INFORMING CLIMATE CHANGE MODELS WITH STAND LEVEL ECOLOGICAL DATA

Valley Oak Woodlands in California
DISCLAIMER

This report was prepared as the result of work sponsored by the California Energy Commission. It does not necessarily represent the views of the Energy Commission, its employees or the State of California. The Energy Commission, the State of California, its employees, contractors and subcontractors make no warranty, express or implied, and assume no legal liability for the information in this report; nor does any party represent that the uses of this information will not infringe upon privately owned rights. This report has not been approved or disapproved by the California Energy Commission nor has the California Energy Commission passed upon the accuracy or adequacy of the information in this report.
ACKNOWLEDGEMENTS

For assistance, we thank Aaron Cole, Corinne Morozumi, Brian Emerson, Caleb Caswell-Levy, Daniella Reagan, Arthur Platel, Tessa Dahlen, Daniela Cusack, Elise Hariton, Rosalie Lawrence, Dustin Mulvaney, Griffin and Bob. For advice and access we thank the members of the Central Coast Rangelands Coalition, Sheila Barry, Dave Brown, Marti Witter, Kimberly Guilliam, Suzanne Goode, Tony Valois, CA State Parks, Fort Hunter Liggett, Sycamore Grove County Park, Hungry Valley SVRA, Christmas Hill Park, Grant County Park, Santa Monica Mountains NRA, Santa Monica Mountains Conservancy, Malibu Creek State Park, Los Padres National Forest, Oak Woodland Conservation Working Group, UC Natural Reserve System, Mark Stromberg, Walt Koenig, Kate McCurdy, Frank Davis, and Claudia Tyler. Valuable discussions and manuscript comments were provided by Pete Raimondi, Kevin Rice, Barry Nickel, Ingrid Parker, Greg Gilbert, Megan Saunders, Sara Maxwell, Blake Suttle, the Zavaleta Lab and two anonymous reviewers. Funding was provided by California Energy Commission (PIER), NSF GFRP, UCSC Environmental Studies Department, UCSC STEPS, CA Native Plants Society, UC Natural Reserve Mildred E. Mathias grant.
PREFACE

The California Energy Commission Energy Research and Development Division supports public interest energy research and development that will help improve the quality of life in California by bringing environmentally safe, affordable, and reliable energy services and products to the marketplace.

The Energy Research and Development Division conducts public interest research, development, and demonstration (RD&D) projects to benefit California.

The Energy Research and Development Division strives to conduct the most promising public interest energy research by partnering with RD&D entities, including individuals, businesses, utilities, and public or private research institutions.

Energy Research and Development Division funding efforts are focused on the following RD&D program areas:

- Buildings End-Use Energy Efficiency
- Energy Innovations Small Grants
- Energy-Related Environmental Research
- Energy Systems Integration
- Environmentally Preferred Advanced Generation
- Industrial/Agricultural/Water End-Use Energy Efficiency
- Renewable Energy Technologies
- Transportation

*Informing Climate Models with Stand Level Ecological Data: Valley Oak Woodlands in California* is the final report for the *Informing Climate Models with Stand Level Ecological Data: Valley Oak Woodlands in California* project (contract number PIR-08-003) conducted by University of California at Santa Cruz. The information from this project contributes to Energy Research and Development Division’s Energy-Related Environmental Research Program.

For more information about the Energy Research and Development Division, please visit the Energy Commission’s website at [www.energy.ca.gov/research/](http://www.energy.ca.gov/research/) or contact the Energy Commission at 916-327-1551.
ABSTRACT

Anticipating species movement under climate change is a major focus in conservation. Bioclimate models are one of the few predictive tools for adaptation planning but do not fully account for (1) climatic tolerances in pre-adult life stages that are potentially more vulnerable to warming; and (2) local-scale movement and use of climatic refugia as an alternative or complement to large-scale changes in distribution. Researchers found through field surveys that California valley oak saplings were more constricted around surface water than adults in the projected contracting area and that the climate envelope for saplings was narrower than that for adults. Findings indicated that valley oaks were more likely to experience constriction around water bodies and eventual disappearance from areas exceeding a maximum threshold temperature rather than a complete shift northward and upslope as predicted by the species bioclimate model. Researchers believed this was the first study to examine the importance of discrete life stage climate sensitivities in determining bioclimate modeling inputs and to identify current climate change-related constriction of a species around microrefugia.

The authors found that the relative importance of top-down and bottom-up forces in limiting oak recruitment shifted across the precipitation gradient. Small mammalian herbivory (top-down) were more important as long-term mean site precipitation increased, and factors related to moisture stress (bottom-up) were increasingly important at lower precipitation levels.

The perceived absence of young cohorts in many valley oaks and other long-lived tree species has raised concerns about their long-term population viability. A comprehensive assessment of natural recruitment across the species distribution has been lacking until now. In this study researchers detected a seven-fold increase in the presence of recruitment over time at 10 sites originally surveyed between 30 and 40 years ago. Results indicated that the species’ long-term conservation prospects may be better than formerly considered.

Keywords: bioclimate modeling, climate change, oak recruitment, microrefugia, valley oak (Quercus lobata), top-down, bottom-up, population regulation, oak recruitment, climate gradient, consumer vs. resource-based limitation, recruitment failure, trees, woodland, reserves, long-term monitoring, biogeography, population dynamics

Please use the following citation for this report:

TABLE OF CONTENTS

Acknowledgements ................................................................................................................................. i

PREFACE ................................................................................................................................................... ii

ABSTRACT .............................................................................................................................................. iii

TABLE OF CONTENTS............................................................................................................................... iv

LIST OF FIGURES .................................................................................................................................. vi

LIST OF TABLES ................................................................................................................................... vii

EXECUTIVE SUMMARY ........................................................................................................................ 1

Introduction ........................................................................................................................................ 1

Project Purpose ................................................................................................................................... 1

Project Results ..................................................................................................................................... 1

Project Benefits ................................................................................................................................... 2

CHAPTER 1: Predicting Species Responses to Climate Change: Demography and Climate Microrefugia in California Valley Oak (Quercus Lobata) ................................................................. 1

1.1 Introduction ................................................................................................................................ 1

1.2 Materials and Methods ...................................................................................................................... 4

1.2.1 Study System ............................................................................................................................ 4

1.2.2 Field Surveys ............................................................................................................................. 4

1.2.3 Valley Oak Bioclimate Model .................................................................................................... 5

1.2.4 GIS and Analysis ....................................................................................................................... 5

1.3 Results .......................................................................................................................................... 7

1.3.1 Constriction of Saplings to Microrefugia ................................................................................ 7

1.3.2 Sapling Climate Envelope ......................................................................................................... 9

1.4 Discussion .................................................................................................................................... 12

1.4.1 Constriction to Microrefugia .................................................................................................... 13

1.4.2 Sapling versus Adult-Based Inputs in Bioclimate Modeling .................................................... 14

1.4.3 Future Valley Oak Distribution .............................................................................................. 16

CHAPTER 2: Shifting Bottom-Up and Top-Down Regulation of Oak Recruitment across a Regional Resource Gradient .............................................................................................................. 17
3.3.2 Recruiting Sites ................................................................................................................. 37
3.3.3 Dendroecology ................................................................................................................. 38
3.4 Discussion ................................................................................................................................. 39
3.4.1 Resurveys: What Accounts for Increased Recruitment over Time? .......................... 39
3.4.2 Episodic Recruitment Events? ........................................................................................ 41
3.4.3 What Factors are Important in Limiting Recruitment in Natural Populations? ..... 41
3.4.4 Conclusions ....................................................................................................................... 42

REFERENCES .......................................................................................................................................... 44

LIST OF FIGURES

Figure 1: Map of Central and Southern Valley Oak Distribution, California, USA .................. 3
Figure 2: Observed Valley Oak Sapling Recruitment (N=26) in Each of the Bioclimate Model-Projected Categories ................................................................. 7
Figure 3: Distance to Streams and Springs for Field Plots with and without Valley Oak Sapling Recruitment in the Projected Persisting/Expanding and Contracting Areas, as Identified by the Valley Oak Bioclimate Model ................................................................. 8
Figure 4: Distance to (a) Lakes/Reservoirs, (b) Rivers, and (c) Groundwater Aquifers for Valley Oak Saplings and Randomly Generated Points throughout the Valley Oak Adult Distribution in the Projected Persisting/Expanding and Contracting Areas, as Identified by the Valley Oak Bioclimate Model ............................................................................................................................................... 9
Figure 5: (a) Mean Maximum August Temperature for the 52 Climate Grid Cells in Recruiting Sites and the Mean Maximum August Temperature of 1000 Random Draws of 52 Cells from across the Adult Distribution. (b) Mean Annual Precipitation for the 52 Cells in Recruiting Sites and the Mean Annual Precipitation of 1000 Random Draws of 52 Cells from across the Adult Distribution ............................................................................................................................................... 10
Figure 6: The Range of (a) August Maximum Temperatures and (b) Average Annual Precipitation Associated with Valley Oak Saplings (N=4219) and Randomly Generated Points throughout the Adult Distribution (N=4219) ............................................................................................................................................... 11
Figure 7: Valley Oak Bioclimate Model Area Inputs Based on the Area of the Current Potential Adult Distribution (black) (Kueppers et al. 2005), and Areas Inputs that Would Be Excluded in a Model Based on the Sapling Climate Threshold (White) ............................................................................................................................................... 11
Figure 8: Conceptual Framework: the Relative Importance of Top-Down and Bottom-Up Regulation to Oak Recruitment Shifts along a Regional Precipitation Gradient ................................................................. 18
Figure 9: Map of Surveyed Valley Oak Distribution and Field Study Sites in California, USA ... 20
Figure 10(a-d): Effects of Mean Annual Site Precipitation on the Importance of Top-Down and Bottom-Up Factors to Valley Oak Sapling Recruitment on (a) Small Mammals, (b) Proximity to Surface Water, (c) Insolation, and (d) Herbaceous Vegetation Height in Ungrazed Sites ............ 22
Figure 11: The Effect of Study Site-Specific Average Annual Precipitation on the Effect Size of Herbivore Exclosures on Valley Oak Seedling Survival across Multiple Planting Experiments . 23
Figure 12: The Effect of Small Mammal Activity, Distance to Surface Water, Insolation and Herbaceous Vegetation Height on Oak Sapling Recruitment in Field Sites with Discrete Recruiting and Non-Recruiting Areas .................................................................................................. 24
Figure 13: Percent of Plots with Valley Oak Saplings under Canopy in Each Study Site, across a Precipitation Gradient ............................................................................................................................. 25
Figure 14: Map of Study Sites and Valley Oak Central and Southern Distribution, California, USA ............................................................................................................................................................ 33
Figure 15: Valley Oak Sapling Recruitment Took Place in at Least One of the Sample Sites in Every Year between 1991 and 2006 and in Multiple Years within Individual Sites ........................................................................... 35
Figure 16: Climate Variables Associated with Grazed and Ungrazed Sites with Sapling Recruitment ............................................................................................................................................... 38
Figure 17: Sapling Diameter at Base with Sapling Age ................................................................................................................................. 39

LIST OF TABLES

Table 1: Results of a General Linear Model Testing the Contributions of Surface Water Distance, Small Mammals, and Interactions of These Factors with Precipitation to Predicting Density of Valley Oak Saplings ................................................................................................................................. 26
Table 2: Results of a Logistic Model Testing the Contributions of Surface Water Distance, Small Mammals, and Interactions of These Factors with Precipitation to Predicting Presence/Absence of Valley Oak Saplings ............................................................................................................................................... 26
Table 3: Survey Sites with Recruitment, Climate, Grazing, and Fire History Status ...................... 37
EXECUTIVE SUMMARY

Introduction
The California valley oak (*Quercus lobata* Nee) is unique to the state and has great biological and cultural significance. Valley oak is reported to be experiencing persistent recruitment failure where dangerously few seedlings survive to adulthood. Climate change poses another threat to its persistence, particularly for juvenile life stages.

Project Purpose
This purpose of this study was to use field data to address three gaps in the understanding of valley oaks:

- Would predictive distribution models be improved with data on saplings as well as adults?
- What controls/regulates their distribution and does it vary along gradients?
- What circumstances permit recruitment in natural populations?

Project Results
Anticipating how species might move in response to climate change is a major focus in conservation. Bioclimate models based on geographic correlations between species distributions and climate are one of the few predictive tools for adaptation planning, but do not fully account for (1) climatic tolerances in pre-adult life stages that are potentially more vulnerable to warming; and (2) local-scale movement and use of climatic refugia outside the boundary of the main distribution as an alternative or complement to large-scale changes in distribution. This study assessed whether these limitations could be overcome with field demographic data. Researchers hypothesized that the valley oak bioclimate model based on adults would overpredict the species' ability to remain where the projected range persists due to higher climate vulnerability of young life stages and underpredict the potential for the species to remain in local-scale refugia where the range contracts. The authors compared the bioclimate model projections against actual locations of saplings and adult trees in natural populations. They found that saplings were more constricted around surface water than adults where the range was projected to contract. They also found that saplings had a narrower climate tolerance than adults. Saplings disappeared at a summer maximum temperature three degrees Celsius (C) below that associated with adults. These findings indicated that valley oaks were more likely to experience constriction around water bodies and eventual disappearance from areas exceeding a threshold of maximum temperature rather than a complete shift northward and upslope as predicted by the species bioclimate model. This was the first study known by the authors to examine the importance of discrete life stage climate sensitivities in determining bioclimate modeling inputs and to identify current climate change-related constriction of a species around microrefugia. These findings illustrated that targeted biological fieldwork can be central to understanding climate change-related movement for long-lived, immobile species.

