits the recruitment of saplings in rangelands, or what controls the transition from seedlings to saplings? As stated in our original proposal, we believe this transition may be the most important bottleneck in oak recruitment in California's oak woodlands, and the Santa Barbara Oak Restoration Program is now in a unique position to be able to address this critical question.

This shift in program emphasis, from oak seedlings to saplings is possible because several necessary conditions are met. Perhaps most importantly, we now have available hundreds of individuals established in our planting experiments. An investigation of the seedling to sapling stage was previously impossible because natural saplings, or seedlings close to becoming saplings, were almost nonexistent at Sedgwick Reserve. The oaks produced as a result of SBCORP plantings are especially valuable for study because they represent four different aged cohorts, including individuals in a range of sizes, and we have detailed history on all individuals (e.g., acorn source, environmental conditions in years of establishment, growth rates, etc.). Second, the extensive infrastructure required to conduct this ambitious large-scale study is already in place. Third, the site, Sedgwick Reserve, is secure and appropriate both for this sort of long-term study and for restoration. In addition, Sedgwick provides access and educational tours to the public, ensuring that the field studies of SBCORP will be a source of information available to Santa Barbara County residents of all ages and interests.

By conducting experiments to determine factors limiting the transition from oak seedling to sapling we will be able to provide information essential to mitigation, restoration, and preservation of oaks in our county and California in general. We will be able to address such questions as: is there a size or age at which seedlings or saplings have a very high likelihood of long-term survival?, what are the growth and survival rates of young oaks at different life stages and under different conditions? A continuation of our seedling physiology study will be especially relevant and valuable since we are observing changes in physiological characteristics of individuals as they approach the sapling life stage, and thus we may be able to assess what characteristics or "performance criteria" are associated with changing probabilities of growth and survival.

Thus, with continued funding at its current level, we will:

- maintain existing SBCORP infrastructure at Sedgwick Reserve, including miles of electric fence, and water system
- design and initiate a long-term study, using seedlings planted 1996-2001, to determine the factors affecting growth and survival of these individuals as they transition to saplings
- monitor yearly the growth and survivorship of all oaks planted in the SBCORP since 1996

- continue physiological measurements on selected oak seedlings to understand their resource use and its relationship to growth and survival to the sapling stage
- conduct outreach through tours at Sedgwick Reserve and through our website

If additional funds become available from the county or from external sources, we would also be able to pursue one or more of the following activities:

- further develop experiments on watering enhancement in order to determine the optimal amount and timing of supplemental watering, and refine design of our "watering-disc"
- conduct experiments to determine the relative benefits of various weed control treatments such as mulching or application of weed cloth
- conduct research on factors limiting the seedling to sapling transition in natural oak recruits, with the goal of developing a prescription for nurturing natural seedlings
- conduct a study of long-term demographic trends in valley oak using tree-ring analyses
- continue monitoring to determine the long-term effects of cattle grazing on diversity and composition of herbaceous vegetation in grassland, oak savanna and oak woodland
- plant additional oaks at appropriate restoration sites on Sedgwick Reserve in years that acorns are available, using methods described in our "prescription"
- advise or assist with off-site restoration plantings conducted in similar large-scale landscape settings on public or privately-owned land

- Bartolome JW, Fehmi JS, Jackson RD, Allen-Diaz B. 2004. Response of a native perennial grass stand to disturbance in California's coast range grassland. *Restoration Ecology* 12:279-289.
- Bilger W, Schreiber U, Bock M. 1995. Determination of the quantum efficiency of photosystem-II and of nonphotochemical quenching of chlorophyll fluorescence in the field. *Oecologia* 102 (4): 425-432.
- Bolsinger CL. 1988. The hardwoods of California's timberlands, woodlands, and savannas, USDA Forest Service, Pacific Northwest Research Station. Resource Bulletin PNW-RB-148. 148 pp.
- Brown R, Davis FW. 1991. Historic mortality of valley oak in the Santa Ynez Valley, Santa Barbara County, 1933-1989. Proceedings of Oak Woodlands and Hardwood Rangeland Management: a Research Symposium. USDA Forest Service General Technical Report PSW-126, pp. 202-207.
- Davis FW, Kuhn W, Alagona P, Campopiano M, Brown RW. 2000. Santa Barbara County oak woodland inventory and monitoring program: pilot mapping and modeling study. A report to the County of Santa Barbara, Dept. of Planning and Development, Santa Barbara, CA: 60 pp. (Report available online at: http://www.biogeog.ucsb.edu/pubs/Technical%20Reports/Technical%20Reports.htm)
- Griffin, JR. 1971. Oak regeneration in the upper Carmel Valley, California. *Ecology* 52(5): 862-868.
- Harrison S, Inouye BD, Safford HD. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology* 17(3):837-845.
- Hayes GF, Holl KD. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* 17(6):1694-1702.
- Jepson WL. 1910. The silva of California. University of California Memoirs 2:1-480.
- Knapp E E, Goedde M A, Rice K J. 2001. Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. *Oecologia* 128:48-55.
- Koenig W D, Mumme R L, Carmen W J, Stanback M T. 1994. Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 75:99-109.

- Muick PC, Bartolome JW. 1987. An assessment of natural regeneration of oaks in California. A report to the California Dept. of Forestry and Fire Protection, Sacramento, CA: 79 pp.
- Ogden GL. 1975. Differential response of two oak species to far inland advection of seasalt aerosol. Ph.D. dissertation, University of California, Santa Barbara, CA. 230pp.
- Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA. 1965. Sap pressures in vascular plants – negative hydrostatic pressure can be measured in plants. *Science* 148:339-346.
- Smith CF.1998. *A flora of the Santa Barbara region, California, 2nd edition*. Santa Barbara Botanic Garden and Capra Press, Santa Barbara, CA.
- Sork V, Davis FW, Smouse P, Apsit V, Dyer R, Fernandez J, Kuhn W. 2002. Pollen movement in declining populations of California valley oak, *Quercus lobata*: Where have all the fathers gone? *Molecular Ecology* 11: 1657-1668.
- Stromberg MR, Griffin JR. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. *Ecological Applications* (4):1189-1211.
- Sudworth GB. 1908. Forest trees of the Pacific slope, USDA Forest Service, 441 pp.
- Swiecki TJ, Bernhardt EA. 1991. Minimum input techniques for restoring valley oaks on hardwood rangeland. Sacramento, CA: Forest and Rangeland Resources Assessment Program, California Department of Forestry and Fire Protection; 79 p.
- Tyler CM, Kuhn B, Davis FW. In press. Demography and recruitment limitations of three oak species in California. *Quarterly Review of Biology*.

VIII. Appendices

- A. Review of oak demography and recruitment (in press, *Quarterly Review of Biology*)
- **B**. Factors limiting valley and coast live oak seedling establishment (conference

proceeding)

DEMOGRAPHY AND RECRUITMENT LIMITATIONS OF THREE OAK SPECIES IN CALIFORNIA

Claudia M. Tyler¹, Bill Kuhn, and Frank W. Davis

Institute for Computational Earth System Science

University of California

Santa Barbara, CA 93106-3060, USA

¹ contact author

email: tyler@lifesci.ucsb.edu

The Quarterly Review of Biology

in press

accepted July 13, 2005

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KEYWORDS

Quercus, oak woodland, population, tree, sapling, seedling establishment, long-lived

ABSTRACT

We review published studies on the demography and recruitment of California oaks, focusing on the widespread dominant species of the foothill woodlands, *Ouercus* douglasii, Q. lobata, and Q. agrifolia, to ascertain the nature and strength of evidence for a decline in populations of these species. The vast majority of studies have been of short duration (less than three years), focused on the acorn and seedling life stages, and conducted at few locations within each species' geographic range. We summarize the extensive body of research that has been conducted on the biological and physical factors that limit natural seedling recruitment of oaks. The oak "regeneration problem" has largely been inferred from current stand structure rather than by demographic analyses, which in part reflects the short-term nature of most oak research. When viewed over longer time periods using field surveys or historical photos, the evidence for a regeneration problem in foothill oaks is mixed. O. douglasii shows very limited seedling or sapling recruitment at present but longer term studies do not suggest a decline in tree density, presumably because rare recruitment is sufficient to offset low rates of mortality of overstory individuals. *Q. agrifolia* appears to be stable or increasing in some areas, but decreasing in areas recently impacted by the disease *Phytophthora ramorum*. Evidence from the few available studies is more consistent in suggesting long term declines in foothill populations of Q. lobata. Long term monitoring, age structure analysis and population models are needed to resolve the current uncertainty over the sustainability of oak woodlands in California.

INTRODUCTION

The oak genus *Quercus*, the largest within the beech family Fagaceae, is widespread throughout the Northern Hemisphere. Oaks are common in temperate and tropical zones within Europe, Asia, and North and Central America and are often a dominant component of forest, woodland, and shrubland communities in these regions. Thought to be of southeast Asian origin (Melville 1982), *Quercus* has evolved into over 500 species of evergreen and deciduous trees and shrubs that occupy a diverse array of habitat and climate types (Manos et al. 1999).

Oaks serve important functions in both human societies and wildlife communities worldwide. Acorns have provided sustenance to indigenous cultures throughout North America and Europe for centuries; other uses of oaks, acorns, and galls have included medicines, dyes, timbers for shipbuilding, and lumber for fuel, railway ties, furniture, and housing (Keator 1998; Johnson et al. 2002). Numerous wildlife species are dependent on oaks for habitat and rely on acorns or oak leaves as a primary food sources (McShea and Healy 2002).

In a number of oak woodlands and savannas throughout the world stands are composed of large, old adults with few individuals in the smaller, younger classes, raising concerns that natural recruitment of the oaks may be insufficient to balance adult mortality. Lack of regeneration has been reported in British oak woodlands (Watt 1919; Shaw 1968a; Shaw 1968b), oak forests in Asia (Saxena and Singh 1984; Singh et al. 1997; Abrams et al. 1999), and North American oak woodlands in California (Holzman 1993; Swiecki et al. 1993), Texas (Russell and Fowler 1999) and Tennessee (Loftis and McGee 1993).

In California, oak forests, woodlands and savannas occupy roughly 45,000 km2, 11% of the state and nearly one-fourth of its wooded landscapes (Davis et al. 1998) (Figure 1). These communities are among the most diverse in North America, containing more than 1400 species of flowering plants, over 300 species of vertebrates, and thousands of invertebrate species. Despite the importance of oaks as a natural resource, a survey conducted in the mid 1980's found that between 3-5 million of California's original 10-12 million acres of oak woodland habitats had been lost largely due to rangeland clearing, agricultural conversion and urban development (Bolsinger 1988); as land conversion has continued since that time, acreage of woodland lost to date is certainly higher. Several species including *Lithocarpus densiflorus*, *Quercus agrifolia*, *Q. kelloggii*, and *Q. chrysolepis* are now threatened by the introduced pathogen, *Phytophthora ramorum*, which has caused extensive mortality in coastal and montane forests from Monterey to Mendocino counties (Rizzo et al. 2002).

Compounding the threat to these systems from habitat conversion and the loss of adult trees, natural recruitment of oaks may be insufficient to maintain current densities within extant populations, as has been observed elsewhere. As early as the beginning of the 20th century, researchers observed that California oaks did not appear to be regenerating well (Sudworth 1908; Jepson 1910). However, more recent quantitative assessments of existing oak stands in California have produced conflicting conclusions about the extent of the "regeneration problem". The few large-scale surveys of oaks in California, which focused primarily on blue oak, *Quercus douglasii*, found that regeneration is highly site specific, making it difficult to generalize about the extent and urgency of population declines in California's oak woodlands (Muick and Bartolome 1987a; Swiecki et al. 1993).

Here we review the scientific literature on the demography of nine species of canopysized oaks found in California, focusing on three species that have received the majority of study and are widespread in central California's foothill woodlands: blue oak (*Q. douglasii*), valley oak (*Q. lobata*), and coast live oak (*Q. agrifolia*) (Figure 1). We summarize the findings of research concerned with species-specific population distribution and abundance, age and size-class structure, and age-specific patterns of mortality and recruitment. Our objectives are to review the experimental findings on factors limiting establishment of oak seedlings and saplings and to describe and evaluate the evidence for a "regeneration problem", that is, for widespread oak population declines in extant stands. Much of the research conducted on California oaks is presented in graduate theses and dissertations, technical reports, and proceedings from scientific conferences. Thus a secondary goal of this review is to synthesize the oak literature from California that may not be readily available to the international scientific community in order to facilitate comparative analyses.

CLASSIFICATION OF OAK DEMOGRAPHY AND REGENERATION STUDIES

We reviewed over 150 published sources, and ultimatley produced a database of 116 distinct studies that focused on one or more of the arborescent oak species in California and contained results relevant to some aspect of oak demography, including oak population age or size structure, change in population structure over time, or stage-specific survival rates. (A complete listing is available online at http://www.biogeog.ucsb.edu/Data/data.htm). The characteristics of this literature can be summarized as follows (Table 1).

1. Two-thirds of studies are published in conference proceedings, technical reports to government agencies, theses, and dissertations; only 23 of the sources have been published in peer-reviewed scientific journals.

