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CONSTRAINTS ON ESTABLISHMENT OF EMORY OAK AT LOWER TREELINE

by

Heather Lynn Germaine

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A Thesis Submitted to the Faculty of the

SCHOOL OF RENEWABLE NATURAL RESOURCES

In Partial Fulfillment of the Requirements  
For the Degree of

MASTER OF SCIENCE

WITH A MAJOR IN RENEWABLE NATURAL RESOURCE STUDIES

In the Graduate College

THE UNIVERSITY OF ARIZONA

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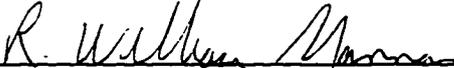
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### ACKNOWLEDGEMENTS

I owe a debt of gratitude to all who helped in the various stages of my research. Thanks to Guy McPherson, Jake Weltzin, Andy Hubbard, Tani Hubbard, Sheila Merrigan, Laurie Abbott, Alicia Nicholas, Shelly Lowe, Karin Rojahn, Debbie Angell, Rob Matson, Kim Suedkamp, Mechelle Meixner, and Rena-Ann P. Abolt for their many hours of excellent field assistance. Thanks to Bob Steidl for his help with data analysis. Special thanks to Guy McPherson for his dedication and guidance, to Jake Weltzin for his extra insights and encouragement, and to Steve Germaine for his never-ending support. I would also like to thank Bill Mannan and Dave Williams for their comments on earlier drafts of this thesis.

This research was funded by the United States Department of Agriculture Cooperative State Research Service, and was completed with the cooperation of the United States Army, in particular Sheridan Stone and John Miller.

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**ABSTRACT**

Encroachment of woody plants has occurred in many of the world's grasslands within the past 3 centuries. Mechanisms underlying these physiognomic shifts have not been adequately described. My objectives were to elucidate the roles of interference, herbivory, acorn maturation date and timing of precipitation on emergence and survival of Emory oak (*Quercus emoryi* Torr.) at lower treeline; and to evaluate how different frequencies of monitoring influence the results of demographic studies with woody plants. Seedling emergence was negatively affected by delays in precipitation and decreased soil moisture content. Seedling survival was negatively affected by overstory and understory interference and vertebrate herbivory. Most seedling mortality was attributed to desiccation. Woody plants should be monitored at least monthly to evaluate emergence and survival after one year. These results indicate that abiotic constraints are the primary factors structuring southwestern oak woodlands and savannas.

## CHAPTER 1

### INTRODUCTION

Investigation of the mechanisms underlying community structure has been a central goal of ecology. Identification of constraints on woody plant establishment represents a tractable problem that is consistent with this goal. However, despite the importance of understanding mechanisms of woody plant establishment and their implications for ecology and management, factors that affect recruitment of this life form are poorly understood (Archer 1989, McPherson 1992).

The lack of mechanistic understanding has fueled a debate about shifts in lower treeline in the southwestern United States. Using repeat photography and historic records in this region, Hastings and Turner (1965) concluded that lower treeline has shifted upslope during the past century. This conclusion is consistent with that of Betancourt et al. (1990) who attributed an upslope shift to warmer and drier conditions since the Pleistocene. Bahre (1991), using techniques similar to those of Hastings and Turner, concluded that lower treeline has remained stable since the 1860's. In contrast to these interpretations, woody plant encroachment into semi-arid grasslands has been observed worldwide (see Archer 1994). Consistent with

worldwide physiognomic shifts, movement of oak woodland into former grassland was demonstrated with the use of stable carbon isotopes (McPherson et al. 1993, McClaran and McPherson 1995).

Regardless of direction, shifts in lower treeline ultimately rely on the presence or absence of woody plant recruitment on either side of the woodland/grassland boundary. Emory oak (*Quercus emoryi* Torr.) is the dominant woody species in southwestern oak savannas. Although Emory oak seedlings are relatively abundant beneath mature oak trees at the woodland/grassland boundary, they are absent from adjacent grasslands (Weltzin and McPherson 1995).

Previous research on Emory oak includes studies of demography (Sanchini 1981, Borelli et al. 1994), mast production (Sanchini 1981), germination and seedbed ecology (Nyandiga and McPherson 1992, Germaine et al. in press), and acorn predation and dispersal (Hubbard 1995, Hubbard and McPherson in press). However, effects of biotic factors on emergence and survival of Emory oak have been investigated only over short temporal scales (McPherson 1993).

Therefore, objectives of the current study were 3-fold: (1) determine the effects of herbaceous interference and herbivory on emergence and survival of Emory oak seedlings; (2) investigate how different frequencies of monitoring influence the results of demographic studies with woody

plants; and (3) determine how the timing of acorn maturation and the timing of the onset of precipitation affect emergence of Emory oak seedlings.

Chapter 2 focuses on the first objective, and includes an assessment of the effects of above- and belowground interference from extant vegetation on emergence and survival, the effects of native herbivores on survival, and the major causes of seedling mortality. Previous demographic studies show little consistency regarding frequency of monitoring. Therefore, data collected in the interference/herbivory experiment were used to evaluate the second objective in chapter 3. Chapter 4 addresses the third objective, which arose from observations of variability in acorn maturation and emergence during the course of the interference/herbivory experiment.