Questions about the relative importance of top-down (consumption by animals) and bottom-up (resource limitation) regulation of populations have long occupied ecologists. Recent work has explored how the strength of consumer- versus resource-based limitation can shift across both
time and space and indicated the need for larger scales of study across spatial resource
gradients. A better understanding of how climate gradients affect population regulation is
integral to conservation ecology, particularly in the context of global change. Researchers
examined the effects of bottom-up (water limitation) and top-down (small mammal herbivory)
forces on valley oak sapling recruitment. They used existing literature on valley oak planting
experiments and field data on natural populations at 26 sites across the species’ distribution to
explore how the factors regulating oak populations shift along a regional precipitation gradient.
This approach allowed researchers to study ecological processes in a long-lived system that
would be impossible to manipulate in a strictly experimental setting. They found that the
relative importance of top-down and bottom-up forces in limiting oak recruitment shifted
across the precipitation gradient. Small mammalian herbivory (top-down) were more important
in wetter areas and factors related to moisture stress (bottom-up) were increasingly important
at lower precipitation levels. These findings emphasized the importance of expanding the spatial
scale of studies on population and community dynamics to better understand variation in the
multiple factors regulating them across resource gradients.

The perceived absence of young trees in many populations of oaks and other long-lived species
has raised concerns about their long-term viability. Researchers explored what circumstances
permit recruitment in natural populations of valley oak. A robust body of literature on planting
experiments conducted mainly on research reserves exists but a comprehensive assessment of
natural recruitment across the whole range of the species has been lacking. A field study
spanning temporal and geographic scales combined tree-ring analysis, historical resurveys, land
steward interviews and field surveys to explain the prevalence, timing, and distribution of
valley oak sapling recruitment. The authors found saplings recruiting from a range of years in a
variety of climates and land management regimes. They detected a seven-fold increase in the
presence of recruitment over time at 10 sites originally surveyed between 30 and 40 years ago.
They would have concluded that sapling recruitment in valley oak woodlands was still absent
or rare if the study had focused only on the sites that were research reserves. These results
indicated that the species’ long-term conservation prospects may be better than formerly
considered and highlighted the importance of field data from sites with a complete range of
climate and land use regimes.

**Project Benefits**

This project benefitted California by improving knowledge about the valley oak, one of the
state’s flagship species that has important biodiversity, cultural and economic value. A better
understanding of how the distribution of this species was likely to shift with climate change
will allow for better land management and adaptation planning.
CHAPTER 1: 
Predicting Species Responses to Climate Change: 
Demography and Climate Microrefugia in California 
Valley Oak (Quercus Lobata)

1.1 Introduction

Species already are responding to climate change through detectable shifts in distributions (Walther 2002; Parmesean and Yohe 2003; Root et al. 2003) and changes in community composition (Brown et al. 1997; Moritz et al. 2008). Species bioclimate models, empirical models based on geographic correlations between species distributions and climate, have been a principal approach to anticipating climate-related species range shifts (Heikkinen et al. 2006) and are one of the few tools available to land managers to guide climate adaptation strategies (Heller and Zavaleta 2009). Bioclimate models are robust predictors of climate change impacts for certain species (Araujo et al. 2005), and some studies confirm that expected regional-scale range shifts northward and upward in elevation are occurring with warming (Rosenzweig et al. 2008). However other species may have more complex distributional responses to climate change that models currently cannot anticipate. There has been considerable debate about bioclimate model assumptions, limitations and reliability (Pearson and Dawson 2003; Thuiller 2004; Hampe 2004; Guisan and Thuiller 2005; Martinez-Meyer 2005; reviewed in Heikkinen et al. 2006; Austin 2007; Botkin et al. 2007; Thuiller 2008) and calls for more ground validation and incorporation of ecological complexity (Araujo et al. 2005; Araujo and Luoto 2007; Keith et al. 2008). While basic bioclimate models can provide relatively rapid assessment of potential changes in species distributions, the risks of inaccurate predictions are significant in the context of efforts to facilitate species persistence and movement through management actions (Hoegh-Guldberg et al. 2008).

We propose two ways to refine and improve predictions of species response to climate change using field data. First, we argue that consideration of life stage-specific climate vulnerability, so far absent in bioclimate modeling, can improve the reliability and precision of model predictions, particularly for long-lived, sessile species. In these species, due to the suite of global changes that have occurred over the past century, current early life stages may experience distinct environmental conditions from those that current adults experienced in their early life stages. Moreover, early life stages may not tolerate the same range of conditions as adults, have been shown to respond differently to environmental gradients than adults (Collins and Carson 2004), and therefore may respond differently to climate change, shaping changes in the species distribution distinct from predictions based on adult climate tolerances. Therefore, analyses based primarily on adults, the focus of most bioclimate models, could mask the responses of early life stages to climate change. Ongoing climate change (Ladochy 2007) has created the opportunity to test models with field data on emerging changes in distributions (Araujo et al. 2005), through a comparison of spatial patterns of adults that established under historic climate conditions and recruits that currently are establishing in warmer conditions.
A second question that can be addressed by refining bioclimate models with field data concerns whether species can persist in microrefugia, microclimates that support small populations of species beyond the boundaries of the climatic limits of their main distributions (Rull 2009; Dobrowski 2010). Most places already are undergoing warming (IPCC 2007), and comparing adult distributions to recruitment patterns in bioclimate model-projected contracting areas (areas from which a species is expected to retreat in response to climate change), can help identify potential climate microrefugia. While there has been extensive work on understanding the role of climate refugia during the Quaternary period (Keppel 2011), as far as we know, no studies on the impacts of current climate change have documented species constriction into local-scale climate refugia. Identifying and protecting potential microrefugia under current climate change is a new priority for conservation and adaptation planning (Keppel 2011), and Hampe and Petit (2005) suggest that the ‘rear edge,’ or projected contracting area, of climate-based range shifts represents an understudied aspect of species response to climate change that is disproportionately important (based on paleoecological studies) to potential recolonization and the maintenance of genetic diversity. While paleoecological studies have addressed the role of regional-scale topographic refugia, other local factors such as areas of high groundwater availability that affect species through mechanisms like plant drought stress may function similarly and deserve examination.

Valley oaks (Quercus lobata Nee), a species endemic to California, USA and of high conservation concern, provide an excellent model system for exploring the potential for life stage analysis to refine bioclimate model projections and for microrefugia to allow persistence within pockets of former species distributions. Because valley oaks are a long-lived, non-mobile species, it is possible to compare the current distribution of adults (which indicates the past distribution of saplings that survived to adulthood) with the current distribution of saplings, (which bounds the possible extent of the future adult distribution). Young valley oaks also may be especially vulnerable to drought effects of climate change (Matzner et al. 2003; Tyler et al. 2006) exacerbated by ongoing anthropogenic changes in California oak woodlands (Gordon et al. 1989, Grulke 2007, Ladochy 2007, Howard and Merrifield 2010). The species is thought to be highly dependent on groundwater (Jepson 1910; Lewis and Burgy 1964; Griffin 1973), and drought stress microrefugia may play an important role in conservation.

California has warmed an average of approximately 1 degree C over the past century (Ladochy 2007), producing discernible signals of this trend in the state’s biota (Kelly et al. 2008; Moritz et al. 2008; Tingley et al. 2009). Thus, we expected to detect field-based evidence of a similar warming-based shift in valley oak woodlands. A regional bioclimate model has been developed for valley oaks using soil and climate parameters associated with adult distribution data (Kueppers et al. 2005). It projects a decrease in extent and a general northward and upward expansion of the species distribution. We conducted a multi-scale observational field study to assess the correspondence between the valley oak bioclimate model projections (Kueppers et al. 2005), and observed patterns of natural sapling recruitment in 30 study sites across the species
distribution (Figure 1). We used data on valley oak sapling distributions within each site to evaluate whether saplings are constricted in extent relative to adults and whether, in particular, emerging microrefugia are related to groundwater availability. Finally, we compared the potential implications of an adult- versus early-life stage focus in generating model predictions. We tested a set of hypotheses (1) that the valley oak bioclimate model would be consistent with regional-scale patterns of sapling recruitment: sites with saplings would be concentrated in the model-projected expanding and persisting areas and reduced in the projected contracting area. (2a) That the model would underpredict the potential for valley oaks to remain in the projected contracting area: sites with sapling recruitment would not be reduced and sapling recruitment would be higher in pockets of local-scale refugia in the projected contracting area; and (2b) that the model would overpredict the potential for valley oak survival in the projected persisting area: the overall climate envelope for saplings would be narrower than that for adults.

Figure 1: Map of Central and Southern Valley Oak Distribution, California, USA

Valley oak presence is represented by grey outlines, and study sites are represented by black circles.

1 We use scale terms as follows: regional-scale, on the order of 100s of kms; landscape-scale, on the order of 10s of kms; and local-scale, on the order of 1 km.
1.2 Materials and Methods

1.2.1 Study System

The distribution of valley oak (Quercus lobata) includes the California Coast Ranges, Central Valley and Sierra Nevada foothills (Griffin and Critchfield 1972), all in a Mediterranean climate with rainy winters and prolonged summer droughts. The 30 sites across this distribution that comprised the field portion of our study included grazed and ungrazed sites (projected contracting areas: 14 ungrazed, 5 grazed; projected persisting and expanding areas: 7 grazed, 3 ungrazed), an elevation range of 300 to 1400 m and a gradient of 45 to 100 cm average annual precipitation. Site community compositions included mixed valley oak, blue oak (Quercus douglasii) and live oak (Quercus agrifolia), mixed oak/conifer, and pure valley oak woodlands, all with valley oak as the dominant tree species. Most sites had a non-native, annual grass understory (Bromus spp., Avena spp.), which has replaced an understory historically dominated by native perennial bunch grasses and forbs (Beetle 1947; Barry 1981; Gordon et al. 1989). Valley oak sapling recruitment is thought to be rare in this system (reviewed in Tyler et al. 2006 and Zavaleta et al. 2007).

We chose study sites based on interviews with land managers to help identify stands with sapling recruitment (N=20); and where previous surveys had been conducted, identified through the literature (N=10) (Figure 1). Sites ranged from 0.5-1 km² in area. Through 215 land manager contacts, we identified 26 sites as ‘recruiting,’ with more than 1 sapling (1.3- 9 cm at base diameter and >0.5 m in height (Zavaleta et al. 2007)) occurring within a 1 km² area. We excluded from our study: areas that were highly disturbed or within 5 m of roads or fencelines, and areas with mixed Q. lobata and Q. garyana adults, which have morphologically indistinguishable saplings. We limited our analyses only to areas within the bounds of our land manager interviews, mainly in the central and southern parts of the distribution. The term ‘adult distribution’ in this paper refers to this subset of the valley oak distribution (Figure 1). Thus, our conclusions are most applicable to oak woodland and savanna in the central and southern portions of the distribution (Figure 1).

1.2.2 Field Surveys

In all sites, to map valley oak saplings and to establish areas with and without recruitment, a field crew conducted a sweep of the entire site and took GPS coordinates for all valley oak saplings (N=4219). To interpret relationships between recruitment and groundwater availability, we mapped springs and streams within each site. For all mapping, we used a Trimble GeoXH 2005, accurate to 0.5 m. In 14 of the 30 sites, we were able to identify discrete, proximate recruiting and non-recruiting areas within the site, allowing for within-site comparative analysis. Non-recruiting areas were defined as areas at least 50 m from any valley oak sapling but within 50 m of a mature adult tree. To assess whether proximity to surface water was related to successful recruitment, we took GPS coordinates of randomly located saplings in recruiting areas and at random points in non-recruiting areas, with approximately one mapped point per 1500 m² of space. Surveys were conducted between late May and August of 2009.
1.2.3 Valley Oak Bioclimate Model
To identify areas of the species distribution projected to expand, persist or contract with climate change, we used a regional bioclimate model for valley oaks projecting a change in distribution by 2100, based on a business-as-usual emissions scenario, similar to the IPCC A1B scenario (Kueppers et al. 2005). The model used multivariate climate and soil envelopes as inputs to determine suitable habitat and based current distribution data on the California GAP analysis, relatively robust locality data for this species (Kueppers et al. 2005). We chose this model over others based on global climate models because of the former’s sensitivity to sub-regional climatic changes from topographic and maritime effects. The model places land areas into one of three climate change projection categories for valley oaks: contracting areas, which are in the current potential distribution but projected to lose valley oaks completely; persisting areas, which are in the current potential distribution and in which valley oaks are expected to remain; and expanding areas, those not in the current potential distribution but into which valley oaks are expected to expand. Areas classified into the three model categories (expanding, persisting and contracting) differ in current climate. Current mean maximum August temperatures and annual average precipitation for areas within the three categories are as follows: contracting: 32.4 °C, 61.1 cm; persisting: 30.1 °C, 103.4 cm; and expanding: 28.4 °C, 143.4 cm (30 year normals, PRISM Climate Group).