2. Blue oak (*Q. douglasii*) has received the large majority of demography-related research effort (Table 1). Both valley oak (*Q. lobata*) and coast live oak (*Q. agrifolia*) have also received considerable attention, while studies of the remaining species account for less than 20% of published research on California oaks. The blue oak woodland type, which ranks first in terms of total land area (Davis et al.1998), ranges from open savannas to dense woodlands (Figure 2). Coast live oak and valley oak rank eighth and ninth, respectively, in terms of extent but, like blue oak, are species where observed limited recruitment is a concern (Griffin 1971; Griffin 1976; Muick and Bartolome 1987a; Bolsinger 1988). These species occur in habitats ranging from closed riparian forests to open savannas, but recruitment has mainly been an issue in open woodland and savanna systems (Figure 3). All three species have been heavily impacted by habitat conversion to agriculture and residential development, raising public and scientific concern for their long term viability (Pavlik et al. 1991).

3. The majority of studies have focused on acorns and seedlings, especially on the factors that affect acorn germination success and seedling survival, while few studies have been conducted on saplings and adults (Table 1.) Most studies were short term (1-2 years) and thus we know little about how the effects of these factors vary over time at a site.

4. There is a conspicuous lack of information about the factors that govern the transition from seedlings to saplings, and from saplings to adults, mainly because saplings are infrequent in most species and because long term study is required. Only four (Allen-Diaz and Bartolome 1992; Swiecki et al. 1997a; Bartolome et al. 2002; Swiecki and Bernhardt 2002) focused on the mechanisms that affect survival or recruitment of saplings within populations.

5. Little is known about rates of and controls on tree mortality and only two studies (Franco 1976; Brown 1991) directly measured adult mortality by following individual trees through time.

6. A substantial number of studies (22) investigated demography of oaks, but nearly all focused on current population or age structure. Only a few studies used tree rings to examine population dynamics over longer time periods.

7. The majority of studies involved field observation of natural or planted individuals for less than two years. Six of the fifteen studies extending over more than 72 months used historical air photos (Franco 1976; Rossi 1979; Scheidlinger and Zedler 1980; Brown 1991; Davis et al. 1995; Callaway and Davis 1998) (Table 1).

8. Although oak woodlands are widespread in California, most research has been conducted in a few areas associated with research field stations, notably the University of California's Sierra Foothill Research Center (Yuba County), Hastings Natural History Reservation (Monterey Co.), Sedgwick Reserve (Santa Barbara Co.), and the Hopland Research and Extension Center (Mendocino Co.).

LIFE HISTORY OF CALIFORNIA OAK SPECIES

For context, we provide a brief description of the life history of California foothill woodland oaks, notably *Q. agrifolia*, *Q. lobata*, and *Q. douglasii*. Although details vary among species, all oaks share this general life cycle (Figure 4).

Flowering and Fertilization (from flower to acorn)

Although the reproductive age is not well documented for these species, it is likely that age at first reproduction for naturally established trees is at least several decades, with maximum production occurring decades later. Mature trees produce flowers during March and April. Oaks are monoecious, bearing the long male catkins and the very small female flowers on a single twig. They are wind pollinated and have limited self-pollination because male flowers generally release their pollen before the stigmas on female flowers of the same tree are receptive (Keator 1998; Sork et al. 2002).

The acorn crop varies widely in quantity from tree to tree and from year to year. Factors that may influence number of acorns produced by a given tree each year include weather, tree age, size, and health, the size of the tree's previous year's fruit crop, and perhaps the

"neighborhood" conditions such as distance to and density of neighboring trees (Koenig et al. 1994; Koenig et al. 1999; Knapp et al. 2001; Sork et al. 2002).

Acorn Development and Dispersal (from acorn to seedling, stage 1)

The length of time required for development and maturation of acorns varies among subgenera. In general, acorns of "white oaks" (subgenus Lepidobalanus) ripen within one year, while acorns of "red oaks" (subgenus Erythrobalanus) and "intermediate oaks" (subgenus Protobalanus) develop and ripen within two years. California's oaks that produce acorns within one year are valley, blue, Engelmann, Oregon, and coast live oak; those that take an additional year to develop acorns are interior live, black and canyon live oak. Acorn drop occurs between September and November (Griffin 1971). While still on the tree, acorns are susceptible to mortality due to heat, fungus, insects (predominately weevils and moth larvae), birds (including jays, magpies, and acorn woodpeckers) and mammals (including mice, squirrels, deer, pigs, and cattle) (Griffin 1980; Koenig et al. 2002). No persistent seed bank is formed because acorns do not survive more than one year.

Most mature acorns that are not eaten or carried away by animals land under or near the canopy of the parent tree. Acorns on the soil surface have a very high likelihood of being killed by heat, desiccation, or predation (Tietje et al. 1991). In a natural landscape, acorns may become buried by one or more means. While some seeds may be buried inadvertently (e.g., by wind-blown litter, or pocket-gopher tailings), acorn-caching animals, in particular western scrub jays, play a critical positive role in natural seedling establishment in central California's oak woodlands. A single scrub jay may cache up to 5,000 acorns in a season, but only relocate and consume half of this number (Carmen 1988). Other caching animals include magpies, stellars jays, ground squirrels, and deer mice.

Acorn germination and shoot emergence (from acorn to seedling, stage 2)

There is no acorn dormancy in the white oaks (e.g., blue and valley oaks), and germination occurs in the late fall. Germination is delayed until early winter or spring for red oaks such as coast live oak (Griffin 1971, Johnson et al. 2002). During late fall and early winter the acorn is especially vulnerable to desiccation if it is on the soil surface depending on the timing of early season rainfall. Most of the initial energy stores of the acorn go toward root growth. It can be months before the shoot is fully expanded and visible above ground (Matsuda and McBride 1986). Seed predators, burrowing animals that consume plant roots, and fungi continue to add the risk of high mortality at this early life stage.

Seedling Development (from seedling to sapling)

Following germination and emergence, seedlings must survive prolonged summer drought, which in the Mediterranean climate of California's foothills, may extend up to six months, or more. While it has been suggested that adult valley oak trees have roots that may tap into the water table, allowing trees to survive summer drought, the roots of new seedlings are generally many meters away from perennial water. Water stress experienced by seedlings is significantly greater than that of saplings and trees (Matzner et al. 2003, Mahall et al. in prep.). An additional stress to the young plant is herbivory by insects and mammals. Older saplings, with considerable belowground growth, may be able to recover from intense herbivory and even complete defoliation, but significant loss of leaves on a new seedling is likely to cause its death. Thus first- and second-year mortality of oak seedlings may be exceptionally high (e.g., Davis et. al. 1991).

Sapling Stages to Maturity (from sapling to tree)

Unless artificially watered, savanna and woodland oaks in California are relatively slowgrowing trees. Competition for light and water in dense stands may reduce growth rates. Sources of mortality at this stage are intensive browsing by deer and cattle, and those sources that also affect adult tree stages, such as fire, disease, and cutting by humans. It is unknown how many years it takes to make the transition from sapling to tree, but it is probably decades. The life span of oaks varies among species. Valley oak is reported to be the largest and longest-lived oak species in North America, reaching ages of 400 - 600years (Pavlick et al. 1991). Blue oaks have been aged to >400 years old (White 1966; Mensing 1988). Coast live oaks are also long-lived but have shorter life spans, perhaps between 200 - 300 years (Snow 1972).

FACTORS LIMITING ESTABLISHMENT OF OAK SEEDLINGS AND SAPLINGS

Field surveys of blue oak, valley oak, and in some cases coast live oak, indicate that in many locations the numbers of seedling and sapling recruits are consistently very low. The factors most often cited as limiting oak recruitment are: acorn diseases, acorn predation, herbivory of established seedlings and saplings, competition between oak seedlings and non-native annual grasses for water, soil compaction by cattle, lack of fire, low rainfall in some years, and low tree population density. Below, we examine the current state of knowledge on these biological and physical factors thought to restrict oak recruitment.

BIOLOGICAL FACTORS

Acorn diseases and insect damage

In an extensive investigation into the impacts of diseases and insect predation, Swiecki et al. (1990) reported a wide array of diseases and insects that damage or kill acorns. They

found high incidences of fungi and evidence of boring and ovipositing by insects in blue oak, valley oak, and coast live oak acorns. Comparing the incidence of insect damage on acorns collected from the canopy to those from the ground, they found significantly greater proportions of insect damage on ground-collected acorns (71 - 96%) compared to acorns still on the tree (5 - 29%). Knudsen (1984) found that 58% of valley oak acorns had evidence of insect damage. Griffin (1980) noted valley oak acorn mortality due to insect damage ranged from 0 - 31% annually over eight years of observation. Dunning et al. (2002) examined insect damage on coast live oak and Engelmann oak acorns and seedlings. They found that the majority of all ground-collected acorns had some insect damage; however, the level of insect damage to acorns of both species was slight (<20% of the entire acorn), and the portions of the acorn most likely to be damaged were the cotyledons (carbohydrate storage) rather than the radicle and epicotyl (growing tips). The degree to which acorn damage reduces germination rates is not clear. Knudsen (1984) reported no difference in growth of seedlings that grew from insect damaged acorns vs. those that showed no evidence of insect damage.

Acorn and seedling predation

Experimental studies have compared the survival and emergence rates of fully exposed acorns to those protected by cages excluding birds and mammals. Predation by small mammals, including mice, gophers, voles, and ground squirrels has been shown to be a major source of acorn and seedling mortality for blue oak (Borchert et al. 1989; Callaway 1992; Adams and McDougald 1995), valley oak (Griffin 1971; Griffin 1980; Knudsen 1984; Callaway 1992; Adams and Weitkamp 1992, Tyler et al. 2002) and coast live oak (Hibberd 1985; Plumb and DeLaseaux 1997; Parikh and Gale 1998; Tyler et al. 2002).

Acorn predation has been found to be extremely high in some cases. Griffin (1971) found that within non-grazed savannas, no ne of 160 sown valley oak acorns produced a seedling. Griffin attributed these substantial losses of acorns and seedlings to both mice and gophers. On Hastings Natural History Reservation, Griffin (1980) placed on the ground under the canopy of an adult valley oak a total of 933 valley oak acorns, all within a deer exclosure, and some protected from birds with mesh screens. After a period of three years, 81% of these acorns had been eaten or carried away. Of the 70 seedlings that emerged, none survived the continued attacks by rodents. Tyler et al. (2002) investigated factors limiting seedling establishment of valley oak and coast live oak, conducting field experiments in which approximately 1000 acorns per species per year were planted in four different years. They found that maximum rates of seedling emergence (i.e., acorn survival and germination) in locations protected from birds and mammals, were 71% in valley oak, and 85% in coast live oak, but in locations open to all seed and seedling predators, maximum emergence rates were significantly lower: 30% in valley oak, and 32% in coast live oak.

The strong associations of natural oak seedlings with shrub canopies reported for coast live oak (Callaway and D'Antonio 1991) and blue oak (Callaway 1992) are likely a result of protection provided by shrubs from shoot herbivory. Callaway and D'Antonio (1991) surveyed naturally occurring coast live oak seedlings and found that the vast majority

were under shrubs, and that these were significantly less browsed than oak seedlings in surrounding open grassland. In field experiments they determined that acorns planted under shrubs had high emergence and survival rates (up to 55% survival to year 2), while no seedlings survived from acorns planted in the open. Herbivory by deer was the suspected cause of mortality of nearly 40% of those dving in the open, as seedlings were removed with no evidence of soil disturbance. Shrubs did not provide protection from acorn predators for blue oaks in similar studies (Callaway 1992); emergence was lower for acorns planted under shrubs due to excavation by gophers there. However, as above, percent survival of emerged shoots was significantly higher under shrubs than in the open, and the majority of mortality in the open was due to herbivory above the soil surface, most likely by deer. Both studies report that animal activity and damage to acorns and shoots varied between microsites. Acorn and seedling removal under shrubs was caused by gophers, which probably use the shrubs as refuge, whereas deer were presumed responsible for shoot herbivory in the open. In addition to providing safe-sites by protecting from deer, shrubs also provide shade. In experiments conducted in a dry year with only 50% of average rainfall, the combination of these facilitative mechanisms, as provided by caging and shading, led to highest survival in blue oak seedlings (Callaway 1992). Rock outcrops may similarly serve as natural safe-sites for oak recruitment (Snow 1972.)

Herbivory and browsing of seedlings and saplings

The role of insects (McCreary and Tecklin 1994) and small mammals in oak seedling mortality has been demonstrated by a number of studies (Griffin 1971; Griffin 1976; Adams et al. 1987; Davis et al. 1991; Adams et al. 1997c; McCreary and Tecklin 1997; Berhardt and Swiecki 1997; Tyler et al. 2002). Leaf defoliation by grasshoppers, root damage by pocket gophers and voles, and bark girdling by mice have all been reported to cause mortality or severe damage to established oak seedlings and saplings. For example, in acorn planting experiments Davis et al. (1991) found that the proportion of blue oak seedlings surviving three years was reduced by half (22% vs. 44%) for seedlings not protected from gophers compared to those protected. Higher rates of damage have been reported for valley oaks seedlings; gophers were responsible for up to 90% of the mortality of planted seedlings (Adams and Weitkamp 1992). In addition, browsing by deer has been noted to significantly reduce growth of oak saplings (White 1966; Griffin 1971). Moderate clipping treatments, which simulated defoliation by insects and light herbivore browsing, were found to result in greater mortality in coast live oaks than in blue oak seedlings; average mortality of shaded one-year-old seedlings in clipped treatments compared to controls for coast live oaks was 82% (clipped) vs. 55% (control), and for blue oaks was 39% (clipped) vs. 35% (controls), suggesting that coast live oak seedlings may be especially vulnerable to such attacks (Muick 1995). Welker and Menke (1990) found that survival of blue oak seedlings in response to simulated browsing was greatly reduced when soil water was depleted rapidly, as might occur when oaks grow with exotic annual grasses rather than native perennials.