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**CHAPTER 2**  
**EFFECTS OF HERBACEOUS INTERFERENCE AND HERBIVORY ON**  
**EMERGENCE AND SURVIVAL OF EMORY OAK SEEDLINGS**

**Abstract**

Woody plants have increased in abundance in many of the world's grasslands during the last 3 centuries. Mechanisms underlying these physiognomic shifts have not been adequately described, despite the importance of these shifts with respect to land use and ecosystem function. The objective of this study was to identify potential biotic constraints on emergence and survival of Emory oak (*Quercus emoryi* Torr.). A large-scale field experiment designed to elucidate the roles of interference and herbivory was established at the oak woodland/semi-arid grassland boundary in southern Arizona, USA. Acorns were planted in July of 1993, 1994, 1995, and 1996 and were subsequently monitored for emergence, survival, and determination of causes of mortality until December 1996. Height of individual seedlings was measured each October, 1993-1996. Emergence of Emory oak seedlings was not affected by herbaceous interference; however it was much lower in the grassland than within adjacent woodland. Survival was reduced by herbaceous interference. Survival of one cohort of seedlings was greater in cleared woodland than in intact

woodland or grassland. In addition to being affected by herbaceous interference, survival of a second cohort was reduced by vertebrate herbivory. Seedling mortality was almost always attributed to desiccation. Seedling height did not differ between interference reduction or herbivore exclusion treatments in the first 15 months of growth, but was subsequently affected by an interaction between overstory vegetation and vertebrate herbivory. Within an overstory type, seedling height was greater in vertebrate-excluded plots than in other treatments. Data from this experiment indicate that although biotic constraints (e.g., vertebrate herbivory) were important for short periods of time, abiotic constraints exerted primary importance in structuring these communities.

## Introduction

Determination of the mechanisms underlying community structure has been a central goal of ecology.

Identification of constraints on woody plant establishment is a tractable problem that is consistent with this goal. A widespread and conspicuous phenomenon that is amenable to this type of approach is the substantial increase in woody plant abundance in many of the world's grasslands during the past 50 to 300 years (Archer et al. 1988). This increase has been the most conspicuous change in the structure of semi-arid grasslands world-wide (Archer et al. 1988) and it has broad implications for "biodiversity, primary and secondary productivity, soil development and stability, livestock and wildlife composition and carrying capacity, recreational opportunities, water quality and water distribution" (Archer 1994). However, despite the widespread knowledge of this phenomenon and its management implications, factors affecting woody plant establishment are poorly understood (Archer 1989, McPherson 1992).

Emory oak (*Quercus emoryi* Torr.), the dominant woody species in southwestern oak savannas, is a recent occupant of some former grasslands (McPherson et al. 1993). However, although Emory oak seedlings are relatively abundant beneath mature oak trees, they are absent from adjacent grasslands (Weltzin and McPherson 1995). Many factors influence

patterns of woody plant recruitment, including biotic (e.g., herbaceous interference, herbivory), abiotic (e.g., shade, precipitation), and edaphic (e.g., soil moisture content, soil nutrients) components. This study was designed to determine the roles of interference and herbivory on recruitment of Emory oak seedlings.

Understanding the roles of herbaceous interference and herbivory on woody plant establishment is fundamental to understanding savanna genesis and maintenance (McPherson 1993). However, studies designed to elucidate the effects of herbaceous interference and herbivory at appropriate scales of resolution are rare. Specifically, the ability to interpret and generalize from most previous studies has been hampered by infrequent sampling (Germaine, Chapter 3), short study periods (Archer 1995), or weak experimental designs (Hairston 1989, Keddy 1989). In addition, there is considerable variability in the presumed role of these 2 factors on seedling establishment. For example, a recent review of savanna dynamics (Skarpe 1992) concluded that large herbivores and belowground interference were the primary factors that control savanna structure and function. Other research on savannas indicates that small herbivores (e.g., Brown and Heske 1990), invertebrates (e.g., McPherson 1993), or competition for light (e.g., Bush and Van Auken 1990) may limit woody plant establishment. Conflicting

results and the general paucity of knowledge concerning the effects of herbaceous interference and herbivory on woody plant recruitment prompted us to execute a long-term in-depth study of these effects and how they might constrain recruitment of woody plants. In particular, it seems clear that determination of the mechanisms and constraints on woody plant recruitment is crucial to our understanding of, and ability to predict changes in vegetation physiognomy.

The objective of this experiment was to investigate the effects of biotic factors on emergence and survival of Emory oak seedlings at the oak woodland/semi-arid grassland boundary in the southwestern United States. Specific objectives were to determine: (1) the effects of above- and belowground interference from extant vegetation on emergence and survival of oak seedlings; (2) the effects of native herbivores on survival of oak seedlings; and (3) the major cause(s) of seedling mortality.

### Study Site

Research was conducted on Fort Huachuca Military Reservation (FHMR) in southeastern Arizona, USA. The study site is located at the mouth of Blacktail canyon (31° 33' N, 111° 35' W) on the northwestern side of the Huachuca Mountains. Soil is from the Terrarossa-Blacktail-Pyeatt complex (fine, mixed, thermic Aridic Paleustalfs; fine, mixed, thermic Aridic Argiustolls; and coarse-loamy, mixed, thermic Aridic Calciustolls, respectively) (Soil Conservation Service 1994).

FHMR is characterized by a semi-arid climate with a mean annual temperature of 14.2°C. Three-fifths of the average annual precipitation (452-mm) occurs from July through October and one-fifth occurs from December through March (long-term data based on Canelo Hills, AZ station, NOAA 1995). A severe foresummer drought between late March and early July is characteristic of this region.

The site is located at the lower-elevation boundary of evergreen oak woodland and semi-arid grassland. The woodland overstory consists almost entirely of the evergreen Emory oak. The herbaceous understory and the grassland includes sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], Texas bluestem (*Andropogon cirratus* Hack.), green sprangletop [*Leptochloa dubia* (H.B.K.) Nees.], plains lovegrass (*Eragrostis intermedia* Hitchc.), three-awns

(*Aristida* L. spp.), and wait-a-minute bush (*Mimosa biuncifera* Benth.). FHMR has not been grazed by livestock for nearly 50 years nor has fire occurred on the study site for at least 20 years.