1.2.4 GIS and Analysis
To explore correspondence of the valley oaks bioclimate model and the distribution of sapling recruitment, we overlaid layers of the model-projected expanding, persisting and contracting areas of the range (scale: 4 km²) (Kueppers et al. 2005) and the current valley oak adult distribution (scale: 1:100,000 km) (California GAP analysis, UCSB 1998, updated 2002). We then generated a null expected proportion of recruiting sites that should occur in each of the three model-projected category areas, based on the proportion of the area of the current adult distribution in each. We used a chi square test to determine whether the expected and observed (based on the GPS coordinates of our field site locations) distributions of recruiting sites differed. We also conducted binomial tests separately on each category to compare the expected likelihood of sites with recruitment in each model-projected category, with the proportion of observed sites falling into each model-projected category. The expanding category for both analyses above included areas within 5 km of a projected expanding edge. Much of the model-projected expanding area did not contain valley oaks, and a 5 km buffer allowed us to examine demography at the potentially expanding edge of the current distribution.

To evaluate whether patterns of recruitment in relation to surface water differed in the model-projected expanding/persisting and contracting areas, we compared the distances of saplings and adults to surface water in each model-projected category at 2 scales. To analyze local-scale hydrologic features, we created our own layer of GPS data on streams and springs at each site. We compared the distance to streams and springs for recruiting and non-recruiting points in the 14 sites with discrete recruiting and non-recruiting areas, in each of the model-projected categories (contracting n=164 points; persisting/expanding n=119 points), using a 2-sample, 2-
tailed T-test. For this and subsequent analyses we combined the projected expanding and persisting areas because they showed qualitatively similar trends.

To compare proximity to water bodies of recruiting and non-recruiting areas at the regional scale, we measured distances to key hydrologic features: rivers, lakes and reservoirs, and ground water basins, for all saplings (N = 4219) and for an equal number of randomly generated points throughout the adult distribution. To map these large hydrologic features, we used the US Water Bodies dataset (USGS and US EPA, ESRI, 2008), the US Rivers and Streams dataset (USGS and US EPA, ESRI, 2008), and the California groundwater basin maps that (CA DWR) (scale: 1:100,000 for all). We compared the distances of saplings and randomly generated points to each of these hydrologic features in the contracting and persisting/expanding model-projected categories, using a 2-sample, 2-tailed T-test with a Bonferroni post-hoc correction.

To determine whether saplings had a narrower climatic envelope than adults, we compared climate parameters in our GIS layer of known valley oak recruitment (based on our field data) to the current adult distribution (California GAP analysis, UCSB 1998, updated 2002). We compiled the PRISM 30-year means (1960-1990, scale: 1 km²) of annual average precipitation, shown to be important to valley oak distribution (Kueppers et al. 2005) and maximum August temperatures, which likely represent the highest levels of drought stress experienced by recruits, associated with both the adult distribution and our sapling layers. We generated a distribution of mean maximum August temperature and annual average precipitation associated with the adult distribution and with the recruiting sites, using a GIS grid of 750 m² cells (based on the average size of our field sites). We compared mean climate values in the recruiting areas (N=52 cells with saplings) to climate values across the adult distribution. For this analysis, to reduce the potential confounding effects of unequal sample size, we resampled 1000 random draws of 52 cells from the adult distribution. We generated a P value by evaluating where the mean of the 52 recruiting values fell within the distribution of means of the 1000 resampled draws of 52 cells from the adult distribution.

To evaluate whether minimum and maximum climate thresholds were different between the sapling and adult climate envelopes, we compared the lowest and highest values of maximum August temperatures and average annual precipitation associated with saplings (N=4219) to randomly chosen points throughout the adult distribution (N=4219). From this we identified the climate values above and below which saplings were not found and calculated the percentages of the adult distribution outside of those values. To estimate how the current valley oak bioclimate model might change if the model inputs were based on climate parameters associated with saplings instead of those associated with adults, we subtracted from the adult-based model inputs all areas above the observed maximum August temperature associated with saplings, and calculated the percent reduction of the area of adult-based inputs.

In all analyses, we transformed data as necessary to address violations of homogeneity of variance and normality. We analyzed the effect of timing of field survey on all variables to ensure that patterns were not due to seasonal differences. We used ArcGIS 10 (ESRI 2010) and Trimble GPS Pathfinder Office software (Trimble Navigation Limited 2005). All statistical analyses were performed using SYSTAT 12 (Systat Software Inc., San Jose, CA, USA).
1.3 Results

The distribution of recruiting sites across the bioclimate model-projected categories (expanding, persisting and contracting) did not differ from the null expected proportion of recruiting sites in each category, based on the proportion of the area of the current adult distribution in each projection category (N=26 sites with recruitment, 26 random locations) (P>0.05) (Figure 2). When we compared the expected and observed numbers of recruiting sites in each category separately the results were as follows: the number of recruiting sites in the projected expanding area was different and more than expected, binomial probability=0.013; the number of recruiting sites in persisting areas was different and less than expected, binomial probability=0.027; the number of recruiting sites in the projected contracting area was not significantly different than expected, binomial probability=0.86. Our study was not designed to analyze grazing effects on recruitment, however in our sites the presence of grazing did not predict whether or not a site had sapling recruitment (unpublished data).

Figure 2: Observed Valley Oak Sapling Recruitment (N=26) in Each of the Bioclimate Model-Projected Categories

Light grey bars represent sites with observed valley oak sapling recruitment (N=26) in each of the bioclimate model-projected categories. Dark grey bars represent 26 locations chosen at random from the valley oak adult distribution, in proportion with the area of the distribution in each of the bioclimate model-projected categories (expanding, persisting and contracting), representing the null model of the expected distribution of recruitment across projected categories. No error bars exist for this figure because the y axis represents known counts.

1.3.1 Constriction of Saplings to Microrefugia

At the local scale, the model-projected contracting and persisting/expanding areas had different associations between oak recruitment and surface water. In the projected contracting area, saplings were closer than adults to surface water (P=0.005, T=2.79, N=164, DF=163); in the
projected persisting/expanding areas, we did not detect significant differences in distance to surface water between adults and saplings (Figure 3).

**Figure 3: Distance to Streams and Springs for Field Plots with and without Valley Oak Sapling Recruitment in the Projected Persisting/Expanding and Contracting Areas, as Identified by the Valley Oak Bioclimate Model**

Bars represent ± standard error.

At the regional scale, in the projected contracting area, saplings were closer to rivers (P<0.00001, T=24.2, DF=5362, N=5364), lakes and reservoirs (P<0.00001, T=23.6, DF=5362, N=5364), and groundwater aquifers (P<0.00001, T=20.9, DF=5362, N=5364) than the adult distribution (Figure 4a,b,c). In the projected persisting/expanding areas, saplings were further away from rivers (P<0.00001, T=-9.3, DF=2667, N=2669), lakes and reservoirs (P<0.00001, T=-18.5, DF=2667, N=2669) and groundwater aquifers (P<0.00001, T=-19.1, DF=2667, N=2669) than the adult distribution (Figure 4a,b,c).
1.3.2 Sapling Climate Envelope

Sapling recruitment was more climatically restricted than the adult distribution, to areas with higher average annual rainfall (P<0.05) and lower maximum summer temperatures (P<0.01) (Figure 5a,b). The range of maximum August temperatures and average annual precipitation associated with recruiting sites was narrower than that associated with the adult distribution (Figure 6), (recruiting sites: minimum=23.5 C, 35.4 cm, maximum=34.6 C, 108.6 cm; adult distribution: minimum=22.5 C, 19.8 cm, maximum=37.6 C, 144.8 cm). For maximum August temperature, the climate envelope of saplings was shifted to the cooler area of the adult distribution: 13.2% of the adult data points occurred at temperatures above the maximum value associated with saplings, and .001% of the adult data points occurred at temperatures below the minimum value associated with saplings (Fig 6a). For average annual precipitation, the climate envelope of saplings was shifted toward the wetter area of the adult distribution: 7% of the
adult data points occurred at precipitation values below the minimum value associated with saplings, and 1.9% of the adult data points occurred above the maximum value associated with saplings (Figure 6b). Based on a threshold of 34.6 degrees C maximum August temperature (the highest value at which we found recruitment), the regional bioclimate model inputs overpredicted areas climatically associated with saplings by 15% (Figure 7).

**Figure 5:** (a) Mean Maximum August Temperature for the 52 Climate Grid Cells in Recruiting Sites and the Mean Maximum August Temperature of 1000 Random Draws of 52 Cells from across the Adult Distribution. (b) Mean Annual Precipitation for the 52 Cells in Recruiting Sites and the Mean Annual Precipitation of 1000 Random Draws of 52 Cells from across the Adult Distribution.

Box and whiskers represent climate values for the valley oak adult distribution. The box edges mark the first and third quartiles, the whiskers mark the upper and lower ranges of the non-outlier points, and stars represent outlier points. Black diamonds represent the mean value in sites with valley oak sapling recruitment.
Figure 6: The Range of (a) August Maximum Temperatures and (b) Average Annual Precipitation Associated with Valley Oak Saplings (N=4219) and Randomly Generated Points throughout the Adult Distribution (N=4219)

Figure 7: Valley Oak Bioclimatic Model Area Inputs Based on the Area of the Current Potential Adult Distribution (black) (Kueppers et al. 2005), and Areas Inputs that Would Be Excluded in a Model Based on the Sapling Climate Threshold (White)
1.4 Discussion

Based on recorded ongoing regional warming (Ladochy et al. 2007), directional species movement in multiple California systems (Morrizt et al. 2008; Kelly and Goulden 2008) and the valley oak bioclimate model (Kueppers et al. 2005), we expected to see evidence of a warming-based shift having already begun to occur in valley oak woodlands. We expected that recruitment patterns today would be consistent with projections of the future species distribution, demonstrating an early signal of distributional shifts. Our first hypothesis was that recruiting sites would be concentrated in the model-projected expanding and persisting areas and reduced in the projected contracting area. This would imply a correspondence between the bioclimate model projections and observed field data. The lack of significant difference between the null expected distribution and the observed distribution of sites with sapling recruitment indicates that the bioclimate model was not consistent with the observed patterns of sapling recruitment (Fig 2). However, the lack of significant difference may have been due to the chi square test’s sensitivity to small sample size (Zar 2010). Therefore, we also examined the differences between observed and expected numbers of recruiting sites in each model-projected category. In the model-projected expanding area there were more recruiting sites than expected by the null model. This finding was consistent with the first hypothesis that sapling recruitment would be concentrated in model-projected expanding and persisting areas. However contrary to this hypothesis, in the model-projected persisting area, there were fewer recruiting sites than expected. In the model-projected contracting area, there was no significant difference between the observed and expected numbers of recruiting sites, also inconsistent with the first hypothesis that recruiting sites would be reduced in the projected contracting area. These results indicate that overall, the bioclimate model successfully predicted areas of potential range expansion, evidenced through increased sapling recruitment in the model-projected expanding area. However, observed patterns of sapling recruitment were not consistent with the model-projected persisting or contracting areas, indicating that other factors aside from regional climate are shaping the future species distribution in these places.

Recent efforts to improve bioclimate modeling include incorporating multiple scales (Kueppers et al. 2005; Seo et al. 2009) and sample sizes (Stockwell and Peterson 2002), and different types of abundance data (Brotons et al. 2004; Chefaoui and Lobo 2008), biotic interactions (Davis et al. 1998; Leathwick 2002; Araujo and Luoto 2007), and demography and dispersal (Iverson and Prasad 2002; Peterson et al. 2002; Keith et al. 2008). The incorporation of spatial demographic data, with a focus on climate-vulnerable life stages and the identification of potential microrefugia, can further refine these efforts and improve predictions of species response to climate change. Instead of overall recruitment patterns consistent with the regional-scale distributional shift projected by the species bioclimate model, our findings support our second hypothesis, suggesting (1) that microrefugia in the form of higher groundwater availability is facilitating valley oak persistence through constricted pockets of sapling recruitment in model-projected contracting areas; and (2) that saplings have a narrower climate envelope than adults, likely restricting the potential for the species to remain in model-projected persisting areas, where these areas exceed sapling-specific climate thresholds.
1.4.1 Constriction to Microrefugia

Evidence, mainly from Quaternary phylogeographic studies (Keppel et al. 2011), suggests that regional-scale climate refugia were important for species persistence through rapid climate fluctuations during the last glacial maximum and later allowed for postglacial recolonization (reviewed in Dobrowski 2010; Keppel et al. 2011). In a current extension of this concept, Loarie et al. (2008) map predictions of future regional-scale climate refugia for endemic species in California and suggest that areas that harbor species with shrinking ranges, such as scattered mountainous areas, may provide good conservation targets. While much historical work focused on large-scale climate refugia there is also some evidence for species’ use of local-scale or microrefugia (also referred to as cryptic refugia), microclimates that supported small populations of species beyond the climatic limits of their main distributions (Rull 2009; Dobrowski 2010). Recently, restriction to favorable microclimates has been shown to occur near the climatic edges of species distributions (Hennenberg and Bruehlheide 2003) and it has been proposed, in theory, that a spatial shift to particular topographic conditions may act as an early indicator of climate change impacts on a species’ distribution (Korner 1999; Thomas et al. 2001). Protecting microrefugia has been suggested as a potential in situ conservation option for species threatened by climate change (Dobrowski 2010), however, actual patterns of climate change-related constriction into microrefugia had yet to be demonstrated with current field data.