Livestock grazing has been implicated as a primary cause for failure of natural oak recruitment, but its effects are not straightforward. Several studies that have examined the association of cattle grazing with oak seedling or sapling abundance have yielded conflicting results. Standiford et al. (1997) conducted surveys of blue oak stands in southern Sierra Nevada woodlands and found that livestock grazing was negatively correlated with blue oak seedling presence, but non-significantly related to the presence of saplings. Analyses of the effects of environmental factors on blue oak sapling abundance conducted by Swiecki et al. (1997b), found that browsing intensity was negatively associated with blue oak sapling presence. However, in their statewide survey of oak woodlands, Muick and Bartolome (1987a) found that patterns of oak recruitment could not be explained by the presence or absence of cattle grazing. In addition, the removal of livestock has not resulted in increased levels of oak recruitment at some sites, even after many decades (e.g., blue oaks, White 1966; valley oaks, Callaway 1992).

Hall et al. (1992) investigated the effects of cattle grazing on blue oak seedling survival, and found that season of grazing played a much greater role in affecting survival than did grazing intensity (stocking density). Seedlings exposed to spring and summer grazing had significantly more damage and lower survivorship than those exposed only to winter grazing. They also found that controls, which excluded cattle but allowed access to deer and other native grazers, were no different from plots grazed by livestock, suggesting that wildlife had an equivalent effect on oak recruitment. Jansen et al. (1997) examined the effects of two grazing systems, traditional (year-round, low intensity) vs. high-intensityshort-duration (HISD) on blue oak sapling growth over 4 years. They found that effects of these grazing regimes did not differ significantly except that browse utilization (the proportion of twigs that were grazed) was higher in the HISD treatment. Interestingly, grazing by cattle has been shown to have positive indirect effects on oak recruitment by reducing the growth of competing herbaceous vegetation. Bernhardt and Swiecki (1997) found that, over a 7 year period, while direct effects of cattle on unprotected seedlings were negative, grazing indirectly improved growth and survival of caged valley oak seedlings and saplings.

Competition with annual grasses

Native perennial grasses, such as *Nasella pulchra* and *N. cernua*, and exotic annual grasses, such as *Avena fatua* and *Bromus mollis*, use water in different ways, both temporally and spatially (Welker et al. 1991; Holmes and Rice 1996; Hamilton et al. 1999). In California, the exotic annuals grow rapidly in the winter and early spring, depleting surface soil layers of water quickly; these annuals flower and complete their life cycle by mid-summer. In contrast, native perennials have slower growth rates and consume soil water at a slower rate so that the plants maintain photosynthesis well into the summer months while water is still available (Holmes and Rice 1996). The roots of annuals are shallower than those of perennials and are more dense within the topsoil layers (Holmes and Rice 1996; Hamilton 1997). It has been hypothesized that the exotic annual grasses deplete near-surface soil water early in the growing season, leaving emerging oak seedlings less water; in contrast, oak seedlings growing among native perennials have access to soil moisture long into the summer. Studies on blue oak and

valley oak have demonstrated that seedling emergence, growth, and survival are significantly reduced when grown with exotic annuals as neighbors versus grown with no neighbors (Gordon et al. 1989; Danielsen 1990; Gordon and Rice 1993). Oak seedlings grown with exotic annual grasses also exhibited reduced emergence and growth rates compared to those grown with native perennials as neighbors (Danielsen 1990; Welker et al. 1991; Gordon and Rice 2000). The negative effects of annual grasses were attributed to their reducing soil moisture more rapidly than perennial neighbors did.

Lending support to this competition hypothesis, several studies that examined various treatment methods found that reduction of grass cover by clearing or mulching (i.e., "weed control") significantly improved seedling survival and/or growth, most strikingly if the seedlings were also protected from herbivores (Swiecki and Bernhardt 1991; Adams and McDougald 1995; Adams et al. 1997b; Adams et al. 1997c; McCreary and Tecklin 1997). Although the grass species were not identified in these studies, it is safe to assume that they were the exotic annual grasses that dominate California grasslands. To examine survival of oak seedlings with and without grass competition, Griffin (1971) planted acorns in plots, half of which were cleared of the herbaceous layer, and all of which were fenced to exclude large herbivores. In savanna plots, 31% of valley and coast live oak acorns, and 88% of blue oak acorns produced seedlings that survived 3 years within the cleared areas, whereas no seedlings emerged within the uncleared section of the plot. The mechanisms of interaction between oak seedlings and herbaceous plants were not discerned in these studies.

PHYSICAL FACTORS

Soil Compaction

Since the majority of California oak woodlands and savannas are used as rangeland for cattle grazing (Bolsinger 1988; Greenwood et al. 1993) it has been speculated that surface soils within these rangelands have been compacted following decades of cattle presence, resulting in soil conditions that reduce oak establishment. Soil compaction leads to increased soil bulk density, which, in turn, reduces the ability of water to penetrate the soil surface and thus increases surface runoff (Bezkorowanjnyj et al. 1993; Trimble and Mendel 1995). The compaction has the potential to reduce the ability of roots to penetrate the surface soil layers (Ferrero 1991), hampering an emerging oak seedling's ability to reach ground water. Research from several systems indicates that the changes in bulk density that occur from grazing vary with the region of study (humid vs. arid) and season and intensity of grazing (Laycock and Conrad 1967; Van Haveren 1983; Stephenson and Veigle 1987). The rate at which soils recover after grazers are removed has been found to vary from a few to many years (Ratliff and Westfall 1971; Braunack and Walker 1985). To our knowledge, there has been no published experimental research that has investigated the relationship between soil bulk density and the establishment or growth of oak seedlings.

Lack of Fire

Some studies have linked past fire events with periods of above average recruitment within blue oak woodlands. These studies aged populations of oaks and determined dates of fires from fire scars. McClaran (1986) and Mensing (1988) found some correlation between fire events and periods of apparent oak recruitment. However, rather than actual new recruitment, the authors acknowledge that the association of tree ages and fire dates may have resulted from temporal concentration of postfire resprouts. This conclusion was reiterated by McClaran and Bartolome (1989) and Bartolome (1991) who suggested that the association of fire and apparent blue oak regeneration was created by removal of older stems by fire and establishment of even-aged stems from resprouting. Contrary to hypotheses about the positive role of fire in oak recruitment, pollen and charcoal evidence suggests that lack of fire (i.e., fire suppression) has led to an increase in coast live oak density in the last 100 years in central coastal California (Mensing 1993).

It has been hypothesized that fire might improve conditions for oak seedling and sapling growth and survival by eliminating herbaceous competitors and by providing a flush of soil nutrients following a burn. Fire has been shown to have variable effects on the survival or growth of existing seedlings, but most studies have not found stimulatory effect of fire on recruitment or resprouting. The effect of wildfire and prescribed burns on the survival rate of Engelmann and coast live oak seedlings was examined by Lathrop and Osborne (1991) on the Santa Rosa Plateau. For the study period of 18 months (from fire to the final observation) the authors found that seedling survival rates were only slightly higher (61%) in the burned areas compared to seedling survival at unburned sites (55%). Other research has found no positive effect of fire treatments on recruitment, survival, and/or growth of blue oak seedlings (Bartolome and McClaran 1988; Bartolome 1991; Allen-Diaz and Bartolome 1992). Swiecki and Bernhardt (2002) conducted research on the survival and regrowth of naturally occurring blue oak saplings burned in a moderate intensity fire. They found that partial or complete topkill from fire did not confer any growth or survival benefits to blue oak saplings, but instead prolonged the period that oak shoots were susceptible to subsequent fires and to other damaging agents. In a statewide survey of the distribution of blue oak saplings, Swiecki et al. (1997b), found that frequent fire was negatively associated with sapling recruitment. Infrequent fire was not correlated or only slightly positively associated with sapling recruitment.

Low rainfall

In multi-year planting experiments interannual variation in seedling emergence and survival can be explained by differences in rainfall. Borchert et al. (1989) found that seedling emergence of blue oaks in a wet year was nearly twice that in dry years. Amount of precipitation following planting also influenced rates of emergence and initial establishment of valley oaks (Griffin 1971; Tyler et al. 2002). In savanna plots protected from large mammals, emergence was 68% in a wet year vs. 0% in a dry year (Griffin 1971); in similar treatments, Tyler et al. (2002) found that emergence was 45% in a wet year, vs. 5% in a dry year, and concluded that rainfall in the first year after planting was the decisive factor in recruitment success of both valley oak and coast live oak seedlings.

In years with below average rainfall there is consistently low emergence and establishment of oaks regardless of caging or weed-control treatments (Griffin 1971; Adams et al. 1997b; Plumb and Hannah 1991), though shading was found to increase survivorship of blue oak (Callaway 1992; Muick 1995) and coast live oak (Muick 1995) seedlings in dry years.

Reduced fecundity due to stand thinning or habitat fragmentation

Oak fecundity may be density-dependent at low stand densities. A study of pollen flow in blue oak found a significant positive correlation between individual acorn production and neighborhood density of potential pollen donors (Knapp et al. 2001). Sork et al. (2002) estimated the average distance of pollen dispersal in a valley oak savanna to be 50 – 150m, and the effective number of pollen donors to be three to five individuals. As oaks become spaced farther apart in the landscape, due to stand thinning or habitat fragmentation, total acorn production and perhaps per capita fecundity decline. At present the demographic consequences of lowered fruit production is poorly understood.

EVIDENCE OF A "REGENERATION PROBLEM"

As in other oak habitats throughout the world, researchers have observed low recruitment rates in California's oak woodlands, raising concerns about population decline. The majority of articles on oak demography make reference to the "oak regeneration problem". This section reviews the evidence for the hypothesis that extant stands of California's foothill oaks are declining. The majority of the data available focuses on blue oak, valley oak, and coast live oak.

The term *regeneration* has several usages, but as applied here in the context of population dynamics, we use *regeneration* to describe the process of replacing individuals lost from mortality; thus it represents a balance of the losses due to mortality with the gains from recruitment that maintain a stable population density over time (Harper 1977; Muick and Bartolome 1987b; Bartolome et al. 1987; Johnson et al. 2002). *Recruitment* is the establishment of new individuals into an age- or size-class of a population. Oak recruitment is generally classified into three size-classes: seedling (the successful germination of an acorn and survival of the seedling), sapling, and tree. *Mortality* is the removal (or death) of individuals from a population, and can occur in any age- or size-class. Mortality may be a result of anthropogenic forces (e.g., cutting) or natural forces, such as wind throw, disease, or old age. To fully and accurately determine whether a regeneration problem exists for a given stand or population, information about both mortality and recruitment is required.

EVALUATION OF STUDY METHODS

We identified nineteen studies that provide quantitative information about current stand structure in California's oak woodlands (Table 2). However, few studies included data on both recruitment and mortality. Four approaches have been used in these studies: 1) age structure analysis of current stands, 2) size structure analysis of current stands, 3)

comparative analysis of historical and current air photos, and 4) comparative analysis of historical and current ground surveys. Each of these approaches has its merits and limitations.

Age structure (tree ring) analyses of current stands

In age-structure analyses the age distribution of adults in the stand is determined by coring or sectioning trees and then counting annual growth rings. This approach provides accurate results for species that produce distinct annual rings (e.g., the deciduous species, such as blue oak and valley oak), but is generally not well suited for those species that do not have distinct rings (e.g., the evergreen oaks, such as coast live oak). At the same time the methods for conducting age-structure analyses are quite laborious since oaks generally have very dense wood, making coring difficult, and there is considerable time required for preparation and reading of cores. By describing a stand's age structure, the goals of these analyses are to determine the years in which the present adults recruited, and to relate those recruitment events to past biological or environmental conditions (e.g., rainfall, fire, historical grazing). Additional information derived from this approach can include individual growth rates (by analyzing ring widths) at different ages or sizes and, potentially, their relationship to past environmental conditions.

The main limitation of this, and similarly any static survey, is that the present age structure represents only the age structure and recruitment history of survivors (Harper 1977). There may have been past peaks in recruitment in cohorts that later experienced much higher mortality rates, for example. Also, one cannot know the entire suite of conditions that existed during those recruitment events. A second important limitation of age structure analyses occurs with species that resprout following cutting or damage by fire. In these cases, a given age cohort may actually represent individuals that *recruited* at many different times, but *resprouted* simultaneously after the same disturbance. Thus the apparent year of recruitment, as inferred from annual growth rings, may not be the year in which the individual established as a seedling, so conclusions about factors promoting natural establishment can be erroneous. For example, in his study of blue oak demography in the Sierra foothills, McClaran (1986) reported that 70-85% of blue oak trees established after fire; similarly Mensing (1988) found that a large peak of recruitment of blue oaks in the Tehachapi Mountains occurred in 1856. While some ecologists cite this work as evidence that fire stimulates oak recruitment, both authors acknowledge that these large cohorts may likely be due to resprouting after fire of adults of various ages.