### Methods

Experiments were conducted on both sides of the oak woodland/semi-arid grassland boundary. The experimental design included 6 grassland blocks, 6 closed-canopy woodland blocks, and 6 cleared woodland blocks. All trees in cleared blocks were mechanically cut to ground-level in January (3 blocks in 1993, 3 blocks in 1994) and stumps were continually hand-treated to minimize resprouting. Blocks were 30 x 30 m and the center 400-m<sup>2</sup> of each block was used in the current study. Half of the blocks (selected at random) received experimental treatments starting in June of 1993 and the other half received experimental treatments starting in June of 1994. All woodland and grassland blocks were within 500 meters of each other, with no more than 10 meters difference in elevation.

Each block contained 9, 3 x 3 m plots. Each plot was randomly assigned 1 of 9 possible combinations of interference reduction (herbicide to remove above- and belowground biomass, clip to remove aboveground biomass, and control) and herbivore exclusion (vertebrate exclusion, invertebrate exclusion, and control). To remove above- and belowground biomass of extant vegetation, plots were sprayed in early summer with glyphosate [trade name 'Roundup'], a non-selective herbicide. Any herbs that established subsequently were removed through hand-weeding. To remove

aboveground biomass, all extant vegetation was clipped 5 cm aboveground. Vertebrates were excluded with hardware cloth exclosures that extended into the ground 30 cm and turned outward to minimize accessibility of fossorial mammals. Invertebrates were excluded by spraying Carbaryl (a broad-spectrum pesticide) weekly during periods of invertebrate activity (April-October).

Several thousand Emory oak acorns ( $n=3969$ ) were collected and screened in July of 1993, 1994, 1995, and 1996 following the procedures of Nyandiga and McPherson (1992). Acorns were planted about 1 cm below the soil surface no later than 2 days after collection. Forty-nine acorns were planted per plot in a 7x7 grid with 10 cm between each acorn. Summer precipitation (the monsoon) was delayed or interrupted in all 4 years; however, we provided supplemental water to the plots in 1993 and 1995. The amount added was equivalent to a 5-mm daily precipitation event for up to 2 weeks, or until precipitation occurred naturally.

Plots were monitored at least twice-weekly for the first 3 months after planting, twice-monthly during the remainder of the growing season (May-October), and once-monthly during the remainder of the year. Monitoring included recording the date of seedling emergence (or re-emergence following defoliation), presence of herbivory, and

cause of mortality for individual seedlings. Seedling emergence was defined as the first observation of a shoot. Herbivory varied from partial leaf defoliation to complete stem cutting. Mortality was categorized as vertebrate, invertebrate, desiccation, or unknown. A seedling was classified as "dead" when all living leaves or buds were removed or desiccated and appeared brown. Desiccation could not be differentiated from other belowground agents of mortality (e.g., damping-off, root herbivory), so this category potentially included other sources of mortality. Seedlings classified as "dead" that re-sprouted from lateral branches were then re-classified as alive (e.g., re-emerged). Seedling survival was monitored for the 1993 and 1995 cohorts through December 1996; however, because emergence in 1994 and 1996 was very low (<2%), monitoring efforts were abandoned after all seedlings had emerged. Individual seedling heights also were obtained every October, 1993-1996.

### Statistical Analyses

Seedling height and emergence data were tested for normality, linearity, and homogeneity of variances by inspection of error residuals (Tabachnick and Fidell 1983). Because data did not meet one or more of the assumptions of analysis of variance (ANOVA), transformations were performed. All assumptions were met after application of the  $\log(x+1)$  transformation for the seedling height data for the 1993 cohort, and the 1995 emergence data. However, transformations ( $x^2$ ,  $1/x$ , square root, arcsine of the square root) did not produce data that met assumptions of ANOVA for the 1993 emergence data and thus data were ranked prior to analysis (Conover and Iman 1981).

ANOVA of transformed or ranked data (as described above) was used to examine the interactive and main effects of overstory type and herbaceous interference on emergence of Emory oak seedlings. Means were compared with Fisher's LSD when appropriate. Repeated measures ANOVA indicated that seedling growth patterns differed for the 1993 and 1995 cohorts; consequently, the 2 cohorts were analyzed separately for emergence, survival, and seedling height. Proportional hazards failure-time analysis was used to examine the main effects of overstory type, herbaceous interference, and herbivory on survival of Emory oak seedlings over time. Repeated measures ANOVA of log-

transformed data was used to examine the interactive and main effects of overstory type, herbaceous interference, and herbivory on the height of seedlings.

## Results

Total emergence in 1994 was 1.2%. No seedlings emerged in the grassland and 1.6 and 2.0% of seedlings emerged in the cleared woodland and intact woodland, respectively. In 1996, only 1 seedling emerged in the intact woodland and no seedlings emerged elsewhere. Total emergence in 1993 and 1995 was 45.8 and 17.0%, respectively. Emergence of the 1993 and 1995 cohorts was not affected ( $P > 0.05$ ) by interactions between overstory type, interference, and herbivory; total emergence was affected ( $P < 0.05$ ) only by the main effect of overstory type. Emergence of both cohorts was greater ( $P < 0.002$ ) in the cleared woodland and intact woodland than in the grassland (Fig. 2.1).