Work on microrefugia has focused mainly on topographic microclimates (Stewart and Lister 2001, Dobrowski 2010), yet other forms of drought stress microrefugia also may exist. Because of valley oaks’ direct use of groundwater (Jepson 1910; Lewis and Burgy 1964; Griffin 1973), we expected that drought stress microrefugia might exist for this species in areas of high groundwater availability, and that these areas would be important for recruitment within model-projected contracting areas. Our finding of different distribution patterns of saplings around surface water between the projected expanding/persisting and contracting areas supported this hypothesis. In the projected contracting areas saplings were more restricted to water bodies, indicating that a climate-based shift in local distribution of valley oaks may be already underway, and that microrefugia, in the form of higher groundwater availability, may play a role in mediating the effects of regional climate change. We saw evidence for this both at the local scale with streams and springs (Figure 3), and at the landscape scale with rivers, lakes and reservoirs, and groundwater basins (Figure 4a,b,c).

Our finding that valley oak saplings grow closer to water bodies in the projected contracting areas, at two scales, likely indicates a higher dependence on groundwater availability during the drought stress-vulnerable seedling-to sapling transition phase (Matzner et al. 2003; Tyler et al. 2006). Because of higher temperatures and lower precipitation in projected contracting areas, seedlings there likely experience higher overall drought stress than seedlings in the projected persisting/expanding areas. With warming, seedlings in these contracting areas may be the first to encounter drought stress thresholds that cause them to require quicker access to the water table, restricting recruitment to areas where the water table is relatively high.

We also found that at the landscape scale (but not at the local scale) saplings grow in areas further from water bodies than adults in the persisting/expanding areas. Reasons for this
finding are not entirely clear. It may indicate that saplings in these areas are less restricted to higher groundwater availability, as temperatures are lower and precipitation is higher, relatively reducing the overall impacts of drought stress and increasing the importance of other environmental stressors such as herbivory (Tyler et al. 2006; McLaughlin and Zavaleta in prep). In persisting/expanding areas, saplings are still within the distribution of adults and our data do not demonstrate an expansion of the distribution.

There were more grazed than ungrazed sites in the projected contracting areas, and more ungrazed than grazed sites in the projected persisting and expanding areas. One hypothesis on oak recruitment failure is that grazing reduces recruitment (Tyler et al. 2006). A potential issue with an uneven distribution of grazing across model-projected categories could exist if grazing impacted distribution of recruitment within a site based on the concentration of cattle around riparian areas (Baily et al. 1996). However we see the opposite trend in our data: more recruitment around riparian areas in projected contracting sites (more of which were grazed) than projected persisting/expanding sites. There may be interactions between grazing, climate and recruitment, but our study was not designed to test these, and grazing does not appear to account for the main effects we report.

1.4.2 Sapling versus Adult-Based Inputs in Bioclimate Modeling

Our finding that key climate parameters associated with saplings are different from those associated with adults suggests that for species with complex life histories, the choice of life stage in parameterizing bioclimate models can be critical and that the valley oak bioclimate model, which is based on climate parameters associated with adults, may overestimate the area in which valley oak will be able persist with climate change. The association of recruiting sites with higher rainfall and lower temperatures (Figure 5 a,b) indicates that sites with saplings may be restricted to cooler and wetter portions of the species distribution. While both mean annual precipitation and maximum August temperature were significant predictors of recruitment, the latter was a stronger predictor. These results suggest a narrowing of the climatic niche for saplings. However short-range dispersal in this species may limit recruitment into areas of newly suitable climate at the cooler and wetter ends of the distribution. Thus what appears in our data as a niche narrowing or contraction may instead be a geographic niche shift, currently undetectable due to dispersal limitation.

The maximum value of maximum August temperatures associated with saplings was lower than that associated with adults, and the minimum value of average annual precipitation associated with saplings was higher than that associated with adults (Figure 6a,b), suggesting that there are potential climate thresholds outside of which adults may still persist but recruitment is unlikely to occur. We were unable to randomly select or stratify study sites according to climate conditions, due to the rarity of sites with sapling recruitment, therefore it is possible that unsampled locations with recruitment at higher temperatures and lower precipitation exist. However our interviews included land stewards with knowledge of these areas, and recruiting stands were not reported. While our analysis of the range of climate parameters associated with recruitment and the full adult distribution necessarily compared areas of unequal size, we argue that our results indicate a true difference in climate tolerances.
between saplings and adults. Since larger data sets tend to capture more extreme values, we might expect to see an overall narrower range of climate values associated with recruitment, constrained at both the lower and upper ends relative to the adult values. Instead, the range of sapling values is skewed in the direction we would predict based on our other results (toward lower maximum August temperatures and higher average annual rainfall). This trend is strongest with maximum August temperatures, with 13.2% of the adult distribution occurring above the maximum temperature value associated with saplings and only .001% occurring below the minimum value associated with saplings. The trend is weaker but still present for average annual precipitation, with 7% of the adult distribution occurring above the maximum temperature value associated with saplings but only 1.9% occurring below the minimum value associated with saplings (Fig 6a,b). If the difference were due to more extreme values being captured by the larger sample size, we would expect to see the effects at both the high and low ends of the climatic ranges. That the differences are more pronounced at the dryer and warmer ends of the spectrum suggests that there are different climatic thresholds for saplings and adults.

Difference in the climate envelope between saplings and adults could be explained by both different vulnerability to drought stress between life stages and by changes in the environment over time. Seedlings are less drought stress tolerant than adults (Matzner 2003; Tyler et al. 2006), and have less direct access to the water table (Lewis and Burgy 1964). Additionally, in a system that has undergone a suite of anthropogenic changes over the past century, climate parameters associated with the current distribution of adults in a long-lived species may be a relict, reflecting recruitment limitation associated with a previous era. Changing environmental conditions in valley oak woodlands likely have increased drought stress in oak seedlings through new stresses including ongoing regional warming (Ladochy et al. 2007), groundwater reductions (Howard and Merrifield 2010), tropospheric ozone exposure (Grulke 2007), and increased herb competition for water from invasive annual grasses (Gordon et al. 1989; Danielson 1990; Danielson and Halvorson 1991). Thus, ambient climate conditions that were tolerable to current adults when they were saplings may no longer be tolerable by today’s recruits.

The use of adult-based bioclimate model inputs may cause the model to overestimate the climate conditions currently necessary for successful recruitment and migration. To explore the extent to which the adult-based valley oak model may overpredict the potential for the species to persist with climate change, we limited inputs to areas within the sapling climate envelope. This reduced model inputs by 15 percent, indicating that future valley oak distributions will be more restricted with climate change than the current adult-based model predicts. Our basic description of a revised climate envelope map based on saplings is intended to illustrate the potential extent of the difference in model inputs based on adults versus saplings. Future work should expand on this basic analysis and involve modeling with a range of multiple sapling-based climate parameters to compare model outputs between sapling-and adult-based inputs.
1.4.3 Future Valley Oak Distribution

Our findings indicate that the valley oak bioclimate model, parameterized by adult-based inputs, overestimates the areas in which the species is likely to persist, by not taking into account sapling-specific climate sensitivities; and also underestimates the potential for small populations of valley oaks to remain within much of the projected contracting area around drought stress-mediating microrefugia. Climate change is predicted to increase drought stress and evapotranspiration (IPCC 2007). If constriction of sapling recruitment around water bodies is due to drought stress, then we would expect this pattern to increase and intensify in the future, ultimately restricting entire populations of valley oak in the projected-contracting zones in pockets of suitable microhabitats. Additionally, we would expect valley oaks to experience complete losses in areas outside the climate envelope associated with sapling recruitment. Our results suggest that a key factor in creating microrefugia is groundwater availability, and that an important factor in differentiating sapling versus adult climate envelopes is maximum summer temperature. These factors are linked in that higher temperatures likely create dryer soil conditions, making high groundwater availability more important to species persistence. Climate change in California may interact with both, increasing temperatures, reducing snowpack and groundwater recharge, and potential increasing the extent of groundwater withdrawal for human use (Hayhoe et al. 2004).

Bioclimate model predictions involving whole-distribution shifts are useful at large scales, but a focus on changes in local species occurrence may be more relevant and actionable for natural resource managers interested in in situ conservation at the level of individually managed landscapes. Our findings support the concern that projections of complete losses of tree species in large parts of their range may be overstated (Pearson 2006), and molecular studies suggest that migration rates for trees may not be fast enough to keep pace with projected rapid warming (McLachlan et al. 2005). Therefore identifying and protecting microrefugia where species may persist would be a critical component of conserving species, populations and genetic diversity within areas projected to lose species with climate change (Dobrowski 2010). Specifically, our results suggest that in Mediterranean systems, where important terrestrial species often depend on access to groundwater (Howard and Merrifield 2010), maintaining groundwater levels and wisely managing riparian areas should be a priority to buffer the system against climate change. More generally, our findings underscore the importance of a focus on life stage specific climate vulnerability in understanding and predicting climate-related species movement. Fortunately, relevant spatial demographic data often are available on the ground and do not represent prohibitive ecological complexity. Their integration into climate change modeling presents an opportunity for collaboration between field ecologists and modelers that could yield significant improvements in model performance, better anticipate potential species movement, and help guide conservation in a warming world.
CHAPTER 2:  
Shifting Bottom-Up and Top-Down Regulation of Oak Recruitment across a Regional Resource Gradient

2.1 Introduction

Since Hairston et al. (1960) presented their “green world” hypothesis, debate has persisted on whether bottom-up forces -- resource availability -- or top-down forces -- higher trophic levels – dominate plant community and population dynamics. This question pervades community ecology and is critical to the development of predictive theory on trophic dynamics (Ovadia and Schmitz 2004). Following Fretwell’s proposition (1977, formalized in Oksanen et al. 1981) that environmental productivity establishes the relative importance of resource versus herbivore control of plant production, it has become clear that bottom-up and top-down forces may act concurrently on populations (Power 1992), and vary in strength with different environmental conditions (Matson and Hunter 1992, Power 1992, Menge 1992) and with local spatial resource gradients (reviewed in Turkington 2009). Because individual species ranges may encompass a wide range of environmental conditions and resource regimes, understanding mechanisms of regional-scale variation of population regulation could improve our ability to predict species responses to environmental change. However it is unclear how regional-scale variation in resource availability affects these relationships across entire distributions, particularly for widely dispersed species with ranges that span critical resource gradients.

Within sites, the strength of top-down and bottom-up effects can shift through time in concert with changes in climate (Meserve et. al. 2003, Mazia et. al. 2004, Ovadia and Schmitz 2004, Post et al. 1999, Spiller and Schoener 2008). In xeric systems, top-down effects often dominate in wet years while bottom-up effects dominant in dry years (Meserve et. al. 2003, Mazia et. al. 2004, Ovadia and Schmitz 2004, Spiller and Schoener 2008). While it has been shown that the relative strength of top-down and bottom-up forces thus varies with climate at individual sites over time, climatic variation through space is a distinct phenomenon and may be equally important in determining patterns of top-down and bottom-up regulation across a species’ distribution. Regional spatial gradients incorporate the long-term effects of various climate regimes on full communities that would be impossible to capture in an intra-annual climate analysis in a single site or experimental setting. In this conceptual context, we explore the relative importance of top-down and bottom-up regulation of populations of a species across its distribution. We chose to focus on California valley oak (*Quercus lobata*), a long-lived species with strong spatial and temporal variation in recruitment whose distribution spans a regional precipitation gradient.