Size structure analyses of current stands

In size structure analyses all individuals in a stand are measured, and assigned to size classes. It is relatively easy to measure the sizes of trees using diameter at breast height (dbh), and of seedlings and saplings using diameter at base (db) and/or height. The main limitation of this method is that any conclusions about population dynamics, and the past or future recruitment or mortality of a stand rely on the assumption that size reflects age. With oaks, as with many tree species, while it is generally true that the largest individuals

are probably old, and the youngest individuals are generally small, it is not always the case that the smallest trees are young. Size and age are not well correlated in blue oaks (McClaran 1986; Harvey 1989), and weakly correlated in valley oaks (Knudsen 1984). As described in the previous section, some species (including blue oak and coast live oak) resprout following cutting or damage by fire, and thus older individuals that have resprouted may be smaller than expected for their age. Therefore, size can be used as a measure of age only in a very broad sense.

Even given this caveat, there are strong arguments for using size class rather than age class to describe the structure of oak populations, and to predict its potential for regeneration. First, mortality risks appear to be much more closely associated with size class than age class. For example, although it may take many years for a sapling to reach a height above the browse layer ($\sim 1.5 - 2$ m), it is then less likely to be killed by large grazers. Larger seedlings and saplings may also be better able to withstand drought and fire. Second, as in many other tree species, reproductive behavior is often size- rather than age-related. Thus size may be the most useful parameter for predictions about the future of given population.

Historical and current air photo analysis

Sequences of historical aerial photos since ~1930's were used to determine the change in tree cover and/or density of several areas. After excluding areas completely converted to other land uses, mortality can then be assumed to be due to natural death or isolated cutting. Since these photos were taken at several times in each study area, this approach can provide valuable information about natural mortality rates and recruitment of individuals into the canopy layer. There are several limitations, however. The time period over which mortality and recruitment rates were observed is at most 70 years -afraction of the life span of an adult oak. Perhaps the main limitation is that in some landscapes, particularly dense woodlands, it may be difficult to accurately determine tree density and species. For example, where valley oak, blue oak, and coast live oak cooccur, the first two deciduous species are easy to distinguish from the latter evergreen species, but may be difficult to distinguish from one another in the aerial photographs. In such cases, and where tree canopies overlap, analyses focus on changes in total tree cover (e.g., Schleidlinger and Zedler 1980; Callaway and Davis 1993; Davis et al. 1995). Without information about changes in density (which would incorporate mortality and recruitment of individuals) of each tree species, conclusions about population dynamics of dense oak stands are limited. This approach may be best suited for use in savanna habitats where the fates of individual trees can be clearly observed (e.g., Brown 1991).

Historical and current ground surveys

The first large-scale mapping of vegetation in California was the Vegetation Type Mapping (VTM) survey directed by A. E. Wieslander from 1919-1945 (Weislander 1935). A tree species was only recorded if: 1) total tree canopy cover in an assessment area was greater than 20%, and 2) that species comprised greater than 20% of the relative tree cover. Thus, the estimate of tree abundance and cover from VTM surveys can be considered conservative since rare individuals or small clusters of trees were generally not recorded. The locations of the original VTM plots were marked on topographic maps (30-minute scale). Comparisons of present day ground surveys in which VTM plots are re-located and sampled, to the original VTM dataset, provide data on changes in oak woodland cover and tree density in the past 50-60 years (e.g., Holzman 1993). Since the uncertainty about the locations of original plots is on the order of 10's to 100's of meters, the comparisons can indicate only approximate levels of change in these systems (Keeley 2004). However, there are no other techniques that provide comparable data on tree density, and thus recruitment and mortality rates, particularly for oak woodlands.

Two other limitations to this approach are 1) it is possible to observe changes only over the past 50-70 years, and 2) due to the sampling criterion of the original surveys (i.e., trees occurring in low densities were not mapped) this method is not well suited for examining change in oak savanna populations, except for stands that formerly had a tree cover of at least 20%.

CURRENT FINDINGS

Blue oak

Eleven of the published studies we reviewed contained information about regeneration status in blue oak woodlands (Table 2). Six were field surveys that included information about the current size structure of the populations. Seedlings ranged from absent to few in three studies (White 1966; Muick and Bartolome 1987a; Bolsinger 1988), and abundant in two studies (Franco 1976; Standiford et al. 1991). The relative abundance of saplings varied among studies, but all reported that saplings were present in most stands. Three field surveys included numerous sites throughout the species' distribution; these found that saplings were relatively rare but present in most plots (Muick and Bartolome 1987a; Bolsinger 1988; Swiecki et al. 1993). Other studies reported that saplings were abundant in most plots in central coastal California (White 1966; Franco 1976), and in the Sierra Nevada (Standiford et al. 1991). Several of the field surveys that collected data at more than one site, examined the relationship between sapling density and environmental factors (Muick and Bartolome 1987a; Swiecki et al. 1991). All found that saplings were more common on mesic sites.

The results of the four studies that examined historical recruitment patterns in blue oak varied. McClaran (1986) and Mensing (1988) found that no trees had established since 1930 and 1864, respectively. White (1966) reported that little recruitment had occurred since 1910. However, Harvey (1989) found that establishment varied among 4 sites in the past 50 years: one had abundant recruits, one had moderate recruitment, and two had little to none.

The two studies that covered a wide area of the range of blue oak, and included some loss or mortality information in their analyses (Holzman 1993; Swiecki et al. 1993) found that while some locations had net losses, i.e., recruitment not balancing mortality, others had increases in tree density or cover, and that most locations had no net change. Davis et al.

(1995) compared historical to current aerial photographs and found that changes in cover varied among sites and regions, but that decreases in tree cover at some sites were offset by increases in tree cover at others. While large changes were noted in individual sites, the mean cover over the entire study region remained virtually unchanged from 1940 to 1988.

In summary, blue oak seedlings and saplings are present but relatively rare in many stands, and absent from some. Some stands have no evidence of tree recruitment within the past 50 years. However, mortality rates of adults are also low: estimated to be 2-4% per decade (Swiecki et al. 1993). The only studies that have examined change over time indicate that most locations show no net change in tree cover or density.

Valley oak

Nearly all of the field studies that inventoried valley oak seedlings and/or saplings (Table 2) found them to be uncommon to absent in most sites, and, in multi-species surveys, at the lowest densities of all oak species observed (White 1966; Griffin 1976; Franco 1976; Thomas 1987; Muick and Bartolome 1987a; Bolsinger 1988). Knudsen (1984) was one exception, finding that seedlings and saplings were common at some sites in the Sacramento Valley within a riparian gallery forest. In addition, Griffin (1976) observed high densities of seedlings in some years in areas excluding cattle and deer.

Although there are few studies on natural recruitment in valley oak, several patterns emerge that merit further investigation. First, the studies that report finding some seedlings (Knudsen 1984; Muick and Bartolome 1987a; Thomas 1987) were conducted within a year or two of previously high rainfall years, suggesting that presence or absence of seedlings may depend on the climatic conditions preceding the survey. This is supported by Griffin (1976), who found that presence of seedlings varied considerably among years, from over 316 recruits in 1970 to only 11 recruits in 1973 – all under the same valley oak adult. Second, rates of sapling recruitment may vary geographically: one study that reported finding no saplings (Brown 1991) was done at one of the driest sites, at the southern extent of the species' range, while the studies that report at least some sapling recruitment (White 1966; Franco 1976; Knudsen 1984) were conducted in wetter, more northern regions. Interestingly, the latter two surveys were also done in preserves with no cattle grazing.

The one study that measured population dynamics found high tree mortality and no tree recruitment between 1938 and 1989 (Brown 1991). Anthropogenic causes such as thinning, may contribute to high mortality of valley oak adults in some areas since they occur on land that is usually used for agriculture (Rossi 1979). Given the generally rare occurrence of seedlings and saplings, current data suggest that in extant savanna stands, valley oak regeneration may not be sufficient to maintain populations at their current levels. However, this conclusion is based on few studies, and thus needs to be tested with additional quantitative studies of natural recruitment and mortality.

Coast live oak

Several field studies (Snow 1972; Griffin 1976; Franco 1976; Muick and Bartolome 1987a) noted that coast live oak seedlings were abundant where adult trees were present, and saplings were uncommon but present in nearly all locations. A state-wide foresters' survey (Bolsinger 1988) found that seedlings and saplings were present but rare compared to other evergreen oak species.

Comparing historical to current aerial photographs, Scheidlinger and Zedler (1980) found that stands dominated by coast live oak varied in the amount of change from 1928 to 1970. They observed an overall decline of 13% cover, but noted that some or all of this loss may have been due to a temporary reduction in crown cover due to a fire just prior to 1970. In central coast California, Callaway and Davis (1998) compared historical aerial photographs from 1947 to those taken in 1989, and recorded oak canopies that were present in the latter photographs only. They found that recruitment was relatively high in coastal sage scrub habitats and very low in grasslands. Field surveys conducted in oak woodlands at the site revealed that coast live oak seedlings and saplings were common where understories were dominated by shrubs, but uncommon in woodlands with herbaceous understories. Only one large-scale ground survey provided more precise information about change in coast live oak stands over time (Holzman 1993), and this study found that tree cover and density had increased since the 1930's.

In summary, coast live oak seedlings have been noted to be abundant in some, but not all locations, saplings are present in many sites, and adult coast live oaks have increased in some stands (Table 2). There are currently no studies that provide quantitative data on mortality rates. Such information would be especially useful to better understand the potential impacts of the large-scale loss of coast live oak stands due to Sudden Oak Death syndrome (Garbelotto et al. 2001; Rizzo et al. 2002; McPherson et al. 2002).

SUMMARY: IS THERE A REGENERATION PROBLEM?

Most studies of California's oaks that report a regeneration problem base that conclusion on the rarity of seedlings and/or saplings (Table 2). As several researchers (Lang 1988; Bolsinger 1988; Swiecki et al. 1993) have noted previously, lack of seedlings or saplings suggests but does not confirm a regeneration problem. Recruitment of seedlings, in particular, can vary considerably among years, depending on acorn crop, rainfall, and other factors. While sapling densities are low in many stands, both sapling and adult survival rates are high. Similar demographic patterns have been reported for long-lived trees in the tropics (Lieberman and Lieberman 1987; Condit et al. 1995).

At present, there are not sufficient quantitative data, particularly on mortality rates, to support the prevalent belief that oaks in California are suffering from a "regeneration problem." The degree to which oak populations are changing appears to vary among species and to vary regionally. Valley oak populations in Central California are declining (Brown 1991). Blue oak populations appear to be regenerating adequately in many locations (Holzman 1993; Swiecki et al. 1993; Davis et al. 1995), particularly in mesic

sites that are not grazed intensively by livestock. Coast live oak may be increasing in some regions (Holzman 1993).

Though we currently lack sufficient evidence of widespread decline in extant stands, those responsible for conservation or management of oaks in California's foothill woodlands may well be justified in maintaining preservation and planting efforts for several reasons. First, even with intervention, seedling and sapling establishment and growth rates are low. If it is demonstrated that mortality in a given stand is exceeding natural recruitment, it will take at least 50 – 100 years to replace functionally the individuals lost. As suggested by Kwit et al. (2004), conservation actions for slow-growing, long-lived species are best pursued before populations decline to a level from which recovery is not possible. Second, evidence suggests that recruitment limitations may be more severe now than in centuries past, in part due to anthropogenic influences (e.g., livestock grazing, stand thinning). Restoration efforts may prove to be challenging and require many years to accomplish. Third, although the major threat to oak woodland habitats is stand loss, through conversion to residential development and agriculture, there are other significant human disturbances within extant stands that increase adult mortality, notably cutting of oaks for firewood or to facilitate agricultural operations.

CONCLUSIONS AND RECOMMENDATIONS

Extensive research has clearly demonstrated what treatments or interventions are necessary to ensure high rates of initial oak seedling establishment. Far less is known about factors limiting establishment of saplings. As discussed by a number of authors, and summarized by McClaran (1986), successful oak recruitment requires a combination of events including abundant acorn production, sufficient rainfall, limited competition for light and water from neighbors, and protection from seed predators, herbivores, and browsers. Any one of these may act as a limiting factor in preventing the recruitment of seedlings and the subsequent transition to sapling and tree. The most significant gaps in our knowledge of seedling and sapling establishment are data on survival rates among size/age classes, and how various treatments or locations influence those rates. Longerterm study, including historical aerial photography, ring-based age structure analysis, and monitoring of permanent plots, is required to determine spatial and temporal variation and trends in oak demography, and in particular causes and rates of mortality within the sapling and adult life stages.

Population models are the best means to predicting the long term consequences of current stage-specific recruitment and mortality rates. Complex, multi-species succession models (i.e., "forest gap models") may not be appropriate for foothill oak populations because the tree layer in oak woodlands is usually comprised of only one or two species, the tree crowns do not interact strongly for light, and there is no evidence of long term successional replacement of tree dominants in these systems. Instead, single-species stage-based matrix transition models (Caswell 2001) can provide insight into the sensitivity of oak regeneration dynamics to changes in seedling and sapling recruitment, mortality rates, or adult fecundity. With such models oak population dynamics can be projected under different ecological assumptions or management and restoration

strategies. Although these models have limitations, they have been used extensively to model extinction risk for rare plants (Menges 2000, Kwit et al. 2004) and in recent years have been refined to account for variations due to factors such as episodic recruitment, correlation in the variation of stage-specific recruitment rates, and temporal autocorrelation in demographic rates (Fieberg and Ellner 2001, Franco and Silvertown 2004). Spatially explicit "landscape models" that account for individual locations, seed dispersal, site heterogeneity and species interactions can provide additional insights although they are more difficult to parameterize and interpret (e.g., Zavala and Zea 2004). Multiple modeling approaches would be welcomed, and the absence of population models for these species is surprising.