Seedling survival in the 1993 cohort was affected by the main effects of herbaceous interference ( $P < 0.0001$ ) and overstory type ( $P < 0.05$ ). After 3.5 years, survival was greatest in herbicided plots (mean  $\pm$  SE =  $11.9 \pm 8.9\%$ ,  $n=100$ ), intermediate in clipped plots ( $5.7 \pm 2.1\%$ ,  $n=42$ ), and least in control plots ( $1.4 \pm 1.0\%$ ,  $n=11$ ) (Fig. 2.2). In addition, survival was significantly greater ( $P < 0.05$ ) in the cleared woodland ( $16.9 \pm 3.5\%$ ,  $n=112$ ) than in the intact woodland or grassland, which did not differ ( $1.1 \pm 1.0\%$ ,  $n=41$ ) ( $P > 0.05$ ) (Fig. 2.3).

Seedling survival in the 1995 cohort was affected by herbivory ( $P < 0.0001$ ) and herbaceous interference ( $P < 0.05$ ).

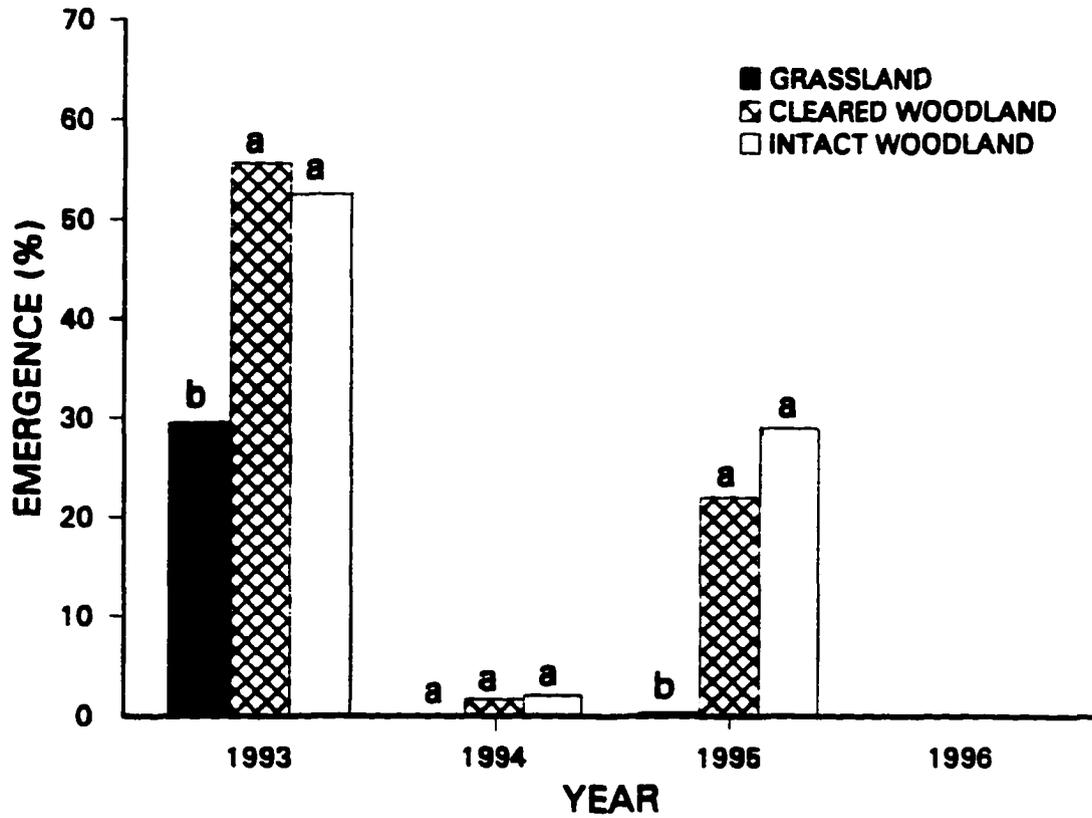


Figure 2.1. Emergence of planted Emory oak seedlings in Blacktail Canyon, Arizona. The 1993 and 1995 cohorts received supplemental water equivalent to a 5-mm daily precipitation event for up to 2 weeks. Within a year, bars with the same letter did not differ ( $P > 0.05$ ) according to Fisher's LSD.