Previous studies have suggested several potential drivers of recruitment limitation in valley oak, including both top-down and bottom-up forces (reviewed in Tyler et al. 2006). Top-down forces known to impact recruitment are wild mammalian herbivores, including gophers (*Thomomys* spp) and ground squirrels (*Spermophilus beecheyi*), and domestic grazing (Griffin 1976, Tyler et al. 2006). Bottom-up forces shown to affect oak recruitment include water
availability as mediated through climate, flood regime and groundwater (Lewis and Burgy 1964, Griffin 1976, Meyer 2002, Kueppers et al. 2005, Tyler et al. 2008), and the potential indirect impacts of herb competition for water (Tyler et al. 2006). Water table levels may substantially impact valley oaks (Brown and Davis 1991, McLaughlin and Zavaleta 2012), which like many oaks in Mediterranean climates (Howard and Merrifield 2010, Miller et al. 2010) is thought to extract water directly from the water table. Exotic annual grasses, the dominant herbaceous vegetation in our study sites, deplete soil moisture more rapidly than native bunch grasses (Danielson 1990) and compete with oak seedlings for water more strongly than natives (Gordon et al. 1989, Danielson and Halvorson 1991). Increased regional N deposition likely favors annual grasses (Allen et al. 2002), and experimental work indicates that nitrogen additions have a negative effect on seedlings, providing a competitive advantage to neighboring annual grasses (Adams et al. 1997).

Valley oak sapling recruitment is thought to be rare and the limiting life stage in this system (reviewed in Tyler et al. 2006 and Zavaleta et al. 2007, McLaughlin and Zavaleta 2012). Such reproductive bottlenecks at young life stages have been observed in multiple tree genera and appear particularly common in Quercus (reviewed in Abrams 2003). Experimental work on valley oak recruitment and seedling performance has yielded no definitive conclusion on the causes of sapling recruitment failure in natural populations (Tyler et al. 2006). Both consumer and resource constraints simultaneously may limit oak recruitment (Macdougall et al. 2010). However, we hypothesize that the relative importance of these factors in limiting recruitment may vary systematically across the species’ distribution with a regional precipitation gradient. Based on the literature on variation of top-down and bottom-up regulation with intra-annual precipitation, we hypothesized that top-down forces -- herbivores -- would be more important in limiting valley oak recruitment in mesic areas of the distribution, and that bottom up forces -- factors impacting water availability -- would be more important in limiting recruitment in xeric areas of the distribution (Figure 8). To explore this hypothesis, we combined analysis of existing experiments with a field study of factors associated with oak regeneration or its absence at 26 sites across the species distribution. Our work addresses a critical gap in trophic cascades theory on how plant population regulation may shift across regional-scale spatial resources gradients.

**Figure 8: Conceptual Framework: the Relative Importance of Top-Down and Bottom-Up Regulation to Oak Recruitment Shifts along a Regional Precipitation Gradient**
2.2 Methods

2.2.1 Study System

Endemic to California, valley oak (*Quercus lobata*) is thought to experience low recruitment at the sapling life-stage (reviewed in Tyler et al. 2006 and Zavaleta et al. 2007), like many other species of oak (Abrams 2003), and is showing long-term declines in certain populations (Brown and Davis 1991). The species distribution spans the California Coast Ranges, Central Valley and Sierra Nevada foothills (Griffin and Critchfield 1972), all in a Mediterranean climate with rainy winters and prolonged summer droughts. Our study included grazed and ungrazed sites and an elevation range of 300-1400 m. Sites included mixed valley oak, blue oak (*Quercus douglasii*) and live oak (*Quercus agrifolia*) woodlands; mixed oak/conifer woodlands; and pure valley oak woodlands. Most sites had a dominant annual grass understory (especially *Bromus* spp. and *Avena* spp.), with a historic understory thought to have consisted largely of native perennial bunch grasses and forbs (Barry 1981).

2.2.2 Analysis of Existing Experiments

To explore how the effects of herbivory, herb competition and water additions, as reported in individual experimental studies, varied with study-site specific climate, we combed the literature for studies on valley oak seedling performance, in which these treatments were applied and data were collected in a comparable manner, with a threshold of at least 5 comparable studies for inclusion in our analysis. With these criteria, we selected 9 planting experiments on herbivory in which both above and below ground exclosures were used, and 9 experiments on herb competition in which weeding treatments were applied. In both sets, we looked at seedling survival data collected after a single growing season and calculated an effect size (log of the response ratio, Hedges 1999) for each treatment from each experiment. We used a linear regression to test the relationship between study site-specific precipitation data (PRISM Climate Group, Oregon State University, http://www.prismclimate.org, created 2009) and the effect size of the treatments.

2.2.3 Field Study Sites

Because natural recruitment was absent at most research reserves, to identify sites in which we could study natural recruitment, we contacted managers of public lands, NGOs and ranchers’ organizations throughout the species distribution (N=215 land managers). We interviewed 114 respondents, and from these identified 16 sites with valley oak sapling recruitment for inclusion in this study. We also included sites that had been previously surveyed (regardless of recruitment status), which we identified through the literature (N=10 resurvey sites) (N=26 total study sites) (Figure 9). Sites ranged from 0.5-1 km² in area. We identified sites as ‘recruiting,’ when there was more than 1 sapling (1.3- 9 cm at base diameter and >0.5 m in height (Zavaleta et al. 2007)) occurring within a 1 km² area. In 14 sites we were able to establish discrete recruiting and non-recruiting areas for within-site comparative analysis (in other sites, sapling recruitment was continuous throughout the accessible stand of adults (N=9)). All non-recruiting and recruiting areas were proximate to each other as part of a continuous stand of valley oak adults. Non-recruiting areas were defined as at least 50 m from any valley oak sapling but within 50 m of a mature adult tree. We excluded from our study areas that were
2.2.4 Field Surveys

In all sites, a field crew conducted a sweep of the entire site and took GPS coordinates for all valley oak saplings (N=4219). To interpret relationships between recruitment and water availability, we mapped springs and streams within each site. We used a Trimble GeoXH 2005, accurate to 0.5 m. To explore factors associated with successful recruitment, 6 m diameter plots were randomly established throughout recruiting and non-recruiting areas with approximately one plot per 1500 m². In recruiting areas, plots were established around randomly chosen saplings and in non-recruiting areas, at random points. In each plot we counted gopher mounds (Engeman 1993) and ground squirrel holes, as a proxy for information on below-ground activity (Romanach et. al. 2005); and recorded species and numbers of seedlings, presence/absence of canopy cover, and a geographic coordinate. To quantify herbaceous vegetation, three 1 m diameter subplots were placed at random throughout the 6 m diameter plot, in which we visually estimated percent cover and measured vegetation height at three random points. In resurvey sites, we established ten 50 m diameter plots, centered on a randomly chosen adult.
valley oak. In each 50 m diameter plot, we established one 6 m diameter plot and used the same plot sampling methods described above. If the resurvey site was found to support valley oak sapling recruitment, the same methods for mapping and surveying recruitment (described above) also were followed. Surveys were conducted between May and August 2009.

2.2.5 GIS and Statistical Analysis

We used ArcGIS 10 (ESRI, 2010), the CA Gap analysis (UCSB biogeography lab 1998, updated 2002) to identify the extent of valley oak distribution, and PRISM precipitation 30 year normals, (PRISM Climate Group, Oregon State University, http://www.prismclimate.org, created 2009). We created our own GIS layer with the locations of plots centers, saplings, and streams and springs. We measured the distance between each plot center and the nearest surface water body, and calculated a measure of insolation (an integrated measure of slope, aspect, elevation and cloudiness (Fu and Rich 2002)) at summer solstice for each plot from a digital elevation model (USGS National Elevation Dataset, cell size: 25 m, created 2009). From field survey data we derived measures of small mammal activity, herbaceous vegetation height, percent total cover and presence/absence of canopy cover for each plot. Height and percent cover were correlated in all plots so we removed percent cover from our analysis. Subplot measurements were combined to a plot-level mean, and we added together the measures of gopher and ground squirrel activity for an overall measure of small mammal activity.

For sites with discrete areas with and without recruitment (N=14), we divided the mean of each measured factor in the recruiting plots by the mean in the non-recruiting plots. With replication at the site level, we analyzed the overall effects of each factor by calculating whether the ratio of the mean of recruiting plots to the mean of the non-recruiting plots was different from one, with a one sample, one-tailed T-test. Because of small sample size and because site-level replication is a conservative measure we set alpha at p<0.1.

To evaluate effects of measured factors across the precipitation gradient, we related the effect on recruitment in each site (mean of recruiting plots/mean non-recruiting plots) to site-specific average annual precipitation (N=14). In analyzing herbaceous vegetation height, we split sites into grazed (N=7) and ungrazed (N=7) because cattle likely would be controlling productivity. We used an ordinary least squares linear regression to analyze the effects of stream distance and herbaceous vegetation height on recruitment along the precipitation gradient. We used a least median squares robust regression to analyze the relationship of insolation effects on recruitment along the precipitation gradient, because the insolation data contained outliers with large leverage. The relationship between the effect of small mammal activity and precipitation was non-linear, and there was no obvious model to fit. The data suggested that there were two distinct regions (above and below the median of precipitation) in which the effect and variability of small mammal activity differed. Therefore we used a T test on means to look for differences in small mammal effects in the higher and lower precipitation sites and a T test on variance to look at consistency of the effect. (Figure 10A-D). In order to explore the potential interactions between regional precipitation patterns and potential nurse-tree effects of shading and hydraulic redistribution, in all sites with sapling recruitment (N=23), we counted the
percentage of recruiting plots located under adult canopy cover in each site and analyzed these values and site-specific average annual precipitation with a linear regression.

**Figure 10(a-d): Effects of Mean Annual Site Precipitation on the Importance of Top-Down and Bottom-Up Factors to Valley Oak Sapling Recruitment on (a) Small Mammals, (b) Proximity to Surface Water, (c) Insolation, and (d) Herbaceous Vegetation Height in Ungrazed Sites**

A y-axis value of 1 indicates no difference between recruiting and non-recruiting areas, a value above 1 indicates a positive association between the factor and recruitment, a value below 1 indicates a negative association between the factor and recruitment.

To incorporate plot-level variance and to take advantage of the entire data set, we ran multiple regression models with replication at the plot level (N= 275 plots with sufficient data for analysis, N sites=26). We used a step-wise logistic multiple regression model to explore relationships between presence/absence of recruitment and the main effects and the interaction of precipitation with small mammal activity, distance to streams and springs, and insolation. We did not include herbaceous vegetation height because of the likely strong impacts of grazing in half of the sites in the data set. We included grazing crossed with small mammals as a model term because of anecdotal evidence that small mammals prefer grazed sites. In a stepwise general linear model, we investigated plot-scale relationships between density of saplings and the same factors above (N=271 plots with sufficient data for analysis, N sites=26). In both models we included secondary and tertiary terms up to a significance of .15 for added fit. We
checked for co-linearity among factors with a Pearson’s correlation matrix. We used AIC values to select the best model, with the requirement that any additional term decrease the AIC value by at least 7 points.

To explore alternative hypotheses, we ran linear regressions on the effects of precipitation and distance to surface water on small mammal activity. To determine whether patterns of seedling recruitment were similar to those of sapling recruitment, we used resurvey sites (N=10) to examine patterns of valley oak seedling recruitment and small mammal activity using the same methods described above for saplings and small mammals. In all data, we checked for violations of homogeneity of variance and normality and transformed when necessary. We analyzed timing of survey with all variables to ensure that patterns were not due to season. Statistical analyses were performed using SYSTAT 12 (Systat Software Inc., San Jose, CA, USA).

2.3 Results

2.3.1 Analysis of Experimental Studies

The effect size of herbivore exclosures in individual planting experiments increased with study site-specific average annual precipitation (P=0.045, adj R²=0.379, F=5.89, DF=1, N=9) (Figure 11). However, we failed to detect a significant trend between the effect size of herb competition in individual planting experiments and study site-specific average annual precipitation (p>0.05).

Figure 11: The Effect of Study Site-Specific Average Annual Precipitation on the Effect Size of Herbivore Exclosures on Valley Oak Seedling Survival across Multiple Planting Experiments

A y-axis value of 0 indicates no effect, below 0 indicates a negative effect, and above 0 indicates a positive effect.
2.3.2 Field Study

Across all sites where we compared discrete recruiting and non-recruiting areas (N=14), we found that areas with saplings had less small mammal activity (p=0.088) and were closer to surface water (streams and springs) (p<0.001) than areas without saplings (Figure 12). There was a mean of two ground squirrel holes and four gopher mounds in each recruiting 6 m diameter plot. We failed to detect a significant difference in herbaceous vegetation height and insolation between recruiting and non-recruiting areas (Figure 12).

Figure 12: The Effect of Small Mammal Activity, Distance to Surface Water, Insolation and Herbaceous Vegetation Height on Oak Sapling Recruitment in Field Sites with Discrete Recruiting and Non-Recruiting Areas

A y-axis value of 1 indicates no difference between recruiting and non-recruiting areas, a value above 1 indicates that the factor was higher in recruiting areas, a value below 1 indicates that the factor was lower in recruiting areas. Standard error shown.

The strength of the effects of small mammal activity, herbaceous vegetation height, distance to surface water and insolation changed with site-specific average annual precipitation (Figure 10A-D). The effect of small mammal activity on sapling recruitment was consistently negative in the higher precipitation sites and became more positive and more variable in lower precipitation sites (Figure 10A): the lower precipitation sites (below the median of 540 mm average annual precipitation) had a mean value of 1 (indicating no effect) in contrast to the higher precipitation sites with a mean value below 1, indicating a negative effect of small mammals (p=0.042; means: 1.0, 0.472).