A comprehensive understanding of oak demography will ultimately require the integration of observational, experimental and modeling components. Here we have recommended general research foci and approaches that we believe will enable the construction of oak population models. These will be necessary to adequately characterize, monitor, and manage California's oak woodlands and savannas for long-term persistence and health, and may contribute to a better understanding of the patterns of regeneration in oak woodlands around the globe.

ACKNOWLEDGEMENTS

We gratefully acknowledge support from the David and Lucille Packard Foundation, and the Santa Barbara County Energy Division during the writing of this review. We received helpful comments and encouragement from M. Borchert, A. Carlson, B. Mahall, D. Odion, and E. Zavaleta. We are especially thankful for the detailed critiques provided by D. Botkin, J. Connell, C. D'Antonio and two anonymous reviewers.

REFERENCES

- Abrams M D, Copenheaver C A, Terazawa K, Umeki K, Takiya M, Akashi N. 1999. A 370-year dendroecological history of an old-growth Abies-Acer-Quercus forest in Hokkaido, northern Japan. *Canadian Journal of Forest Research* 29:1891-1899.
- Adams T E, McDougald N K. 1995. Planted blue oaks may need help to survive in Southern Sierras. *California Agriculture* 49:13-17.
- Adams T E, Weitkamp W H. 1992. Gophers love oaks to death. *California Agriculture* 46:27-29.
- Adams T E, Sands P B, McHenry W B. 1997b. Weed control improves survival of transplanted blue oak. *California Agriculture* 51:26-30.
- Adams T E, Sands P B, Weitkamp W H. 1988. Artificial regeneration of blue and valley oak in California. UC Dept of Agronomy and Range Science, Agricultural Exp Station, Range Science Report: 9 pp.
- Adams T E, Sands P B, Weitkamp W H, Stanley M E. 1997c. Oak seedling establishment by artificial regeneration on California rangelands. Pages 213-222 in *Proceedings of a* symposium on oak woodlands: ecology, management, and urban interface issues, technical coordinators N H Pillsbury, J Verner and W D Tietje. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-160.
- Adams T E, Sands P B, Weitkamp W H, McDougald N K, Bartolome J. 1987. Enemies of white oak regeneration in California. Pages 459-462 in *Proceedings of the symposium on multiple-use management of California's hardwood resources*, technical coordinators T R Plumb and N H Pillsbury. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. General Technical Report PSW-100.
- Allen-Diaz B, Bartolome J W. 1992. Survival of *Quercus douglasii* (Fagaceae) seedlings under the influence of fire and grazing. *Madrono* 39:47-53.
- Bartolome, J W. 1991. Effects of fire and browsing on regeneration, growth, and survival of blue oak. A report to the California Dept. of Forestry and Fire Protection, Sacramento, CA: 5 pp.
- Bartolome J W, McClaran M P. 1988. Effect of fire and grazing on blue oak regeneration. A report to the California Department of Forestry and Fire Protection, Sacramento, CA: 17 pp.

- Bartolome J W, McClaran, M P, Allen-Diaz B H, Dunne J, Ford L D, Standiford R B, McDougald N K, Forero L C. 2002. Effects of fire and browsing on regeneration of blue oak. Pages 281-286 in *Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape*, technical coordinators R B Standiford, D McCreary and K L Purcell. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-184.
- Bartolome J W, Muick P C, McClaran M P. 1987. Natural regeneration of Californian hardwoods. Pages 26-31 in *Proceedings of the symposium on multiple-use management of California's hardwood resources*, technical coordinators T R Plumb and N H Pillsbury. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. General Technical Report PSW-100.
- Bernhardt E A, Swiecki T J. 1997. Effects of cultural inputs on survival and growth of direct seeded and naturally occurring valley oak seedlings on hardwood rangeland.
 Pages 310-311 in *Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues*, technical coordinators N H Pillsbury, J Verner and W D Tietje. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-160.
- Bezkorowanjnyj P G, Gordon A M, McBride R A. 1993. The effect of cattle foot traffic on soil compaction in a silvo-pastoral system. *Agroforestry Systems* 21:1-10.
- Bolsinger C L. 1988. The hardwoods of California's timberlands, woodlands, and savannas, USDA Forest Service, Pacific Northwest Research Station. Resource Bulletin PNW-RB-148. 148 pp.
- Borchert M I, Davis F W, Michaelsen J, Oyler L D. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. *Ecology* 70:389-404.
- Braunack M V, Walker J. 1985. Recovery of some surface soil properties of ecological interest after sheep grazing in a semi-arid woodland. *Australian Journal of Ecology* 10:451-460.
- Brown R W. 1991. Historical mortality of Valley Oak (*Quercus lobata*, Nee) in the Santa Ynez Valley, Santa Barbara County, California :1938-1989. M.A. thesis: 49 pp. University of California, Santa Barbara, CA.
- Busing R T, Spies T A. 1995. Modeling the population dynamics of Pacific yew. USDA Forest Service Pacific Northwest Research Station. Research note PNW-RN-515.
- Callaway R M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73:2118-2128.

- Callaway R M, D'Antonio C M. 1991. Shrub facilitation of coast live oak establishment in central California. *Madroño* 38:158-169.
- Callaway R M, Davis F W. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. *Ecology* 74:1567-1578.
- Callaway R M, Davis F W. 1998. Recruitment of *Quercus agrifolia* in central California: the importance of shrub-dominated patches. *Journal of Vegetation Science* 9:647-656.
- Carmen W J. 1988. Behavioral ecology of the California scrub jay (*Aphelocoma coerulescens* Californica): a non-cooperative breeder with close cooperative relatives.Ph.D. dissertation: 334 pp. University of California, Berkeley, CA.
- Caswell H. 2001. Matrix population models: construction, analysis and interpretation. Second edition. Sinauer, Sunderland, Massachusetts.
- Condit R S, Hubbell S P, Foster R B. 1995. Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65:419-439.
- Danielsen K C. 1990. Seedling growth rates of *Quercus lobata* Nee. (Valley oak) and the competitive effects of selected grass species. M.A. thesis: 74 pp. California State University, Los Angeles, CA.
- Davis F W, Borchert M I, Harvey L E, Michaelsen J. 1991. Factors affecting seedling survivorship of blue oak (*Quercus douglassii* H.&A.) in central California. Pages 81-86 in *Proceedings of the symposium on oak woodlands and hardwood rangeland management*, technical coordinator R B Standiford. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-126.
- Davis F W, Brown R, W, Buyan B, Kealy J. 1995. Vegetation change in blue oak and blue oak/foothill pine woodland. A report to the California Department of Forestry and Fire Protection, Sacramento, CA: 34 pp.
- Davis, F W, Stoms D M, Hollander A D, Thomas K A, Stine P A, Odion D, Borchert M I, Thorne J H, Gray M V, Walker R E, Warner K, Graae J. 1998. The California Gap Analysis Project --Final Report. Santa Barbara, University of California.
- Dunning C E, Paine T D, Redak R A. 2002. Insect-oak interactions with coast live oak (*Quercus agrifolia*) and Engelmann oak (*Q. engelmannii*) at the acorn and seedling stage. Pages 205-218 in *Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape*, technical coordinators R B Standiford, D McCreary and K L Purcell. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-184.

- Ferrero A F. 1991. Effect of compaction simulating cattle trampling on soil physical characteristics in woodland. *Soil and Tillage Research* 19:319-329.
- Fieberg J, Ellner S P. 2001. Stochastic matrix models for conservation and management: a comparative review of methods. *Ecology Letters* 4:244-266.
- Franco G M M. 1976. Grazing effects on oak distribution in Jasper Ridge and adjacent areas. M.A. thesis: 33 pp. Stanford University, Palo Alto, CA.

Franco M, Silvertown J. 2004. A comparative demography of plants based on elasticities of vital rates. *Ecology* 85:531-538.

- Garbelotto M, Svhira P, Rizzo D M. 2001. Sudden oak death syndrome fells three oak species. *California Agriculture* 55:9-19.
- Gordon D R, Rice K J. 2000. Competitive suppression of *Quercus douglasii* (Fagaceae) seedling emergence and growth. *American Journal of Botany* 87:986-994.
- Gordon D R, Rice K J. 1993. Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology* 74:68-82.
- Gordon D R, Welker J M, Menke J W, Rice K J. 1989. Competition of soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. *Oecologia* (Berlin) 79:533-541.
- Greenwood G B, Marose R K, Stenbeck J M. 1993. Extent and ownership of California's hardwood rangelands. A report to the California Dept of Forestry and Fire Protection, Sacramento, CA: 119 pp.
- Griffin J R. 1971. Oak regeneration in the upper Carmel Valley, California. *Ecology* 52:862-868.
- Griffin J R. 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. *American Midland Naturalist* 95:422-435.
- Griffin J R. 1980. Animal damage to valley oak acorns and seedlings, Carmel Valley, California. Pages 242-245 in *Proceedings of the symposium on the ecology, management, and utilization of California oaks*, technical coordinator T R Plumb. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. General Technical Report PSW-44.
- Hall L M, George M R, McCreary D D, Adams T E. 1992. Effects of cattle grazing on blue oak seedling damage and survival. *Journal of Range Management* 45:503-506.

- Hamilton J G. 1997. Environmental and biotic factors affecting the occurrence of the native bunchgrass *Nassella pulchra* in California. Ph.D. dissertation: 145 pp. University of California, Santa Barbara, CA.
- Hamilton J G, Holzapfel C, Mahall B E. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* 121:518-526.
- Harper J L. 1977. Population biology of plants. Academic Press, New York, New York.
- Harvey L E. 1989. Spatial and temporal dynamics of a blue oak woodland. Ph.D. dissertation: 170 pp. University of California, Santa Barbara, CA.
- Hibberd M. 1985. A comparison of water stress and site conditions for *Quercus agrifolia* in relation to controls on distribution. M.A. thesis: 71 pp. San Diego State University, San Diego, CA.
- Hickman J C, editor. 1993. *The Jepson Manual: higher plants of California*. Berkeley and Los Angeles, CA, University of California Press.
- Holmes, T H and Rice, K J. 1996. Patterns of growth and soil-water utilization in some exotic annuals and natire perennial bunchgrasses of California. *Annals of Botany* 78:233-246.
- Holzman B A. 1993. Vegetation change in California's blue oak (*Quercus douglasii*) woodlands 1932-1992. Ph.D. dissertation: 120 pp. University of California, Berkeley, CA.
- Jansen H C, Snow R R, Treber G A, Bell F L. 1997. Effects of livestock grazing on blue oak saplings. Pages 313-320 in *Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues*, technical coordinators N H Pillsbury, J Verner and W D Tietje. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-160.

Jepson W L. 1910. The silva of California. University of California Memoirs 2:1-480.

- Johnson P S, Shifley S R, Rogers R. 2002. *The ecology and silviculture of oaks*. CABI Publishing, New York, New York.
- Keator G. 1998. The life of an oak. Heyday Books. Berkeley, CA.
- Keeley J E. 2004. VTM plots as evidence of historical change: goldmine or landmine? *Madroño* 51:372-378.

- Knapp E E, Goedde M A, Rice K J. 2001. Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. *Oecologia* 128:48-55.
- Knudsen M D. 1984. Life history aspects of *Quercus lobata* Nee in a riparian community, Bobelaine Audubon Sanctuary, Sutter County, California. M.S. thesis: 135 pp. Sacramento State University, Sacramento, CA.
- Koenig W D, McCullough D R, Vaughn C E, Knops J M H, Carmen W J. 1999. Synchrony and asynchrony of acorn production at two sites in coastal California sites. *Madroño* 46:20-24.
- Koenig W D, Knops J M H, Carmen W J. 2002. Arboreal seed removal and insect damage in three California oaks. Pages 193-204 in *Proceedings of the fifth* symposium on oak woodlands: oaks in California's changing landscape, technical coordinators R B Standiford, D McCreary and K L Purcell. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-184.
- Koenig W D, Mumme R L, Carmen W J, Stanback M T. 1994. Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 75:99-109.
- Kwit C, Horvitz C C, Platt W J. 2004. Conserving slow-growing, long-lived tree species: input from the demography of a rare understory conifer, *Taxus floridana*. *Conservation Biology* 18: 432-443.
- Lang F J. 1988. Oak regeneration assessment a problem analysis. A report to the California Dept. of Forestry and Fire Protection, Forest and Rangeland Resources Assessment Program (FRRAP), Sacramento, CA: 78 pp.
- Lathrop E W, Osborne CD. 1991. Influence of fire on oak seedlings and saplings in southern oak woodland on the Santa Rosa Plateau Preserve, Riverside County, California. Pages 366-370 in *Proceedings of the symposium on oak woodlands and hardwood rangeland management*, technical coordinator R B Standiford. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-126.
- Laycock W A, Conrad P W. 1967. Effect of grazing on soil compaction as measured by bulk density on a high elevation cattle range. *Journal of Range Management* 20:136-140.
- Lieberman D, Lieberman M. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). *Journal of Tropical Ecology* 3:347-358.
- Loftis D L, McGee C E, editors. 1993. Oak regeneration: serious problems, practical recommendations; symposium proceedings, Knoxville, Tennessee, September 1992. USDA Forest Service, Southeastern Forest Experiment Station. General Technical Report SE-84.