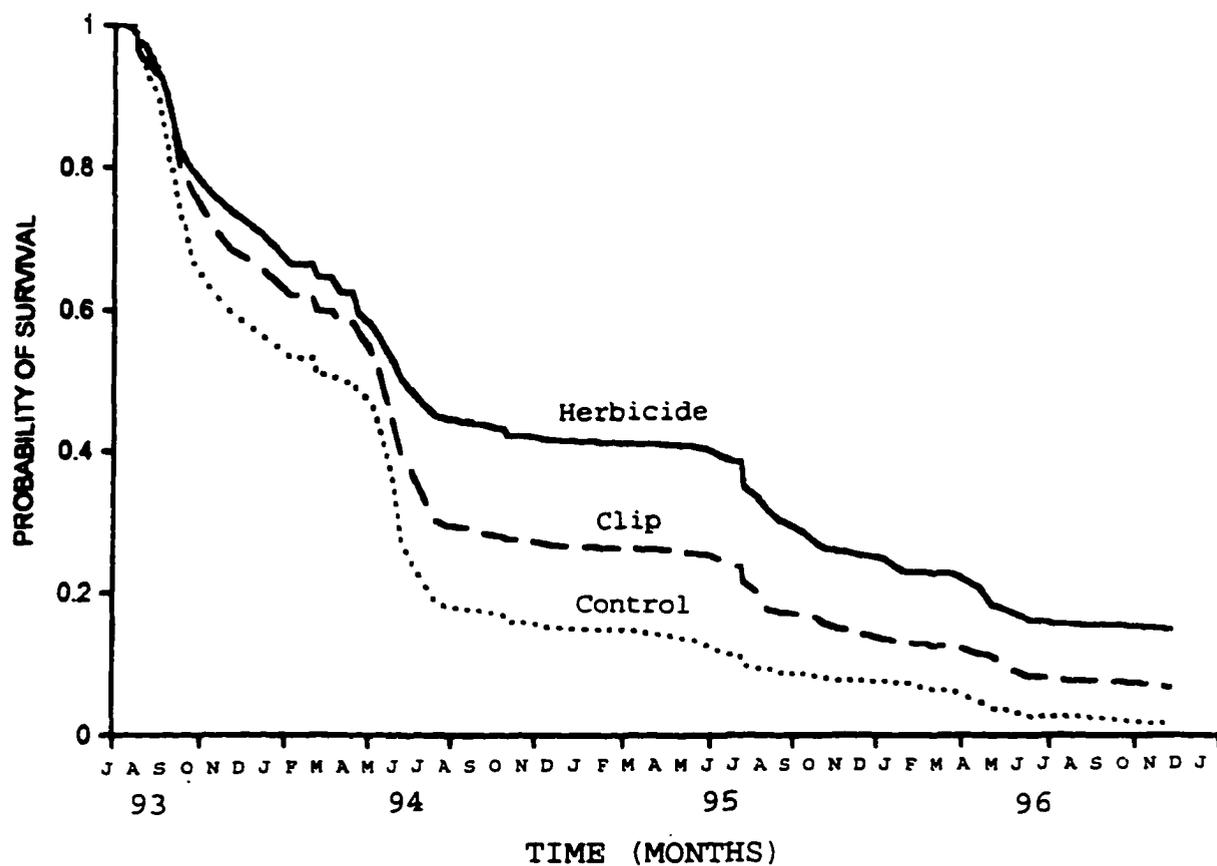


Figure 2.2. Survival curves of Emory oak seedlings planted 19 July 93 in different interference reduction treatments. See text for explanation of experimental treatments.

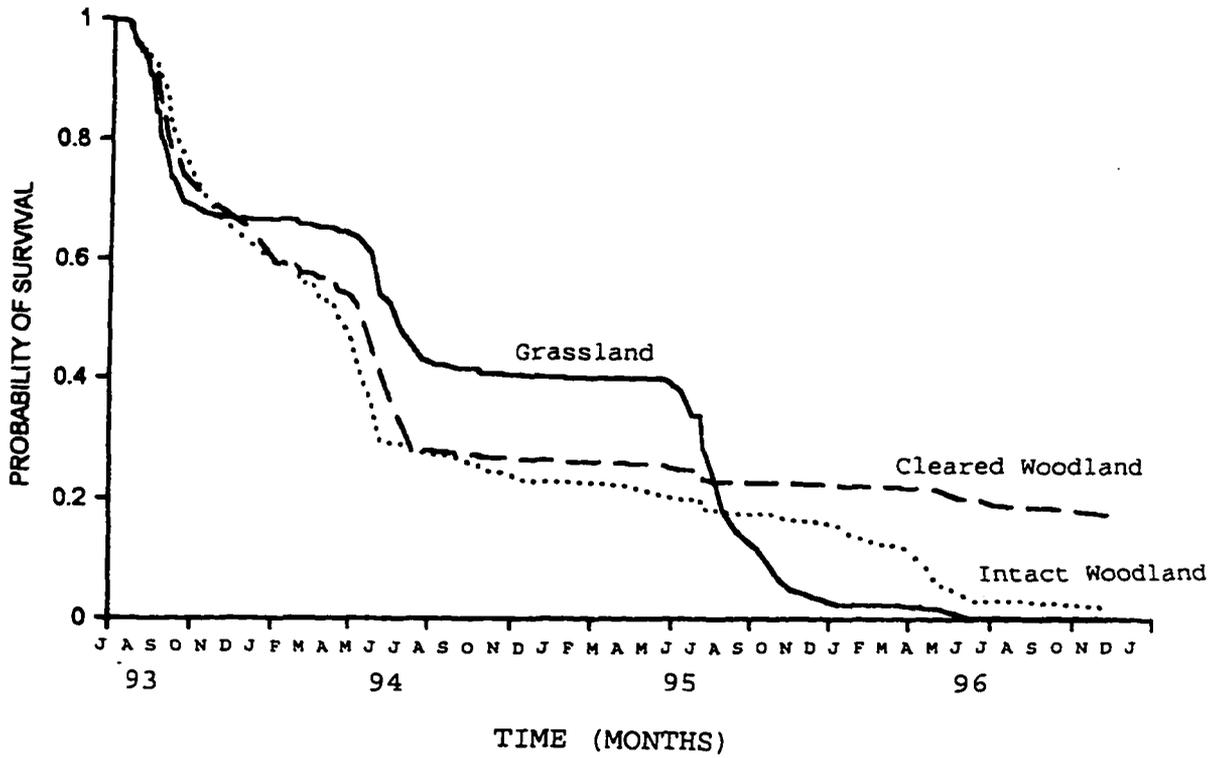


Figure 2.3. Survival curves of Emory oak seedlings planted 19 July 93 in different overstory treatments. See text for explanation of experimental treatments.

After 1.5 years, survival was greater ( $P < 0.05$ ) in plots with vertebrates excluded ( $9.3 \pm 4.8\%$ ,  $n=39$ ) than invertebrate-excluded or control plots, which did not differ ( $0.7 \pm 0.7\%$ ,  $n=2$ ) ( $P > 0.05$ ) (Fig. 2.4). In addition, seedling survival was greater ( $P < 0.05$ ) in herbicided plots ( $11.3 \pm 5.6\%$ ,  $n=40$ ) than in clipped or control plots, which did not differ ( $0.5 \pm 0.5\%$ ,  $n=1$ ) ( $P > 0.05$ ) (Fig. 2.5).