The effects of multiple drivers of water availability on sapling recruitment decreased with precipitation. In lower precipitation sites, recruiting areas were closer to surface water than non-recruiting areas (OLS regression, p<0.001, adj R²=0.555, F=17.23, df=12, N=14) (Figure 10B). In sites above 750 mm of annual average precipitation, recruiting areas were of equal distance or further from surface water than non-recruiting areas. Precipitation also had a significant
effect on the relationship between insolation and recruitment (LMS regression, p<0.05, R²=0.4, df=12, N=14) (Figure 10C). In lower precipitation sites, recruiting areas had lower insolation than non-recruiting areas and in higher precipitation sites, recruiting areas had higher insolation than non-recruiting areas. In ungrazed sites, the effect of herbaceous vegetation height on sapling recruitment was stronger in lower precipitation sites, (OLS regression, p=0.044, adj R²=0.508, F=7.196, df=12, N=14) (Figure 10D). The direction and magnitude of difference in vegetation height shifted along a precipitation gradient, with shorter vegetation in recruiting areas than in non-recruiting areas in lower precipitation sites and taller vegetation in recruiting than in non-recruiting areas in higher precipitation sites. This relationship was not seen in grazed sites. Vegetation height was correlated with total percent cover (p=0.004, adj R²=0.811). In all recruiting sites, percent of recruiting plots under the canopy decreased as precipitation increased (p=0.013, adj R²=0.835, F=7.282, df=21, N=23) (Figure 13).

Figure 13: Percent of Plots with Valley Oak Saplings under Canopy in Each Study Site, across a Precipitation Gradient

In a general linear model predicting sapling density, the terms in the best fit model were (1) distance to surface water, (2) an interaction between precipitation and surface water distance, and (3) an interaction between precipitation and small mammal activity (p=0.015, adjusted R²=0.026, F-ratio=3.518, N=271) (Table 1). In a logistic multiple regression model predicting the presence/absence of recruitment in each plot, the terms in the best model were (1) distance to surface water, (2) an interaction between precipitation and surface water distance and (3) an interaction between precipitation and small mammals (p<0.0001, Nagelkerke’s R²=0.131, df=3, N=275) (Table 2).
2.3.3 Other Factors Potentially Driving Small Mammal Activity

Across all plots, we saw an increase in the absolute amount of small mammal activity with precipitation (P<0.001, adj. R²=0.028, DF=1, F=11.68, N=361). In our resurvey sites, patterns of seedling recruitment, small mammal activity and precipitation were similar to the patterns we saw with saplings (P=0.059, adj. R²=0.297, DF=1, F=4.804, N=10).

2.4 Discussion

We undertook these analyses to explore shifts in the relative strength of top-down vs. bottom-up forces on *Q. lobata* sapling recruitment, as influenced by a regional precipitation gradient. Our results suggest that the relative importance of these factors shifts predictably over the gradient. As precipitation increased, top-down effects - small mammal herbivory - became relatively more important in regulating sapling recruitment. As precipitation decreased, bottom-up effects - factors mediating drought stress and water availability - became relatively more important in regulating sapling recruitment.

2.4.1 Top-Down Drivers: The Effects of Herbivory Increase with Precipitation

Several lines of evidence suggest that small mammalian herbivores – top-down forces – became relatively more important to recruitment as precipitation increased. Our analysis of herbivore
Exclosure treatment effects in the experimental literature showed an increasing effect of herbivores on seedling survival with increasing study-site specific precipitation. Results of our field study of sites with discrete recruiting and non-recruiting areas showed consistent negative effects of small mammal activity in the higher-precipitation sites, but not in the lower-precipitation sites. In our multiple regression models, the term ‘small mammals crossed with precipitation’ emerged as more significant than small mammals alone in predicting both presence/absence and densities of saplings. In both models, this interaction was driven by a stronger negative relationship between small mammals and saplings in higher-precipitation sites. In total, these results, drawn from multiple analyses and scales, indicate that top down forces -- small mammals -- were relatively more limiting to valley oak sapling recruitment at higher-precipitation sites.

The increase in the strength of small mammal effects that occurred in higher precipitation sites could relate to an overall increase in herbivore pressure. Previous work on the impacts of precipitation or soil moisture on small mammal activity is inconclusive, with some showing positive associations between precipitation or soil moisture and gopher activity (Romanach et al. 2005) and others showing no relationship (Bandoli 1981). In our study, we saw an increasing trend in overall small mammal activity with precipitation, but while small mammal activity in non-recruiting plots increased with precipitation, in recruiting plots it stayed relatively constant (data not shown). This may indicate that while overall numbers of small mammals increased along the precipitation gradient, there may be a threshold, reached in higher precipitation sites, over which sapling recruitment is unlikely.

Because of the correlative nature of our data, it is possible that small mammals were responding to saplings rather than limiting saplings or that another factor is affecting both. A demonstrated preference by ground squirrels for lower cover (Balph and Balph, 1996), by gophers for higher soil cohesion (Vleck 1981), higher soil moisture (Romanach et. al. 2005) but not saturated soils (Ingles 1949), and by both gophers and ground squirrels for more productive vegetation and certain species (Eviner and Chapin 2005) may impact the distribution of small mammal activity. However, several lines of argument support the hypothesis that small mammal activity was driving sapling distributions more than that saplings were driving small mammal activity: (1) In our resurvey sites, patterns of seedling recruitment, small mammal activity and precipitation were similar to the patterns we see with saplings, small mammal activity and precipitation. That independent of saplings, these similar patterns of seedling recruitment and small mammals existed suggests that small mammals were driving the distribution of sapling recruitment rather than saplings driving small mammal distributions. (2) Ground squirrel burrow systems can remain in place for many decades if undisturbed (personal communication T. Salmon) and gophers often remain in areas that they inhabit if there is not a reason to move (personal communication J. Reichman). As our dendrochronological analysis (Mclaughlin and Zavaleta in review) places recruitment dates from seedling to sapling life stages at an average of 10 years previous, the general locations of burrow systems are likely to have been established prior to sapling recruitment, suggesting that small mammal distributions were in place prior to sapling recruitment. (3) Soil moisture may affect small mammal distributions, potentially confounding the effects of distance to stream and small mammal activity on saplings. However,
we did not see similar trends in small mammal activity and saplings relative to stream distance
(unpublished data), indicating that saplings and small mammals were responding
independently to soil moisture gradients away from surface water. Soils in our plots were
never fully saturated as to exclude small mammals.

Contrary to our expectations, nearly half of the lower precipitation sites showed positive
associations of small mammal activity with recruitment (Figure 10A). This could have resulted
from the role of gophers and ground squirrels as seed distributors (Griffin 1976), and disturbers
(Hobbs and Mooney 1991), potentially ‘weeding’ around an established seedling or sapling,
leaving it in place but removing the surrounding shallower rooted vegetation surrounding
(personal observation). While deer may also browse oaks (Tyler et al. 2006), relative impacts of
deer in relation to small mammal herbivory on a closely related species (Quercus garryana) were
minimal (Macdougall et al. 2010), and because of the broad scale of deer movement, we could
not address deer herbivory in this study.

2.4.2 Bottom-Up Drivers: The Effects of Water Availability Decrease with Precipitation

Multiple factors impacting drought stress and water availability showed qualitatively similar
trends, becoming increasingly important in regulating sapling recruitment at the dryer end of
the precipitation gradient. Streams and springs are areas where groundwater reaches the
surface, indicating relatively high water availability to terrestrial plants in the proximate
surrounding rooting zone (Bilby 1988, reviewed in Mikkelson and Vesho 2000, Castello et al.
2000). Groundwater withdrawal in California has increased substantially over the last half
century (Howard and Merrifield 2010). Work on blue oak has shown higher productivity of
herbaceous vegetation under adult trees when summer water potentials were high (indicating
groundwater access), than when summer water potentials were low (Callaway et al. 1991). This
suggests that oaks compete with herbaceous vegetation for soil moisture in the upper horizons
and is consistent with the theory that seedling and sapling performance may vary with
groundwater availability. In our study, distance to surface water (a proxy for groundwater
accessibility) emerged as the most consistently significant factor impacting recruitment, and the
magnitude of the effect increased with lower precipitation. We saw this pattern in sites with
discrete recruiting and non-recruiting areas: in lower-precipitation sites, we found adults
throughout the site, but found saplings only in close proximity to streams and springs; in
higher-precipitation sites, recruitment was not constricted around streams and springs.
Distance of saplings to surface water averaged 69.6 m at the dryer end of the precipitation
gradient and 168.5 m at the wetter end of the precipitation gradient (McLaughlin and Zavaleta
2012.) We also saw this pattern in our multiple regression models, where the interaction
between distance to surface water and precipitation strongly predicted both the
presence/absence and density of saplings at the plot level across all study sites. In both models,
the interaction was driven by an increase in the strength of the relationship between distance to
surface water and recruitment with lower precipitation. Oak seedlings can resprout repeatedly
after the stem has been disturbed by fire or browsing (Tyler et al. 2006), and thus older
seedlings may develop a long tap route potentially tapping the water table and facilitating a
transition to the sapling phase.
The impact of canopy cover on recruitment shifted along the precipitation gradient, with % recruiting plots under canopy increasing in the lower precipitation sites, while total canopy cover in lower precipitation sites was substantially lower than in higher precipitation sites. Contrary to an expected Janzen-Connel effect of lower offspring survival with proximity to a parent (Janzen 1970, Connel 1971), adult facilitation of offspring, through shading or hydraulic redistribution of groundwater into upper soil layers (Dawson 1993, Caldwell et al. 1998), may play an important role in supporting sapling recruitment in lower precipitation sites. In higher precipitation sites, host-specific pathogens or predators may be facilitated by higher moisture availability (Givnish 1999). Thus, density dependent mortality, in addition to lower drought stress and potentially more light limitation, could explain the patterns we saw of lower sapling recruitment under canopy at higher precipitation sites.

Microtopographic effects on sapling recruitment also shifted across the precipitation gradient of our field sites. Topographic positioning on a landscape can have a large effect on the amount of solar radiation experienced by an individual (Dobkin et. al. 1987). Puerta-Pinero and Gomez (2007) showed that microclimatic differences in insolation affected seedling performance in Quercus ilex. In sites where we compared recruiting and non-recruiting areas, the effects of insolation on recruitment increased with decreasing precipitation (Figure 10C), with recruitment clustered in areas of lower insolation at lower-precipitation sites. However, neither insolation nor insolation by precipitation emerged as a significant term in the multiple regression models, potentially indicating the relative importance of other factors and reflecting the high variability of topography across sites.

Experimental work suggests that annual grasses compete strongly for water with small oaks (Gordon et al 1989, Danielson 1990, Danielson and Halvorson 1991). In our field study, we interpreted a lower herbaceous vegetation height in recruiting than non-recruiting areas as indicating either (1) competition between the sapling and the surrounding herbaceous vegetation, such that the productivity of herbaceous vegetation is lower when the sapling is present and/or (2) that saplings are growing in areas where other herbaceous vegetation is less productive and thus less competitive. While the current height of herbaceous vegetation in recruiting areas would not have had a direct impact on the prior establishment of a valley oak recruit, the shift in relative height between recruiting and non-recruiting areas across a rainfall gradient indicates changing levels of competition between the species. We found that the effect of herb competition decreased with precipitation in ungrazed sites (Figure 10D). In lower-precipitation sites, we saw the largest difference in height between recruiting and non-recruiting areas across a rainfall gradient, with shorter herbaceous vegetation in recruiting areas than in non-recruiting areas, and in higher-precipitation sites, we saw the opposite relationship.

2.4.3 Conservation Implications and Conclusions

Recruitment failure in many species of oak, and potential cascading impacts on other native species, is a pressing conservation concern. By focusing on natural populations in a broad range of study sites, we address how predictable variation in environmental forces may be driving these patterns of decline. Our study reconciles conflicting results in the literature on valley oak recruitment limitation: while both top-down and bottom-up factors impact
recruitment, these factors vary systematically along a regional spatial precipitation gradient. Our results can be used to anticipate the relative importance of these drivers, helping guide conservation and restoration strategies across the species distribution. For example, at dryer sites, management strategies that protect riparian areas and maintain water table levels could increase the likelihood of recruitment. Understanding the multiple dynamic factors regulating how particular species respond to environmental stressors across regional resource gradients is fundamental to the development of effective conservation in the context of global change. Continued integration of a more explicit and representative spatial dimension into community ecology is integral to the continued development of theory on resource versus consumer-based limitation of populations.
CHAPTER 3: 
Missing Young Cohorts Found: an Assessment of 
Valley Oak (Quercus Lobata) Recruitment in Natural 
Populations

3.1 Introduction

Long-lived species may be threatened in ways that are undetectable in the current distribution 
of adults due to reproductive bottlenecks in younger life stages. The phenomenon of missing 
young cohorts in tree populations has been observed in multiple genera: Populus (Ripple and 
Larson 2000), Acer (Belden and Pallardy 2009), Pinus (Perrakis and Agee 2006) and others 
(Lopez and Terborgh 2007). Quercus species appear prone to recruitment failure (reviewed in 
Abrams 2003, Pulido and Diaz 2005, Acacio 2007). Recruitment failure is of particular concern in 
light of forest declines worldwide (Allen et al. 2010).