- Lull H W. 1959. Soil compaction on forest and range lands. U.S. Forest Service Misc. Publ. 768. 33pp.
- Manos, P S, Doyle J J, Nixon K C. 1999. Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* Subgenus *Quercus* (Fagaceae). *Molecular Phylogenetics and Evolution* 12: 333-349.
- Matsuda K, McBride J R. 1986. Difference in seedling growth in morphology as a factor in the distribution of three oaks in central California. *Madroño* 33:207-216.

Matzner S L, Rice K J, Richards J H. 2003. Patterns of stomatal conductance among blue oak (*Quercus douglasii*) size classes and populations: implications for seedling establishment. *Tree Physiology* 23: 777-784.

- McClaran M. 1986. Age structure of *Quercus douglasii* in relation to livestock grazing and fire. Ph.D. dissertation: 119 pp. University of California, Berkeley, CA.
- McClaran M P, Bartolome J W. 1989. Fire-related recruitment in stagnant *Quercus* douglasii populations. Canadian Journal of Forest Research 19:580-585.
- McCreary D D, Tecklin J. 1994. Grasshoppers continue to hamper oak restoration efforts. Oaks 'n Folks Newsletter: 9:4-5. Integrated Hardwoods Range Management Program, University of California.
- McCreary D D, Tecklin J. 1997. Effects of seedling protectors and weed control on blue oak growth and survival. Pages 243-250 in *Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues*, technical coordinators N H Pillsbury, J Verner and W D Tietje. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-160.
- McPherson B A, Wood D L, Storer A J, Kelly N M, Standiford R B. 2002. Sudden oak death: disease trends in Marin County plots after one year. Pages 751-764 in *Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape*, technical coordinators R B Standiford, D McCreary and K L Purcell. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-184.
- McShea W J, Healy W M, eds. 2002. Oak forest ecosystems : ecology and management for wildlife. Johns Hopkins University Press, Baltimore, MD
- Melville, R. 1982. The biogeography of Nothofagus and Trigonobalanus and the origin of the Fagaceae. *Botanical Journal of the Linnean Society of London*. 85: 75-88.
- Menges E S. 2000. Population viability analyses in plants: challenges and opportunities. *Trends in Ecology and Evolution* 15:51-56.

- Mensing S A. 1988. Blue Oak (*Quercus douglasii*) regeneration in the Tehachapi mountains, Kern County, California. M.A. thesis: 71 pp. University of California, Berkeley, CA.
- Mensing S A. 1993. The impact of European settlement on oak woodlands and fire: pollen and charcoal evidence from the transverse ranges, California. Ph.D. dissertation: 216 pp. University of California, Berkeley, CA.
- Muick P C. 1995. Effects of shade and simulated herbivory on seedling emergence, survival and growth of two California oaks: coast live oak (*Quercus agrifolia* Nee.) and blue oak (*Quercus douglasii* Hook. and Arn.). Ph.D. dissertation: 104 pp. University of California, Berkeley, CA.
- Muick P C, Bartolome J W. 1987a. An assessment of natural regeneration of oaks in California. A report to the California Dept. of Forestry and Fire Protection, Sacramento, CA: 79 pp.
- Muick P C, Bartolome J W. 1987b. Factors associated with oak regeneration in California. Pages 86-91 in *Proceedings of the symposium on multiple-use management of California's hardwood resources*, technical coordinators T R Plumb and N H Pillsbury. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. General Technical Report PSW-100.
- Parikh A, Gale N. 1998. Coast live oak revegetation on the central coast of California. *Madroño* 45:301-309.
- Pavlick B M, Muick P C, Johnson S G, Popper M. 1991. *Oaks of California*. Cachuma Press. Los Olivos, California.
- Plumb T R, Hannah B. 1991. Artificial regeneration of blue oak and coast live oaks in the central coast. Pages 74-80 in *Proceedings of the symposium on oak woodlands and hardwood rangeland management*, technical coordinator R B Standiford. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-126.
- Plumb T R, De Lasaux M C. 1997. An evaluation of coast live oak regeneration techniques. Pages 231-242 in *Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues*, technical coordinators N H Pillsbury, J Verner and W D Tietje. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-160.
- Ratliff R D, Westfall S E. 1971. Non-grazing and gophers lower bulk density and acidity in annual-plant soil. United States Forest Service Pacific Southwest Forest and Range Experimental Station. Research Note PSW-254.

- Rizzo D M, Garbelotto M, Davidson J M, Slaughter G, Koike S T. 2002. *Phytophthora ramorum* as the cause of extensive mortality in *Quercus* spp. and *Lithocarpus densiflorus* in California. *Plant Disease* 86:205-214.
- Rossi R S. 1979. Land use and vegetation change in the oak woodland-savanna of northern San Luis Obispo County, California, (1774-1978). Ph.D. dissertation: 337 pp. University of California, Berkeley, CA.
- Russell F L, Fowler N L. 1999. Rarity of oak saplings in savannas and woodlands of the Eastern Edwards Plateau, Texas. *The Southwestern Naturalist* 44:31-31.
- Saxena A K, Singh J S. 1984. Tree population structure of certain Himalayan forest associations and implications concerning their future composition. *Vegetatio* 58:61-69.
- Scheidlinger C R, Zedler P H. 1980. Change in vegetative cover of oak stands in southern San Diego County: 1928-1970. Pages 81-85 in *Proceedings of the symposium on the ecology, management, and utilization of California oaks*, technical coordinator T R Plumb. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. General Technical Report PSW-44.
- Shaw M W. 1968a. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales: I. A preliminary study of acorn production, viability and losses. *Journal of Ecology* 56:565-583.
- Shaw M W. 1968b. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales: II. Acorn losses and germination under field conditions. *Journal of Ecology* 56:647-660.
- Singh S P, Rawat Y S, Garkoti S C. 1997. Failure of brown oak (*Quercus semecarpifolia*) to regenerate in central Himalaya: a case of environmental semisurprise. *Current Science* 73:371-374.
- Snow G E. 1972. Some factors controlling the establishment and distribution of *Quercus agrifolia* Nee and *Q. engelmannii* Greene in certain southern California oak woodlands. Ph.D. dissertation: 105 pp. Oregon State University, Corvallis, Oregon.
- Sork V L, Bramble J. 1993. Ecology of mast-fruiting in three species of north American deciduous oaks. *Ecology* 74:528-541.
- Sork V L, Davis F, Smouse P E, Apsit V J, Dyer R J, Fernandez J, Kuhn B. 2002. Pollen movement in declining populations of California valley oak, *Quercus lobata*: Where have all the fathers gone? *Molecular Ecology* 11:1657-1668.
- Standiford R B, McDougald N, Phillips R, Nelson A. 1991. South Sierra oak regeneration weak in sapling stage. *California Agriculture* 45:12-14.

- Standiford R B, McDougald N, Frost W, Phillips R. 1997. Factors influencing the probability of oak regeneration on southern Sierra Nevada woodlands in California. *Madroño* 44:170-183.
- Stephenson G R, Veigle A. 1987. Recovery of compacted soil on pastures used for winter cattle feeding. *Journal of Range Management* 40:46-48.

Sudworth G B. 1908. Forest trees of the Pacific slope, USDA Forest Service, 441 pp.

- Swiecki T J, Bernhardt E. 2002. Effects of fire on naturally occurring blue oak (Quercus douglasii) saplings. Pages 251-259 in Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape, technical coordinators R B Standiford, D McCreary and K L Purcell. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-184.
- Swiecki T J, Bernhardt E A. 1991. Minimum input techniques for restoring valley oaks on hardwood rangeland. A report to the California Dept. of Forestry and Fire Protection, Sacramento, CA: 79 pp.
- Swiecki T J, Bernhardt E A, Drake, C. 1993. Factors affecting blue oak sapling recruitment and regeneration. A report to the California Dept. of Forestry and Fire Protection, Sacramento, CA: 131 pp.
- Swiecki T J, Bernhardt E A, Drake C. 1997a. Factors affecting blue oak sapling recruitment. Pages 157-161 in *Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues*, technical coordinators N H Pillsbury, J Verner and W D Tietje. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-160.
- Swiecki T J, Bernhardt E A, Drake C. 1997b. Stand-level status of blue oak sapling recruitment and regeneration. Pages 147-156 in *Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues*, technical coordinators N H Pillsbury, J Verner and W D Tietje. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-160.
- Swiecki T J, Bernhardt E A, Arnold R A. 1990. Impacts of diseases and arthropods on California's rangeland oaks. A report to the California Dept. of Forestry and Fire Protection, Sacramento, CA: 94 pp.
- Thomas T W. 1987. Population structure of the valley oak in the Santa Monica Mountains National Recreation Area. Pages 335-340 in *Proceedings of the* symposium on multiple-use management of California's hardwood resources, technical coordinators T R Plumb and N H Pillsbury. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. General Technical Report PSW-100.

- Tietje W D, Nives S L, Honig J A, Weitkamp W H. 1991. Effect of acorn planting depth on depredation, emergence, and survival of valley and blue oak. Pages 14-20 in *Proceedings of the symposium on oak woodlands and hardwood rangeland management*, technical coordinator R B Standiford. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-126.
- Trimble S W, Mendel A C. 1995. The cow as a geomorphic agent a critical review. *Geomorphology* 13:233-253.
- Tyler C M, Mahall B E, Davis F W, Hall M. 2002. Factors limiting recruitment in valley and coast live oak. In Pages 565-572 in Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape, technical coordinators R B Standiford, D McCreary and K L Purcell. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-184.
- Van Haveren B P. 1983. Soil bulk density as influenced by grazing intensity and soil type on a shortgrass praire site. *Journal of Range Management* 36:586-588.
- Watt A S. 1919. On the cause of failure of natural regeneration in British oak woods. *Journal of Ecology* 17:175-203.
- Weislander A E. 1935. A vegetation type map of California. *Madroño* 3:140-144.
- Welker J M, Menke J M. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought. *Functional Ecology* 4:807-818.
- Welker J M, Gordon D R, Rice K J. 1991. Capture and allocation of nitrogen by *Quercus douglasii* seedlings in competition with annual and perennial grasses. *Oecologia* 87:459-466.
- White K L. 1966. Structure and composition of foothill woodland in central coastal California. *Ecology* 47:229-237.
- Zavala M A, Zea E. 2004. Mechanisms maintaining biodiversity in Mediterranean pinoak forests: insights from a spatial simulation model. *Plant Ecology* 171:197-207.

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TABLE 1. Classification of oak demography and regeneration studies in California. Data are numbers of published studies in each category.	<mark>O. chrysolepis</mark> 7		<u>Fire</u> 10	<mark>61-72</mark> 2	 * Acorn - fate of acorns including germination rates, depredation rates, or damage from other biological factors; Emerg - processes or agents that affect survival from acorn to seedling or initial emergence/recruitment of seedlings; Seed - factors that influence the survival and growth of existing seedlings and saplings; Adult - fate of adults including sources of mortality, and factors that affect growth and survival; Demog - quantified population or stand demographics; Graz - effects of grazing on population structure or life stage survival rates; Fire - effects of fire on population structure through changes in survival rates of life stages;
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Classificatic	Species studied <u>O. douglasii</u> 75	Life stage studied <u>Acorn</u> <u>S</u> 46	Study type* <u>Acorn</u> 16	Study length (months) <u>0</u> <u>1-1</u> 26 <u>30</u>	* Acorn - fatt Emerg - proc Seed - factors Adult - fate o Demog - quar Fire - effects Change - spa

			study measured?	ed?		
Source	species	<u>study approach</u> recruitment <u>mortality</u> findings	<u>ecruitment mor</u>	<u>tality</u>	findings	
McClaran 1986	BO	age-struct	yes r	ou	lack of tree recruitment since ~1930	
Mensing 1988	BO	age-struct		no	lack of tree recruitment since ~1860	
Harvey 1989	BO	age-struct		no	tree recruit. in past 50 yrs varied among sites from none to abundant	
White 1966	BO	size-, age-struct		no	few seedlings;saplings common; little tree recruitment since 1910	
Franco 1976	BO	size-struct		no	seedlings and saplings abundant in ungrazed site	
Muick & Bartolome 1987a	BO	size-struct		no	saplings present in most sites; sapling:tree density > 1:10 for most regions	s
Bolsinger 1988	BO	size-struct		no	seedlings & saplings uncommon to absent in many sites	
Standiford et al. 1991	BO	size-struct		no	many seedlings, saplings rare to abundant	
Swiecki et al. 1993	BO	size-struct	yes y	yes	sapling recruits present in low density at 11/15 sites; adult mortality low	
Davis et al. 1995	BO	air photo	ı	ı	tree cover increased at some sites, decreased at others; stable overall	
Holzman 1993	BO	plot resurvey	yes y	yes	numbers of trees constant or increased at most sites since 1932	
Knudsen 1984	ΛΟ	size-, age-struct	yes	no	seedlings & saplings relatively abundant, esp on mesic sites; ungrazed	
White 1966	ΛO	size-struct		no	no saplings in 2 out of 4 stands; 9 saplings per 306 trees	
Griffin 1976	ΟΛ	size-struct		no	seedlings & saplings rare in all grazed sites	
Griffin 1976	ΛO	size-struct		yes	seedlings common some years in ungrazed sites; high seedling mortality	
Franco 1976	ΟΛ	size-struct		no	seedlings and saplings present but uncommon in ungrazed site	
Thomas 1987	ΟΛ	size-struct		no	seedlings absent from 3, abundant at 1 ungrazed site; saplings uncommon	ч
Muick & Bartolome 1987a	ΟΛ	size-struct		no	saplings absent from most sites; seedlings present in 4 out of 6 plots	
Bolsinger 1988	ΛO	size-struct		no	seedlings & saplings uncommon to absent in most sites	
Brown 1991	ΛO	air photo		yes	number of trees decreased; no visible recruitment	
Snow 1972	CLO	size-, age-struct	yes	ou	younger/smaller classes of trees present but uncommon in most sites	
Griffin 1976	CLO	size-struct		no	seedlings abundant	
Franco 1976	CLO	size-struct		no	seedlings and saplings abundant in ungrazed site	
Muick & Bartolome 1987a	CLO	size-struct		ou		٨
Bolsinger 1988	CLO	size-struct		no		h
Callaway & Davis 1998		size-struct		no	()	and
Schleidlinger & Zedler 1980	-	air photo		ı	tree cover increased at some sites, decreased at others; decline overall	liv /
Callaway & Davis 1998	CL0	air photo		no	decreased in grasslands	٨
Holzman 1993	CLO	plot resurvey	yes y	yes	tree density increased at most sites since 1932	

TABLE 2.