All survival curves of both cohorts were visually similar, regardless of differences between treatments (Fig. 2.2-2.5). Survival was characterized by periods of low seedling mortality punctuated by periods of high seedling mortality. Newly emerged seedlings, regardless of cohort or treatment combination, experienced a period of high mortality from the first month up to 6 months after planting (August-January). Subsequent episodes of high seedling mortality generally occurred from late March through August. However, seedling survival in the 1993 cohort did not decline substantially in 1995 until July through November (Fig. 2.2 & 2.3), and mortality during this period was particularly high in the grassland (Fig. 2.3).

The primary agents responsible for seedling mortality in the first 6 months after planting differed between the 1993 and 1995 cohorts. Specifically, vertebrates caused minimal mortality in 1993 compared to 1995.

Desiccation accounted for most of the initial seedling

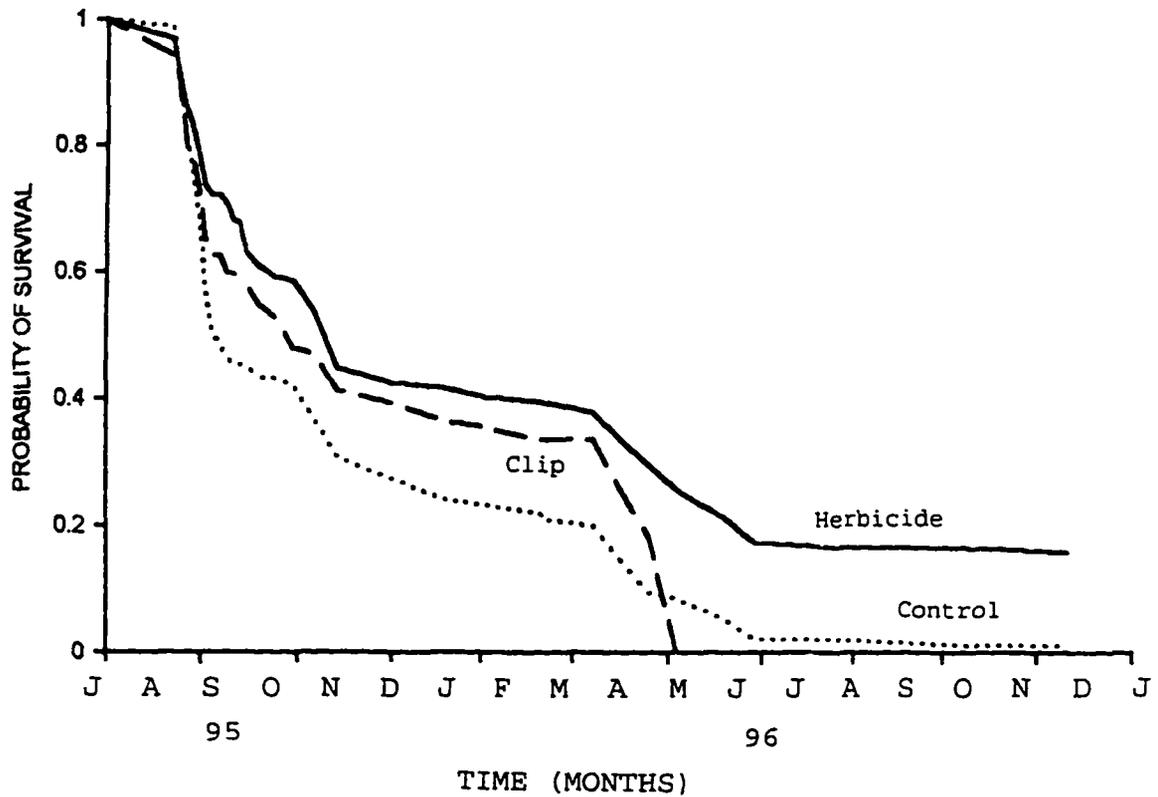


Figure 2.4. Survival curves of Emory oak seedlings planted 18 July 95 in different interference reduction treatments. See text for explanation of experimental treatments.