Valley oak, endemic to the California floristic province, appears to be declining with potential 
cascading impacts on other native species and important ecosystem services (Pavlick 1991). 
Now reduced to 10% of its pre-European settlement extent, the current distribution spans the 
California Coast Ranges, Central Valley and Sierra Nevada foothills, all in a Mediterranean 
climate with rainy winters and summer droughts. Mortality rates in adults outpace observed 
recruitment into the canopy (Brown and Davis 1991) and >85% of past survey studies reported 
the complete absence of saplings in natural populations (Zavaleta et al. 2007). These 
demographic patterns suggest a high risk of future losses in this species. Most of the species 
distribution occurs on private rangelands, and less than 4% is formally protected (Underwood 
et al 2009), making the study and conservation of this species uniquely challenging.

Extensive changes in California oak woodlands since European settlement could help explain 
valley oak recruitment failure. Potentially increasing drought stress on young oaks: invasive 
annual grasses now dominate an understory thought to have consisted previously of native 
forbs and grasses (Gordon et al. 1989), likely increasing water competition with young oaks 
(Gordon et al. 1989, Danielson and Halvorson 1991) and increased regional N deposition likely 
 favors annual grasses (Allen et al. 2002); temperatures have increased approximately 1 degree C 
regionally (Ladochy et al. 2007); ground water levels have decreased (Howard and Merrifield 
2010); and increased tropospheric ozone levels, may reduce seedling WUE (Grulke et al. 2007). 
Fire and land use have changed, potentially impacting recruitment: indigenous Californians 
managed oak woodland ecosystems through fire (Anderson 2007); fire suppression has 
increased (Keeley and Fotheringham 2001); and wild grazers have been replaced by domestic 
grazers (Anderson 2005). In concert or individually, these changes in California oak woodlands 
may have increased stress on oak seedlings.

Recruitment in valley oaks appears to have been limited for decades, but research gaps have 
prevented a comprehensive assessment of the species’ conservation status (Tyler et al. 2006). 
Early observational work documented demographic patterns but did not relate environmental
factors to recruitment. More recently experimental work has focused on identifying mechanism for recruitment failure, however most of these studies were conducted at a handful of research reserves, a limited representation of the species distribution (Tyler et al. 2006). Experimentally, several drivers have been shown to impact seedling performance, including wild herbivores, domestic grazers, herb competition and water availability (reviewed in Tyler et al. 2006), but the importance of these drivers on recruitment in natural populations remain unclear.

Our study combines historical resurveys, interviews with land stewards, field surveys targeting natural recruitment, GIS analysis and dendroecology to address these current gaps in the research and assess the conservation status of valley oaks in natural populations. We address the questions of (1) how the status of sapling recruitment in valley oak woodlands has changed over the past 40 years (2) whether recruitment patterns are explained by changes in fire, grazing or climate; and (3) whether recruitment is synchronous within or across sites, confined to particular years or related to specific regional-scale events. Our approach suggests a framework for studying and conserving other long-lived species experiencing recruitment failure.

3.2 Methods

We focused our study on sapling rather than seedling recruitment as the sapling stage appears to be the main bottleneck to reproduction in valley oak (Tyler et al. 2006). Saplings also have lower mortality and a greater chance than seedlings of surviving herbivory (Bartolome et al. 2002), drought, and fire (Swiecki and Bernhardt 2002), making sapling rather than seedling recruitment a better indicator of future population viability.

3.2.1 Field Sites

All survey sites had dominant valley oak adult cover, and most sites had an annual grass understory (Bromus spp. and Avena spp.). Sites ranged from 0.5-1 km². We surveyed two sets of sites. Set 1, “targeted recruitment sites” (N=18), selected based on the presence of sapling recruitment and set 2, “resurvey sites,” selected based on the existence of previous surveys (N=10) (Figure 14).
Because natural recruitment was absent at most research reserves, we contacted managers of public lands, NGOs and ranchers’ organizations throughout the species distribution to identify sites to study natural recruitment (N=215 land managers). We interviewed 114 respondents, and from these identified 18 sites with valley oak sapling recruitment. We identified sites as “recruiting” when there was more than 1 sapling (1.3-9 cm at base diameter and >0.5 m in height (Zavaleta et al. 2007)) occurring within a 1 km² area. Sapling densities per site ranged from 2 to 900 saplings per km². We excluded from the study areas that were highly disturbed or...
within 5 m of human development; and areas with mixed *Q. lobata* and *Q. garyana* adults, which overlap in the northern part of the *Q. lobata* distribution and have morphologically indistinguishable saplings. Thus, our conclusions are most applicable to oak woodland and savanna in the central and southern portions of the species distribution. Surveys were conducted between late May and August of 2009.

Zavaleta et al. (2007) identified 18 historic surveys on valley oak. Ten remained in our study based on our ability to relocate and access the site and quality of original data. We compared presence/absence instead of densities of saplings because quantitative data on sapling densities was insufficient in the original surveys.

### 3.2.2 Field Surveys

In all sites with valley oak sapling recruitment, a field crew conducted a sweep of the entire site and took geographic coordinates for all valley oak saplings. To explore factors associated with successful recruitment, 6 m diameter plots were randomly established throughout the site with approximately one plot per 1500 m². We mapped each plot with a geographic coordinate and in each plot recorded species and numbers of seedlings, and counted gopher mounds and ground squirrel holes. To quantify herbaceous vegetation, three 1 m diameter subplots were placed at random throughout each 6 m diameter plot, in which we measured vegetation height at three random points. For more detail on survey methods see (McLaughlin and Zavaleta 2012). In resurvey sites, we established 10 randomly located 50 meter diameter plots, centered on a mature adult valley oak. In each 50 m diameter plot, we established one 6 m diameter plot and used the same plot sampling methods described above. If the resurvey site was found to support valley oak sapling recruitment, the methods for surveying recruitment (described above) were followed. We gathered information on land-use history from site managers.

### 3.2.3 Dendroecology

We obtained sapling samples for dendroecological analysis at a subset of our sites. When possible, saplings were randomly selected, however land manager preferences also directed selection. We sampled 2-6 saplings at 10 sites that spanned a range of climate and land use, and measured diameter at base and height of each sample. We used the bottom surface for ring analysis. We sanded each sample, and counted and measured each ring under a microscope. We established a date of recruitment based on the earliest year present. Since young oak seedlings may resprout after the stem has been browsed (Tyler et al. 2006), our recruitment dates do not necessarily represent the date of seedling establishment, but represent the year in which the seedling remained above ground with a viable stem and began a successful transition to the sapling stage. We compared recruitment dates with PRISM average annual precipitation, Calfire fire history, and valley oak masting data from 1994-2009 (W. Koenig).

### 3.2.4 GIS Analysis

We used ArcGIS 10 (ESRI, 2010), the CA Gap analysis (UCSB biogeography lab 1998, updated 2002) to identify the extent of valley oak distribution and we created our own GIS layer with the locations of our plots centers, study site centers and all saplings. We identified the extent of the valley oak distribution covered by our phone and email inquiries to land managers and excluded all other areas of the distribution as described above (Figure 14). We used PRISM
3.2.5 Statistical Analysis

3.2.5.1 Resurveys

Because of the small N and high variability of resurvey sites, we set our alpha for resurvey site analyses at 0.1 (all other analyses use an alpha of 0.05). We used a Pearson Chi Squared test to compare the proportion of recruiting and non-recruiting sites during the first set of surveys and the 2009 resurveys. To look for changes in regional climate, land-use and fire history that might have been driving the overall increase in sites with sapling recruitment, we compared the 15 year periods before each original survey to the 15 year period between 1990 and 2005, in terms of fire history, mean average annual precipitation and grazing status (grazed or ungrazed). The 15 year time period was established by the recruitment dates of the oldest and youngest sampled saplings (Figure 15). We used a paired, two-tailed T test to compare the mean climate values for each resurvey sites before the 1st and 2nd sets of surveys, and a Pearson Chi Square test to look for differences in presence/absence of a major fire and presence/absence of grazing between the time periods before the first and second sets of surveys.

**Figure 15: Valley Oak Sapling Recruitment Took Place in at Least One of the Sample Sites in Every Year between 1991 and 2006 and in Multiple Years within Individual Sites**

The Y axis represents different sites and where saplings were sampled for dendroecological analysis, and the x axis shows date of recruitment for each sapling.
In order to look specifically at differences between the resurvey sites that had recruitment and did not have recruitment during the 2009 surveys, we compared average annual precipitation, maximum August temperatures, herbaceous vegetation height, small mammal activity and valley oak seedling densities in the sites that had sapling recruitment to the sites that did not have sapling recruitment in the 2009 surveys, with two-sample, two-tailed T tests, and a Pearson Chi Square test to look for differences in presence/absence of a major fire and presence/absence of grazing in the time period before the 2nd surveys. We also tested whether mean sapling densities at sites designated as research reserves were different than non-research reserves with a 2 sample, 2 tailed T test bootstrapped with 1000 resamples.

3.2.6 Recruiting sites
We mapped our targeted recruiting sites onto statewide climate and fire history maps and recorded average annual precipitation, maximum August temperatures and whether or not the site had experienced a fire between 1985 and 2005. In order to explore impacts of grazing on recruitment, we looked at plot densities of saplings in grazed and ungrazed sites with a two-tailed two sample T-test. To explore potential interactions between climate and grazing, we looked for climatic differences between the grazed and ungrazed recruiting sites, using a 2-tailed 2 sample T-test with a Bonferroni correction to compare average annual precipitation and maximum August temperatures.

3.2.7 Dendroecology
To establish the relationship between size and age in our sapling samples, we analyzed ring count and diameter at base, and ring count and height with linear regressions. To look for differences in sapling growth rates due to differences in climate or land use, we did an ancova on the relationship between size and ring count on grazed versus ungrazed sites and on a categorical delineation of high and low precipitation (above and below the mean).

To evaluate whether year of recruitment was associated with site- and year-specific precipitation, we compared precipitation values during recruitment years to the average values of all years over which recruitment took place according to our samples (1991-2005). To determine whether recruitment was associated with wetter than average precipitation years, we compared the ratio of site-specific precipitation from the recruitment year to the site-specific average precipitation (1991-2005) to 1 in a 1-tailed, 1 sample T test. We also used a general linear model to examine whether fire history (year of a major fire), valley oak annual masting and site- and year-specific precipitation predicted recruitment dates, including 1 year time lags for each factor. All statistical analyses were performed using SYSTAT 12 (Systat Software Inc., San Jose, CA, USA).

3.3 Results
3.3.1 Resurveys
There was a significant increase in sites supporting sapling recruitment between the original surveys and our 2009 resurveys (P>0.01) (Table 3). The period before the second (2009) survey was wetter than the period preceding the first survey in all sites (p<0.0001). We did not find significant differences in grazing or fire during the periods preceding each set of surveys. In
comparing the sites that did and did not support sapling recruitment in the 2009 resurveys, we found that herbaceous vegetation was marginally significantly higher in the sites that did not support recruitment (p=.071, T=2.01, N=10, DF=8). We did not find significant differences in average annual precipitation, maximum August temperatures, seedling densities or small mammal activity between the sites that did and did not support saplings in the 2009 resurveys (P>0.1). Resurveys showed sapling densities between 2 and 179 saplings per kilometer squared. The sites that were natural reserves had lower sapling densities (N=3, mean .66 saplings per K²), than sites that were not natural reserves (N=7, mean 76 saplings per K²), (P<0.05) (Table 3).

Table 3: Survey Sites with Recruitment, Climate, Grazing, and Fire History Status

<table>
<thead>
<tr>
<th>Site</th>
<th>Saplings</th>
<th>Precip</th>
<th>Grazed</th>
<th>Fire</th>
<th>Saplings</th>
<th>Precip</th>
<th>Grazed</th>
<th>Fire</th>
</tr>
</thead>
<tbody>
<tr>
<td>PO Hill</td>
<td>R</td>
<td>589</td>
<td>683</td>
<td></td>
<td>638</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sedgwick</td>
<td>R</td>
<td>552</td>
<td>638</td>
<td></td>
<td>660</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SA2</td>
<td></td>
<td>547</td>
<td>660</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plasket Ridge</td>
<td></td>
<td>486</td>
<td>21</td>
<td>683</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bear Trap</td>
<td></td>
<td>780</td>
<td>54</td>
<td>917</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chews Ridge</td>
<td></td>
<td>905</td>
<td>148</td>
<td>983</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nacimiento</td>
<td></td>
<td>526</td>
<td>179</td>
<td>617</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SA 1</td>
<td></td>
<td>512</td>
<td>42</td>
<td>611</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cheseboro</td>
<td></td>
<td>479</td>
<td>88</td>
<td>514</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jasper Ridge</td>
<td>R</td>
<td>615</td>
<td>2</td>
<td>694</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Sapling numbers in Survey 2 represent number of saplings per K². ‘R’ designates sites that are natural reserves.