FIGURE LEGENDS

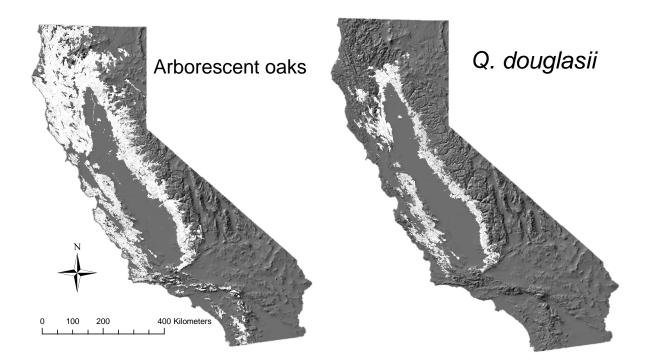
FIGURE 1. MODERN GEOGRAPHICAL DISTRIBUTION OF CANOPY-SIZED OAKS IN CALIFORNIA (AREAS OF OCCURRENCE IN WHITE). DATA FROM DAVIS ET AL 1998. A) ALL NINE ARBORESCENT SPECIES COMBINED; B) *Q. DOUGLASSII*, BLUE OAK; C) *Q. LOBATA*, VALLEY OAK; D) *Q. AGRIFOLIA*, COAST LIVE OAK.

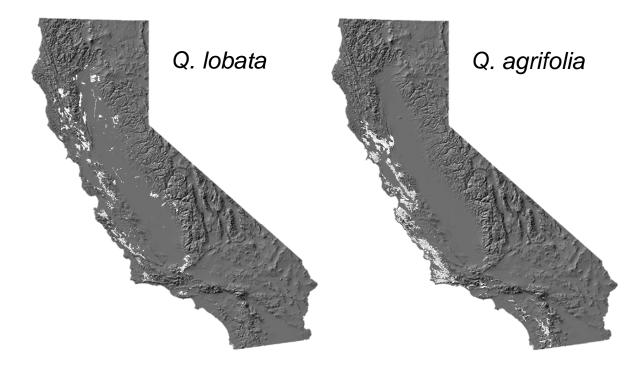
FIGURE 2. BLUE OAK WOODLAND, SEDGWICK RESERVE, SANTA BARBARA COUNTY, CALIFORNIA. SEEN HANGING FROM THE TREE BRANCHES IS THE EPIPHYTIC "LACE LICHEN", *RAMALINA MENZIESII*. PHOTO BY C. TYLER.

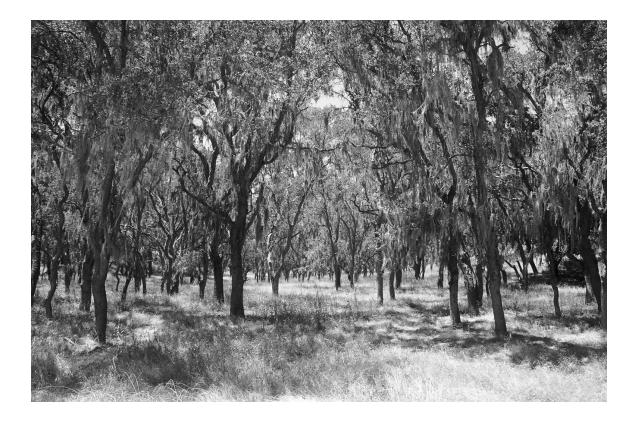
FIGURE 3. FOOTHILL OAK WOODLAND AT SEDGWICK RESERVE, SANTA BARBARA COUNTY, CALIFORNIA, COMPRISED OF EQUAL PROPORTIONS OF *Q. LOBATA* AND *Q. AGRIFOLIA*. IN THE IMMEDIATE BACKGROUND IS COASTAL SAGE SCRUB VEGETATION WITH SCATTERED *PINUS SABINIANA*, *Q. AGRIFOLIA* AND *Q. DOUGLASII*. PHOTO BY F. DAVIS.

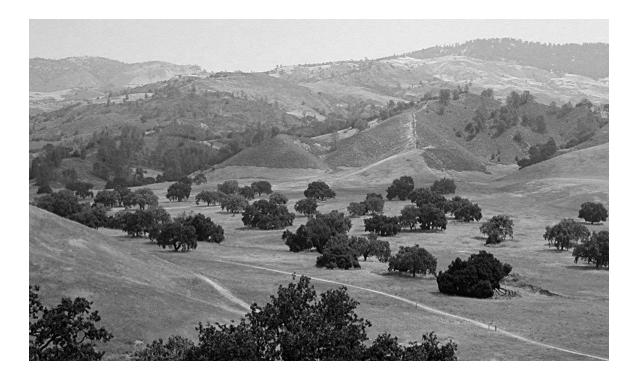
FIGURE 4. CONCEPTUAL MODEL OF THE LIFE HISTORY STAGES OF OAKS.

Appendix A

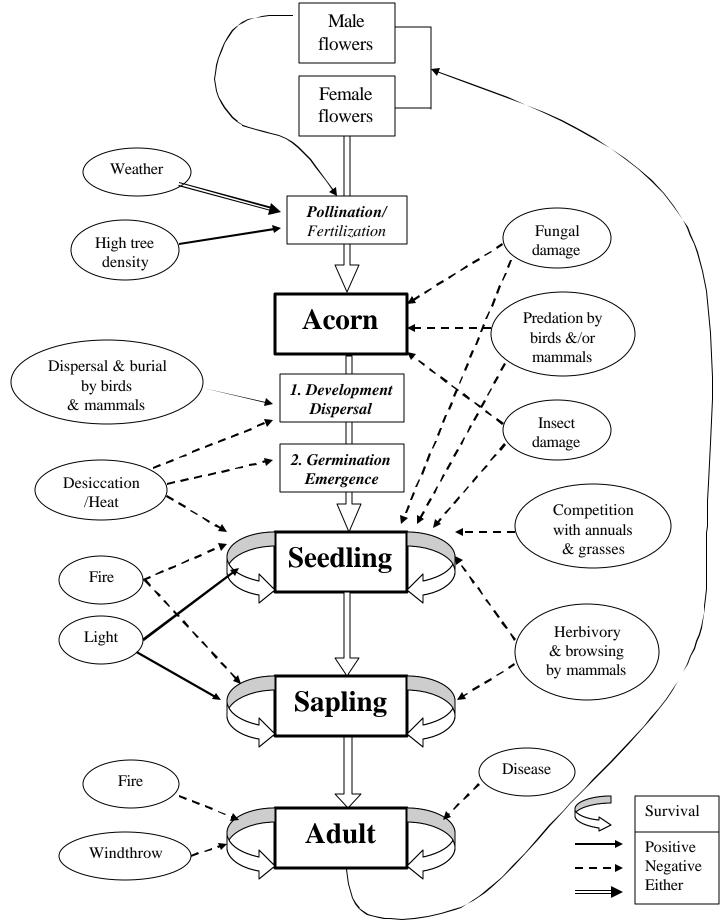








Appendix A



Factors Limiting Recruitment in Valley and Coast Live Oak¹

Claudia M. Tyler,² Bruce E. Mahall,³ Frank W. Davis,⁴ and Michael Hall⁵

Abstract

The Santa Barbara County Oak Restoration Program was initiated in 1994 to determine the major factors limiting recruitment of valley oak (Quercus lobata) and coast live oak (Q. agrifolia). At Sedgwick Reserve in Santa Barbara County, California, we have replicated large-scale planting experiments in four different years to determine the effects of cattle and other ecological factors on oak seedling establishment in oak savannas and woodlands. In 33 large experimental plots (50 x 50 m) we planted acorns collected from O. lobata and O. *agrifolia* on the site. Fifteen of these large plots are controls, open to grazing, fifteen exclude cattle with the use of electric fence, and three are ungrazed in large ungrazed pastures. Within the plots, experimental treatments included: 1) protection from small mammals such as gophers and ground squirrels, 2) protection from large animals such as cattle, deer, and pigs, and 3) no protection from mammalian grazers. In winters 1997, 1998, 2000, and 2001, we planted approximately 1,000 acorns of each species. Results confirm that seed predation and herbivory by small mammals are a significant "bottleneck" to oak seedling recruitment on the landscape scale. Comparing results among years indicates that lack of late winter rainfall can significantly reduce oak emergence and establishment. Survivorship of protected acorns and seedlings is comparable in grazed and ungrazed areas.

Introduction

Oak woodland and savanna habitats, among the most diverse communities in North America, have suffered significant losses in the past century (Bolsinger 1988), primarily due to agricultural conversion and urban development. In addition, natural regeneration of the keystone species (in the genus *Quercus*) of these systems appears to be insufficient to maintain current populations. Many reasons for this lack of recruitment have been proposed including: 1) intense browsing of saplings and seedlings from large mammals (both deer and introduced cattle) (Griffin 1971); 2) acorn predation by cattle, deer, ground squirrels and others (up to 100 percent predation in some cases) (Borchert and others 1989); 3) trampling by cattle (Griffin 1973); 4) underground root attack from fossorial rodents (primarily gophers); 5)

¹ An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.

² Assistant Research Scientist, Institute for Computational Earth System Science, University of California, Santa Barbara, CA 93106 (e-mail: tyler@lifesci.ucsb.edu)

³ Professor, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106.

⁴ Professor, Donald Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106.

⁵ Beef Specialist, Animal Science Department, Cal Poly State University, San Luis Obispo, CA.

competition with exotic annual grasses for water (Danielson and Halvorson 1991); and 6) soil compaction by cattle (Braunack and Walker 1985).

More than 75 percent of oak woodland in California is grazed by cattle, making cattle the most pervasive anthropogenic influence on these ecosystems. Thus, the effects of cattle grazing must be a central theme in a comprehensive investigation of natural regeneration and restoration in today's oak savanna/woodland communities. Although cattle have been implicated as a primary cause of the failure of natural oak recruitment (Griffin 1973), their effects are clearly not straightforward. Even in areas that have not been grazed by cattle for almost 60 years (e.g., the U.C. Hastings Reserve), there is still a lack of significant oak regeneration.

The Santa Barbara County Oak Restoration Program was initiated in 1994 with the goals of determining the major factors limiting recruitment by valley oak (*Quercus lobata*), and coast live oak (*Q. agrifolia*). and identifying cost-effective techniques for large-scale oak restoration in grazed savannas. The primary foci of this program are the effects of cattle, small mammals, and interannual weather variations. Here we present preliminary results from four years of experimental plantings in this long-term oak regeneration program.

Methods

Research was conducted on the Sedgwick Reserve, a 5,883-acre (2,382-ha) ranch located in the Santa Ynez Valley in Santa Barbara County, California. The climate is Mediterranean, with hot dry summers and cool wet winters. Mean annual rainfall is 397 mm. Total precipitation (as recorded at the nearest National Weather Service recording station) for the rain years 1996-1997, 1997-1998, 1998-1999, 1999-2000, and 2000-2001 was 298 mm, 828 mm, 309 mm, 387 mm, and 649 mm, respectively. Under a cooperative grazing agreement with the College of Agriculture at California Polytechnic University, San Luis Obispo, students and faculty from Cal Poly maintained and cared for the cattle herd at Sedgwick, and assisted with the application of grazing treatments in our experiments.

Our large experimental plots were 50 x 50 m. Fifteen of these large plots were controls, open to grazing, and fifteen excluded cattle with the use of electric fence. These plots were established in 1995. They were chosen as pairs, with one randomly selected to be fenced to exclude cattle. In addition, three single 50 x 50 m plots were established in 1996 in three large ungrazed areas.