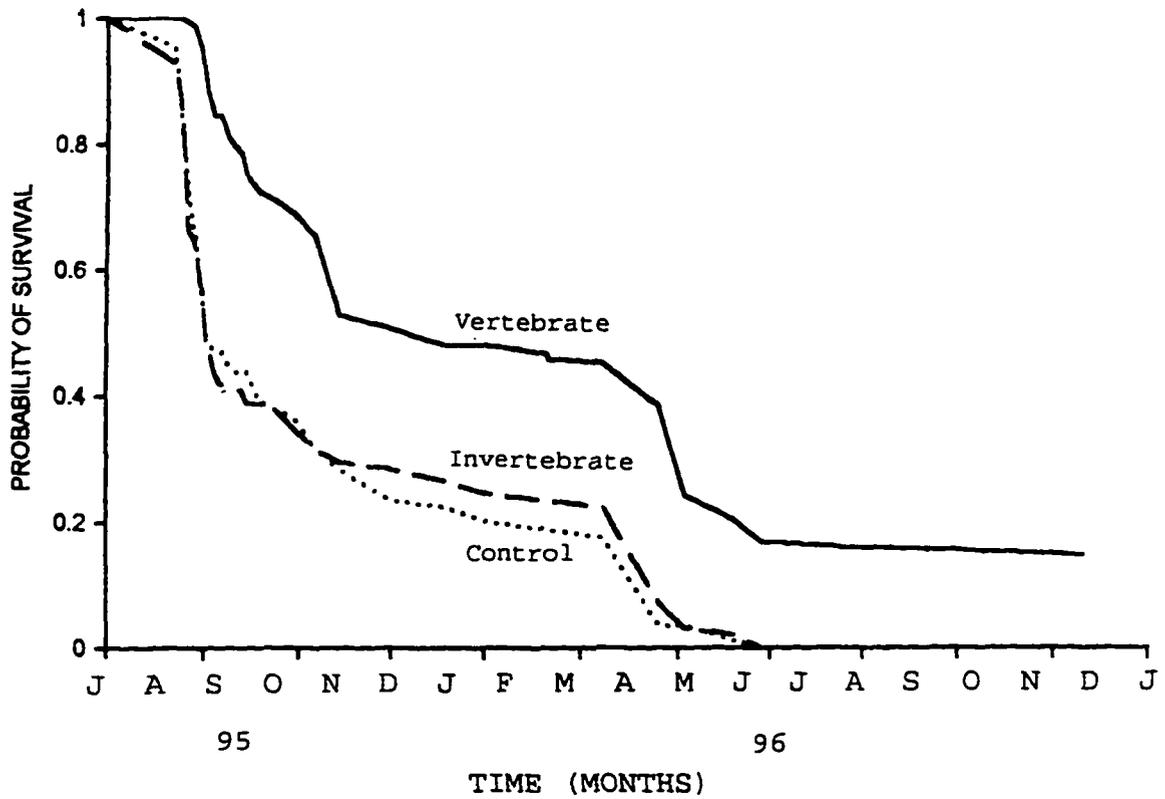


Figure 2.5. Survival curves of Emory oak seedlings planted 18 July 95 in different herbivore exclusion treatments. See text for explanation of experimental treatments.

mortality in the 1993 cohort (range=55.9 to 79.5%) and was the greatest in the woodland (79.5%) and in plots with all extant vegetation present (73.1%) (Table 2.1). The proportion of seedlings that desiccated decreased as the amount of extant vegetation decreased (73.1, 65.5, and 58.6% for control, clipped, and herbicided plots, respectively); however, seedling mortality caused by vertebrates increased (9.8, 15.9, and 28.2% for control, clipped, and herbicided plots, respectively). Invertebrate and vertebrate herbivory, respectively, accounted for 32.8 and 2.2% of early seedling mortality in the grassland and 12.3 and 31.8% in the cleared woodland.

Early seedling mortality in the 1995 cohort was caused by desiccation and vertebrate herbivory. In vertebrate-excluded plots, desiccation accounted for 89.5% of seedling mortality. In plots accessible to vertebrates, desiccation accounted for 34.0%, whereas vertebrate herbivory accounted for 58.0%. Invertebrate herbivory accounted for less than 9% of seedling mortality in the 1995 cohort.

Regardless of treatment combination, high seedling mortality was attributed to desiccation between late March and August, 1993, 1994, and 1996. A similar period of high mortality occurred in July-November in 1995. Desiccation accounted for greater than 90% of seedling mortality in nearly all plots.

Table 2.1 Cause of mortality (percent) of 2 cohorts of Emory oak seedlings in Blacktail Canyon, Arizona.

Period	Main Effect <sup>1</sup>	Treatment	Cause of Mortality <sup>2</sup>			
			V	I	D	U
(Cohort #1)						
19 Jul 93-	HI	Herbicide	11.8	16.0	72.2	0.0
10 Feb 94		Clip	6.3	21.0	72.8	0.0
		Control	7.6	17.5	74.9	0.0
	OT	Intact Wdlnd	3.9	14.6	81.5	0.0
		Clrd Wdlnd	15.3	15.3	69.3	0.0
		Grassland	2.3	32.3	65.4	0.0
9 Apr 94-	HI	Herbicide	5.4	1.8	90.2	2.7
31 Aug 94		Clip	7.4	1.1	85.1	6.3
		Control	6.3	1.0	90.1	2.6
	OT	Intact Wdlnd	5.7	1.1	89.8	3.4
		Clrd Wdlnd	10.0	1.9	85.2	2.9
		Grassland	0.0	0.0	92.3	7.7
14 Jul 95-	HI	Herbicide	1.3	0.0	96.2	2.5
17 Nov 95		Clip	0.0	0.0	100.0	0.0
		Control	4.5	0.0	95.5	0.0
	OT	Intact Wdlnd	8.3	0.0	91.7	0.0
		Clrd Wdlnd	0.0	0.0	100.0	0.0
		Grassland	0.0	0.0	98.2	1.8
4 Apr 96-	HI	Herbicide	11.8	5.9	82.4	0.0
12 Jun 96		Clip	9.5	0.0	85.7	4.8
		Control	0.0	5.9	94.1	0.0
	OT	Intact Wdlnd	11.3	1.9	87.0	0.0
		Clrd Wdlnd	0.0	15.4	76.9	7.7
		Grassland	0.0	0.0	100.0	0.0

Table 2.1 Continued.

Period	Main Effect <sup>1</sup>	Treatment	Cause of Mortality <sup>2</sup>			
			V	I	D	U
(Cohort #2)						
18 Jul 95-	HI	Herbicide	43.1	8.7	46.2	2.1
13 Jan 96		Clip	36.0	7.5	54.3	2.1
		Control	39.0	4.0	56.5	0.5
	HE	Vertebrate	0.0	8.9	89.5	1.6
		Invertebrate	59.3	4.0	35.2	1.5
		Control	57.8	7.3	33.3	1.6
4 Apr 96-	HI	Herbicide	6.0	0.0	92.5	1.5
26 Jul 96		Clip	4.5	0.0	95.5	0.0
		Control	0.0	0.0	100.0	0.0
	HE	Vertebrate	0.0	0.0	100.0	0.0
		Invertebrate	6.1	0.0	91.8	2.0
		Control	15.2	0.0	84.8	0.0

<sup>1</sup> HI=herbaceous interference, OT=overstory type, HE=herbivore exclusion.