3.3.2 Recruiting Sites

In total, we found 25 sites with valley oak sapling recruitment (Figure 14) with sufficient information for this study’s analyses, ranging in average annual precipitation from 421.2-974.2 mm with a mean of 610.6 mm, and maximum August temperatures from 23.5-34.6 C with a mean of 30.2 C. Seven of the 25 sites with sapling recruitment experienced a major fire in between 1985 and 2005. Twelve of the 25 sites were grazed. Numbers of saplings per site ranged from between 10 and 990. We failed to detect differences in sapling densities between grazed and ungrazed sites (grazed, mean= 3.5 saps per plot, ungrazed, mean=3.2 saps per plot) (P>0.05). Annual average precipitation was higher (P=0.004) and maximum August temperatures were lower (P<0.0001) in grazed than non-grazed recruiting sites (Figure 16).
Figure 16: Climate Variables Associated with Grazed and Ungrazed Sites with Sapling Recruitment

3.3.3 Dendroecology

Recruitment was not restricted to particular years, took place in at least one of the sampled sites in every year between 1991 and 2006, and occurred in multiple years within each individual site (Figure 15). There was a weak association of recruitment with years of higher than average rainfall ($P<.067$, $T=1.5$, $N=43$, $DF=42$). Fire history and masting (with 1 year time lags) did not improve predictions of recruitment in a general linear model. Diameter at base significantly predicted ring counts in saplings ($P<.0001$, adj. $R^2=.45$, $F=37.1$, $N=45$) (Figure 17), however we did not detect a relationship between ring count and height ($p>0.05$). We also did not find significant differences in the relationship between ring counts and diameter between grazed and ungrazed sites (Figure 17) or between high and low precipitation sites ($P>0.05$).
We did not detect a difference in sapling growth rates between grazed and ungrazed sites.

3.4 Discussion

Our results show more recruitment in valley oak woodlands than had been reported in previous work (Tyler et al. 2006) and we saw a seven fold increase in sites supporting sapling recruitment over time (Table 3). Saplings can recruit in large numbers in a variety of land-use types and climates. The absence of valley oak saplings is not a persistent condition across the distribution, and our results do not support an argument for enormous, rare recruitment events.

3.4.1 Resurveys: What Accounts for Increased Recruitment over Time?

We expected that grazing (Griggs 1986), fire (Van Leer and Watt 1993), climate (Kueppers et al. 2005) and herbivory and herb competition (reviewed in Tyler et al. 2006) limit recruitment in natural populations of valley oaks. To explain the increase in recruitment in our resurvey sites, we looked for fire, climate and land-use signals that might have triggered a large-scale recruitment event between surveys. We also looked at differences between sites that did and did not support recruitment in the second survey. Our sample size for resurveys (N=10) made it difficult to draw conclusions across all sites, thus we discuss below some general trends within regional groups to prompt further research.

We did not detect regional changes in fire or grazing between the first and second surveys. However, we found that average annual precipitation was higher in the time period preceding the 2009 resurveys than in the time periods preceding the original surveys, indicating that the
overall increase in recruitment during the second survey may be related to a preceding period of wetter years. We note that our resurvey sites represent a disproportionately wet portion of the species distribution and thus may overestimate the current state of recruitment in the species.

In comparing the resurvey sites with and without recruitment, we found that neither climate, grazing, fire history nor small mammal activity predicted which sites supported recruitment. Seedling densities did not differ between sites with and without sapling recruitment, thus sapling recruitment may be responding to factors distinct from those controlling seedling recruitment (Davis et al. 2011), and the presence of seedlings may not ensure successful recruitment into the adult population. The only marginally significant factor differentiating resurvey sites that did and did not support recruitment was herbaceous vegetation height, indicating a potential effect of herb competition in these sites. However, recruitment at each individual site may not be responding to the same drivers, and some general patterns emerge when we group the sites by climate.

The three coolest and wettest of the resurvey sites, in the Los Padres National Forest (Chews Ridge, Bear Trap, and Plaskett Ridge), all picked up sapling recruitment between the first and second surveys. Changes in climate and fire between surveys could explain this change in recruitment. Average annual precipitation was higher in the time period before the second survey than the first survey, and all three sites experienced one of the largest fires recorded in California between survey periods. The paper reporting the original surveys anecdotally reported dense growth of pine seedlings and saplings in the understory, with a suggestion by the author that pines might eventually replace oaks in those systems (Griffin 1976). Our survey data did not detect dense pine growth in the understory (unpublished data). A lack of fire in the above resurvey sites prior to the first survey may have allowed for the dense accumulation of pines in the understory, which have been shown to inhibit oak recruitment in other systems (Van Lear and Watt 1993). In Arizona, Barton (1999) found that the proportion of oaks to pines increased in a post-fire recovery period. The 1977 fire in the three Los Padres resurvey sites, followed by a series of 6 consecutive wetter-than-average years, may have facilitated the recruitment of young oaks in this system. Grazing, present continuously before both surveys, does not appear to drive the change in recruitment in these sites.

Three drier sites that picked up sapling recruitment in the second survey were Chesebro Canyon, in the Santa Monica Mountains and Nacimiento and SA 1, in Fort Hunter Liggett. While none of these sites experienced a major fire between surveys, there were changes across sites in both grazing and climate. Precipitation was higher in the time period before the second surveys than before the first surveys. Recruitment at each of these sites was highly constricted around surface water (Mclaughlin and Zavaleta 2012), indicating drought stress limitation on recruitment. All three sites were grazed before the first survey and grazing was removed between the two sets of surveys, consistent with the theory that grazing may impact recruitment in these systems. Potential impacts of grazing and possible interactions between grazing and climate are discussed further below.
3.4.2 Episodic Recruitment Events?

Recruitment failure in valley oak could be explained by rare, episodic recruitment events in response to regional drivers (Mensing 1988). Therefore, we examined whether recruitment was clustered in particular years within and across sites, consistent with this theory. Our results support an argument for the importance of site-specific conditions over an episodic regional-scale driver in facilitating recruitment. We saw high asynchrony both across and within sites in the timing of recruitment (Figure 15). Recruitment occurs in at least one site in every year over the time period covered by our samples (1991 to 2006), and there are multiple recruitment dates in each individual site. We found a weak correlation between recruitment years and wetter-than-average years but also saw some recruitment in dryer-than-average years, indicating that climate may be an important but not synchronous driver of episodic recruitment across sites. We saw no correlations between fire and grazing history and recruitment dates. Overall these findings suggest that repeated recruitment occurred in response to a suite of site-specific characteristics or conditions, rather than in response to a regional environmental signal prompting a large-scale recruitment event. However, as Davis et al. (2011) suggest, episodic recruitment could occur in response to complex suites of events such as synchronously timed wet years and masting events. We did not detect this trend in our model of recruitment dates, weather and masting data, however our masting data was not site specific, and a model including more comprehensive, site-specific masting data may perform better. Alternatively, such synchronously timed events may create seedling banks that develop extensive root structures, allowing them to resprout after being browsed. The recruitment of persistent seedling banks after high rainfall and mast years could allow seedlings to establish and then take advantage of subsequently reduced herbivore pressure (Macdougal et al. 2010, Davis et al. 2011) or other favorable local conditions or microhabitats and recruit into the sapling stage in subsequent years.

We found a strong correlation between diameter at base and ring count (Figure 17), contrary to reports in the literature (Knudsen 1984) that size and ring count have weak correspondence in this species. Size structure analysis may be a better tool for measuring population dynamics of valley oak than was previously thought (Tyler et al. 2006).

3.4.3 What Factors are Important in Limiting Recruitment in Natural Populations?

Valley oak saplings likely are limited by multiple factors. In addition to consumer-based limitation (Davis et al. 2011), water availability appears to be important in controlling sapling recruitment. High rainfall years have been associated with higher emergence rates of valley oak seedlings in planting experiments (Davis et al. 2011). Sites with sapling recruitment were overall cooler and wetter than the adult distribution on average, and shorter distances to surface water were associated with sapling recruitment (McLaughlin and Zavaleta 2012). Further supporting this theory, in our resurvey study, a period of wetter years was associated with a seven-fold increase in sites supporting sapling recruitment. We also found that herbaceous vegetation height (a proxy for herb competition for water availability) was the only factor that differed in resurvey sites with and without recruitment. However, the fact that we did not detect a difference in precipitation between sites that did and did not pick up recruitment during the second survey, and that we found only a weak association of wetter
than average rainfall years with sapling recruitment dates, indicate that water availability is not
the only factor driving sapling recruitment.

Valley oak saplings occur near human development even when absent in nearby oak
woodlands (Kuhn 2010). Many of the recruiting sites we located were in heavily disturbed oak
woodlands, including recreational areas, active military areas, and working rangelands.
Human disturbance may reduce herbivore pressure (Kuhn 2010). It also can remove annual
grasses that compete strongly with seedlings for water, comparable to cases where gopher
disturbance to annual grasses allowed for the reestablishment of native forbs (Hobbs et al.
2004).

Well-timed grazing also could remove competition from around oak seedlings. While it has
been argued that livestock grazing is responsible for recruitment failure (Griggs 1986), and there
is evidence that grazing exclosures can improve seedling performance, studies do not show a
consistent negative effect of grazing on recruitment or a consistent positive effect of removing
cattle (Tyler et al. 2006). Several findings from this study indicate that grazing can be
compatible with oak recruitment. Nearly half (46%) of our recruiting field sites were grazed, as
were half of the resurvey sites that picked up recruitment. We did not see differences in
recruitment densities in grazed versus ungrazed sites, and tree ring analysis indicated similar
sapling growth rates in grazed and ungrazed sites. Our results do not support the argument
that grazing is the primary driver of sapling recruitment failure in natural populations.

Climate and grazing may interact to determine impacts on young oaks. Multiple site managers
interviewed for this study indicated that climate and availability of alternative vegetation were
important factors in whether or not cattle would browse oak seedlings. Recent studies in which
winter/spring grazing was beneficial to oak seedling performance when cattle were removed
during the driest part of the season (Tyler et al. 2008) corroborate the theory that grazing may
be compatible with valley oak conservation under some circumstances, and that climate and
grazing may interact in impacting young oaks. Further, we found that grazed sites with
recruitment were wetter and cooler than ungrazed sites with recruitment (Figure 16). We also
observed that in the three wettest resurvey sites that picked recruitment, grazing was present
through both survey periods, however at the three driest sites that picked up recruitment,
grazing was removed between survey periods. In addition to reduced grazing pressure on oak
seedlings due to the availability of other vegetation, higher precipitation sites also may be more
resilient to grazing because of saplings are less restricted to surface water than in dryer sites
(McLaughlin and Zavaleta 2012), avoiding the concentrated impacts of cattle convergence
around riparian areas. However, we also saw grazing and oak recruitment in drier-than-
average sites and in sites with year-round grazing, indicating that other factors aside from
climate and grazing also drive recruitment.

3.4.4 Conclusions
Our results emphasize the importance of reconciling recent trends toward a mechanistic focus
in ecology with the roots of the discipline: natural history and broad scale observation (Sagarin
and Pauchard 2010). They also suggest that complex conservation issues, such as biodiversity
loss in long-lived species, require a holistic approach that transcends the boundaries of research
reserves. Had we focused only on research reserves in this study, we would have concluded that sapling recruitment in valley oaks was absent or rare, as is asserted commonly in the literature. Yet this is not the case across the species distribution, which includes a wider range of climate and land-use regimes. Though they provide invaluable research environments, reserves may not be representative of species distributions in terms of climate and land-use. A focus on work solely from these places may contribute to a misunderstanding of a species’ conservation ecology. Our findings illustrate the need for caution in over-extending conclusions derived from ecological conditions on research reserves.

Drivers of valley oak recruitment are complex and depend on interacting local and regional factors. Collaboration with private landowners and land stewards is critical to understanding important interactions with land use and to developing viable conservation strategies. Much of the recruitment we documented occurs on rangelands and heavily used recreational lands, and the species’ preservation will depend heavily on matrices of public and private lands.
REFERENCES

Predicting Species Responses to Climate Change: Demography and Climate Microrefugia in California Valley Oak (Quercus Lobata):


Danielson, KC (1990) Seedling growth of Quercus lobata Nee (valley oak) and the competitive effects of selected grassland species. M.Sc. Thesis, California State Univ. at Los Angeles, CA.


**Shifting Bottom-Up and Top-Down Regulation of Oak Recruitment across a Regional Resource Gradient:**


**Missing Young Cohorts Found: an Assessment of Valley Oak (Quercus Lobata): Recruitment in Natural Populations:**


Ecological Applications 13: 1355-1374.


Kuhn, B. A. 2010. Road systems, land use, and related patterns of Valley oak (Quercus lobata Nee) populations, seedling recruitment, and herbivory. University of California at Santa Barbara, California, USA.