Within the plots, experimental treatments included: 1) protection from small mammals such as gophers and ground squirrels (*fig. 1a*), 2) protection from large animals such as cattle, deer, and pigs (*fig. 1b*), and 3) no protection from mammalian grazers (*fig. 1c*). Large cages were constructed of 4 ft high, 2 x 4 inches mesh galvanized wire (12 gauge); they were round (diameter = 18 inches) and supported at one side with a 5 ft t-post, and at the other side with a 4 ft rebar. Smaller cages to exclude small mammals were cylinders constructed of 3 ft high hardware cloth (mesh size = 0.5 inches); they were sealed at both ends with aviary wire. In positions with cages (small mammal exclusion), the cages were set 12 inches into the ground. Each of these treatments was replicated five times within each plot for each species.

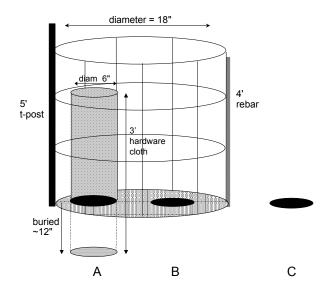


Figure 1—Treatments used for acorn plantings. A: caged and fenced to prevent grazing and herbivory by both large and small mammals (this treatment is referred to as "no rodents"). B: fenced to prevent grazing by large animals. C: open. These treatments are replicated in both 1) plots that are grazed by cattle and 2) plots that are fenced to exclude cattle.

Following the onset of consistent seasonal rains (December or January), at each planting location holes were augured to a depth of 12 inches, soil replaced and two viable acorns planted 1-2 inches below the soil surface. We planted acorns collected from *Quercus lobata* and *Q. agrifolia* on the site in the fall of the same year. Prior to planting, acorns were placed into buckets of water. Acorns that floated were discarded; we planted only acorns that sank and appeared viable. Acorns and seedlings did not receive supplemental watering through artificial irrigation.

In winters of four years, 1996-1997, 1997-1998, 1999-2000, and 2000-2001, we planted approximately 1,000 acorns of each species. In 1996-1997, and 1997-1998, we planted in all 33 plots. In January 1998 (El Niño year), the trees in the middle of two of these plots were blown over. The broken trunks and downed large limbs made future planting in these plots unfeasible. Because the plots are paired, we removed the two sets of plots (total of four) from additional planting experiments, reducing the number of plots in 1999-2000, and 2000-2001 to 29: 13 fenced, 13, unfenced, and 3 in large ungrazed pastures.

Results

2000-2001 Planting

Grouping all treatments, 17 percent of Q. *lobata* seedlings emerged, and 26 percent of Q. *agrifolia*. There were striking differences in emergence rates among experimental treatments (*fig. 2*). The highest seedling emergence was found in locations that were protected from both rodents and large grazers. It appears that there were no differences in initial emergence rates in large grazed versus ungrazed plots, indicating that cattle grazing did not affect emergence of oak seedlings. At

present, grouping all treatments, there are 405 newly emerged seedlings from the 2000-2001 plantings (160 *Q. lobata* and 245 *Q. agrifolia*).

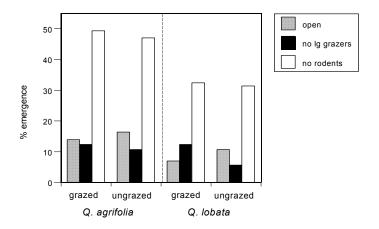


Figure 2—Total percent emergence of seedlings planted in 2000-2001 with various levels of protection from herbivores. Data are from May/June 2001.

1999-2000 Planting

The highest emergence and survivorship has been for seedlings that are protected from small mammals (*fig. 3*). However, mortality of 1-year-old seedlings, especially *Q. agrifolia*, has occurred over the past year. It appears that there was relatively higher mortality for both species in the large ungrazed plots. In terms of actual seedling numbers, there are currently 337 established 1-year-old seedlings (273 *Q. lobata*, and 64 *Q. agrifolia*). Fifty percent of these seedlings are in the treatment protected from rodents.

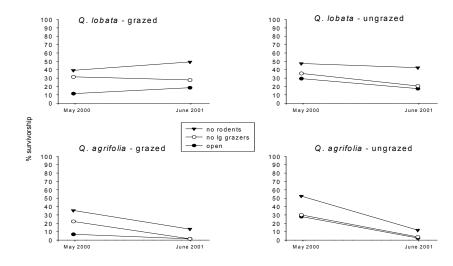


Figure 3—Percent survivorship of 1-yr-old seedlings (planted in 1999-2000) in large plots grazed by cattle, vs. those fenced to exclude cattle. Data are totals for three experimental treatments (*fig. 1*) for two sampling dates

1997-1998 Planting

The highest seedling/sapling establishment rates are for those protected from small mammals (*fig. 4*). In nearly all treatments highest mortality thus far appears to have occurred in the first season after emergence. However, it is interesting to note that there was higher mortality for both species in the plots that have been ungrazed (see "no rodent treatment," *fig. 4*). In terms of actual seedling numbers, there are currently 526 established three-year-old seedlings (300 *Q. lobata*, and 226 *Q. agrifolia*). Sixty-seven percent of these seedlings are in the treatment protected from rodents.

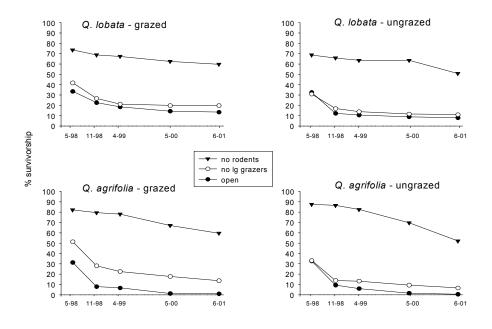


Figure 4—Percent survivorship of 3-yr-old seedlings (planted in 1997-98) in large plots grazed by cattle, vs. those fenced to exclude cattle. Data are totals for three experimental treatments (*fig. 1*) for five sampling dates.

1996-1997 Planting

Out of 2,112 acorns planted in 1996-1997, a total of 13 four-year-old established seedlings have survived, or less than 1 percent of each species planted *(table 1)*. There are presently 4 four-year old *Q. agrifolia* seedlings, and 9 four-year old *Q. lobata*. Our results suggest that the treatment that was most successful in terms of oak establishment was that which excluded small mammals. There are no seedlings surviving from the 1996-1997 planting that were in the open.

			Planting year	r	
	1996-1997	1997-1998	1998-1999	1999-2000	2000-2001
Quercus lobata	0.9	21.6	-	29.4	17.2
Quercus agrifolia	0.4	16.3	-	6.9	26.4
No. planted per sp	1,056	1,386		928	928

Table 1—*Percent survival of seedlings of each species in each age class to June 2001 (all treatments combined). No acorns were planted in 1998-1999 because acorns were unavailable.*

Discussion

Results from our four large-scale planting experiments indicate that several factors play a role in limiting or promoting seedling recruitment of oaks, most notably rainfall and herbivory by small mammals. Abundant rainfall in late winter, as seen in the El Niño year 1997-1998, can significantly enhance emergence and survivorship, while very low rainfall, as seen in 1996-1997, results in low seedling numbers. The effects of annual variation in precipitation levels, which are directly related to soil-moisture levels, on oak establishment have been described in previous studies. Griffin (1971) proposed that reduced rainfall greatly reduced establishment of blue and valley oak in central California. Plumb and Hannah (1991) concluded that low rainfall was the primary cause for poor success in regeneration work with coast live oak. In our study, which aims to determine cost-effective methods for oak restoration on a large landscape scale, plants have not been artificially watered because a) irrigation is expensive and may be economically infeasible on a large scale, and b) the long-term survivorship of saplings following weaning of supplemental watering is unknown. However, it is clear that adequate rainfall in the first year after planting will directly affect the success of restoration efforts.

As observed in all four planting years, at all planting sites, in both grazed and ungrazed plots, and for both oak species, seed predation and herbivory by small mammals (most likely gophers and ground squirrels, both of which are abundant at the site) significantly reduces oak seedling recruitment. The role of small mammals in oak seedling mortality has been suggested by a number of studies (e.g., Adams and others 1987, Adams and others 1997, Berhardt and Swiecki 1997, Borchert and others 1989, Davis and others 1991, Griffin 1976, McCreary and Tecklin 1997). However, in cases where seedlings are protected from herbivory with the use of window screening or tree shelters, it is difficult to separate the effects of small mammals from insects, since these treatments exclude both. The present study indicates that small mammals play a major role in limiting recruitment of valley and coast live oak.

Finally, although there appears to be no difference in initial seedling emergence in large grazed vs. ungrazed plots, our results suggest that there may be higher mortality in ungrazed plots. These latter plots, which have been ungrazed since January 1995, now have dense herbaceous vegetation. It is possible that this thick cover of thatch and grasses either 1) negatively affected the oak seedlings directly by competing for water (Gordon and Rice 1993), or 2) attracted higher densities of herbivores. We believe that the higher mortality was due to the latter, in particular herbivory by insects. This past summer (2001) we observed an outbreak of grasshoppers at our site, and many of our seedlings, in all treatments, were defoliated. Previous studies have found that reducing cover of grasses, either by weeding or grazing, significantly enhanced emergence or survivorship in oaks (Adams and others 1997, Berhardt and Swiecki 1997, McCreary and Tecklin 1997). While reduced competition was one outcome of these treatments, several studies note that weed control also reduced damage by animals that are attracted to thick herbaceous cover, such as voles (Bernhardt and Swiecki 1997) and grasshoppers (McCreary and Tecklin 1994).

Acknowledgments

This research has been funded by the Santa Barbara County Oak Restoration Program through the Energy Division at Santa Barbara County's Planning and Development Department. We thank Bill Kuhn for assisting with planting nearly every year for this project, and for support of other aspects of this research. We thank Mike Williams, Virginia Boucher, and Mark Reynolds for support at Sedgwick Reserve. We thank Cal Poly San Luis Obispo staff and students for managing the grazing operation. Tom Griggs provided helpful comments on this manuscript.

References

- Adams, T.E.; Sands, P.B.; Weitkamp, W.H.; McDougald, N.K.; Bartolome, J. 1987. Enemies of white oak regeneration in California. In: Plumb, T.R.; Pillsbury, N.H., technical coordinators. Proceedings of the symposium on multiple-use management of California's hardwood resources; November 12-14, 1986; San Luis Obispo, CA. Gen. Tech. Rep. PSW-100. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 459-462.
- Adams, T.E.; Sands, P.B.; Weitcamp, W.H.; Stanley, M.E. 1997. Oak seedling establishment by artificial regeneration on California rangelands. In: Pillsbury, N.H.; Verner, J.; Tietje, W.D., technical coordinators. Proceedings of the symposium on oak woodlands: ecology, management, and urban interface issues; March 19-22, 1996; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-160. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 213-222.
- Berhardt, E.A.; Swiecki, T.J. 1997. Effects of cultural inputs on survival and growth of direct seeded and naturally occurring valley oak seedlings on hardwood rangeland.
 In: Pillsbury, N.H.; Verner, J.; Tietje, W.D., technical coordinators. Proceedings of the symposium on oak woodlands: ecology, management, and urban interface issues; March 19-22, 1996; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-160. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 301-312.
- Bolsinger, C.L. 1988. The hardwoods of California's timberlands, woodlands, and savannas. Resource Bulletin PNM-RB-148. Portland. OR: Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture; 148 p.
- Borchert, M.I.; Davis, F.W; Michaelsen, J.; Oyler, L.D. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. Ecology 70(2): 389-404.
- Braunack, M.V.; Walker, J. 1985. Recovery of some surface soil properties of ecological interest after sheep grazing in a semi-arid woodland. Australian Journal of Ecology 10(4): 451-460.

- Danielson, K.C.; Halvorson, W.L. 1991. Valley oak seedling growth associated with selected grass species. In: Standiford, R.B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; October 31-November 2, 1990; Davis, CA. Gen. Tech. Rep. PSW-126. Berkeley, CA. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.
- Davis, F.W.; Borchert, M.; Harvey, L.E.; Michaelson, J.C. 1991. Factors affecting seedling survivorship of blue oak (*Quercus douglasii*) in central California. In: Standiford, R.B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; October 31-November 2, 1990; Davis, CA. Gen. Tech. Rep. PSW-126. Berkeley, CA. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.
- Gordon, D.R.; Rice, K.J. 1993. Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. Ecology 74(1): 68-82.
- Griffin, J.R. 1971. Oak regeneration in the upper Carmel Valley, California. Ecology 52(5): 862-868.
- Griffin, J.R. 1973. Xylem sap tension in three woodland oaks of central California. Ecology 54(1): 152-159.
- Griffin, J.R. 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. American Midland Naturalist 95(2): 422-435.
- McCreary, D.D.; Tecklin, J. 1994. Grasshoppers continue to hamper oak restoration efforts. Oaks 'n Folks Newsletter: 9(2) 4-5; Integrated Hardwoods Range Management Program, University of California.
- McCreary, D.D.; Tecklin, J. 1997. Effects of seedling protectors and weed control on blue oak growth and survival. In: Pillsbury, N.H.; Verner, J.; Tietje, W.D., technical coordinators. Proceedings of the symposium on oak woodlands: ecology, management, and urban interface issues; March 19-22, 1996; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-160. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 243-250.
- Plumb, T.R.; Hannah, B. 1991. Artificial regeneration of blue oak and coast live oaks in the central coast. In: Standiford, R.B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; October 31-November 2, 1990; Davis, CA. Gen. Tech. Rep. PSW-126. Berkeley, CA. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 74-80.