<sup>2</sup> V=vertebrate-induced mortality, I=invertebrate-induced mortality, D=desiccation, U=mortality due to unknown causes

Seedling height of the 1993 cohort was affected by an interaction between overstory type and herbivory ( $P < 0.05$ ); however, these factors did not affect growth until after 15 months. Within an overstory type, seedling height was greatest in vertebrate-excluded plots than invertebrate-excluded or control plots. Within vertebrate-excluded plots there were no consistent patterns of growth with respect to overstory type. However, after 3.5 years, only one seedling was alive in the grassland in a vertebrate-excluded plot (height = 19.5 cm), whereas 60 seedlings were alive in vertebrate-excluded plots in the cleared woodland; 60% of these seedlings exceeded 19.5 cm in height, and the tallest seedling was 61 cm tall. Consistent with the first 15 months of growth in the 1993 cohort, seedling height for the 1995 cohort (at 15 months) was not affected by main or interactive effects of any treatment ( $P > 0.05$ ).

### Discussion

In this experiment, emergence of Emory oak seedlings was very low in the grassland; however, low emergence did not result from high levels of herbaceous interference. In fact, herbaceous interference did not affect emergence in grasslands or woodlands. Within either type of overstory, an Emory oak seedling has an equal probability of emerging regardless of extant herbaceous vegetation. However, emergence was higher within woodlands, including within large gaps (i.e., cleared woodland), than in grasslands. Therefore, the absence of very young Emory oak seedlings in grasslands adjacent to woodlands is constrained by some other factor(s) or life-history stage, such as seed dispersal (e.g., Crawley 1992, Tilman 1997). In fact, low seed dispersal is recognized as a potential constraint to seedling establishment in these grasslands. Dispersal of Emory oak acorns is 10-fold higher at the woodland boundary than into the grassland (Hubbard 1995). Nonetheless, acorns dispersed into grasslands have a higher probability of escaping predation than those dispersed within woodlands (Hubbard 1995).

Although herbaceous interference did not affect emergence of Emory oak, seedling survival increased with removal of all herbaceous interference (Fig. 2.2 & 2.3). Thus, survival of young seedlings represents an additional

constraint on oak seedling recruitment into grasslands. Belowground interference clearly constrains survival of Emory oak seedlings. These results are consistent with previous research on woody seedling/grass interactions (Bush and Van Auken 1990, Adams et al. 1992, McPherson 1993), and highlight the importance of rapid early root growth. Seedlings with the ability to access water deeper in the soil profile within the first growing season decrease interference from extant herbs and increase likelihood of survival (McPherson 1993). In addition to the effects of belowground interference, aboveground interference also constrained survival of seedlings up to 3.5 years, which is consistent with Wilson and Tilman's (1993) nutrient-rich, but not nutrient poor treatments.

In addition to effects of herbaceous interference, survival of the 1993 cohort also was affected by overstory type, reflecting effects of interference at a larger spatial scale (Fig. 2.3). Survival increased with overstory removal, indicating that the positive effects of the canopy (e.g., decreased daytime soil temperature, increased soil nutrients) were masked or overridden by negative effects (e.g., shade, decreased soil moisture beneath trees due to interception of precipitation). This finding is consistent with research on northern red oak (*Quercus rubra* L.) in which survival was greatest with complete removal of the

overstory and initial removal of the understory (Crow 1992).

In addition to effects of herbaceous interference, survival of the 1995 cohort also was affected by herbivory (Fig. 2.4). Seedling survival was greatest in vertebrate-excluded plots, with vertebrate-induced mortality accounting for more than 50% of seedling mortality within the first 6 months in plots accessible to vertebrates (Table 2.1). A majority of the seedlings in vertebrate-accessible plots were individually excavated by vertebrates (mammals or birds) within 1 month after emergence. The vertebrates ate the acorns and left the stems, leaves, and roots on the soil surface, thus eliminating any potential for the seedling to survive. This behavior was observed only during a few weeks of this 42-month study. Thus, vertebrate-induced mortality was extremely variable and unpredictable.

Animal densities and feeding habits can demonstrate considerable intra- and interannual variability (Vaughan 1986). For example, food items not eaten during one season or year may constitute the largest proportion of the diet during another period, in part because the absence of preferred food items causes dietary shifts. Thus, studies of herbivory over short temporal scales may give a misleading impression of the importance of herbivory in structuring a system. These data clearly show that herbivore-induced mortality is extremely variable.

Vertebrate herbivory was a critical factor during one year (1995) for one cohort of seedlings, but was a negligible phenomenon during the remainder of the study, especially compared to the effects of abiotic factors.

Other than the large proportion of vertebrate-induced seedling mortality in the first 6 months of the 1995 cohort, all periods of high seedling mortality were attributed primarily to desiccation (Table 2.1). Periods of high mortality generally corresponded to periods of low precipitation (Fig. 2.6). In addition, 1 to 12 months of below-normal precipitation occurred prior to large declines in seedling survival. Drought has been cited as the leading cause of seedling mortality in many studies of woody plant survival (Pase 1969, Griffin 1971). As predicted by Prentice (1986), abiotic factors (in this case, precipitation) exert considerable control over survival of Emory oak seedlings and therefore community structure at relatively long spatial scales.

Seedling height did not vary between treatments in the first 15 months of growth. Thus, studies performed over short temporal scales (i.e., less than 1.5 years) are not representative of early seedling growth and the factors that affect it. After 15 months, seedlings in the 1993 cohort were affected by an interaction between overstory type and herbivory. As expected, within an overstory type, seedling

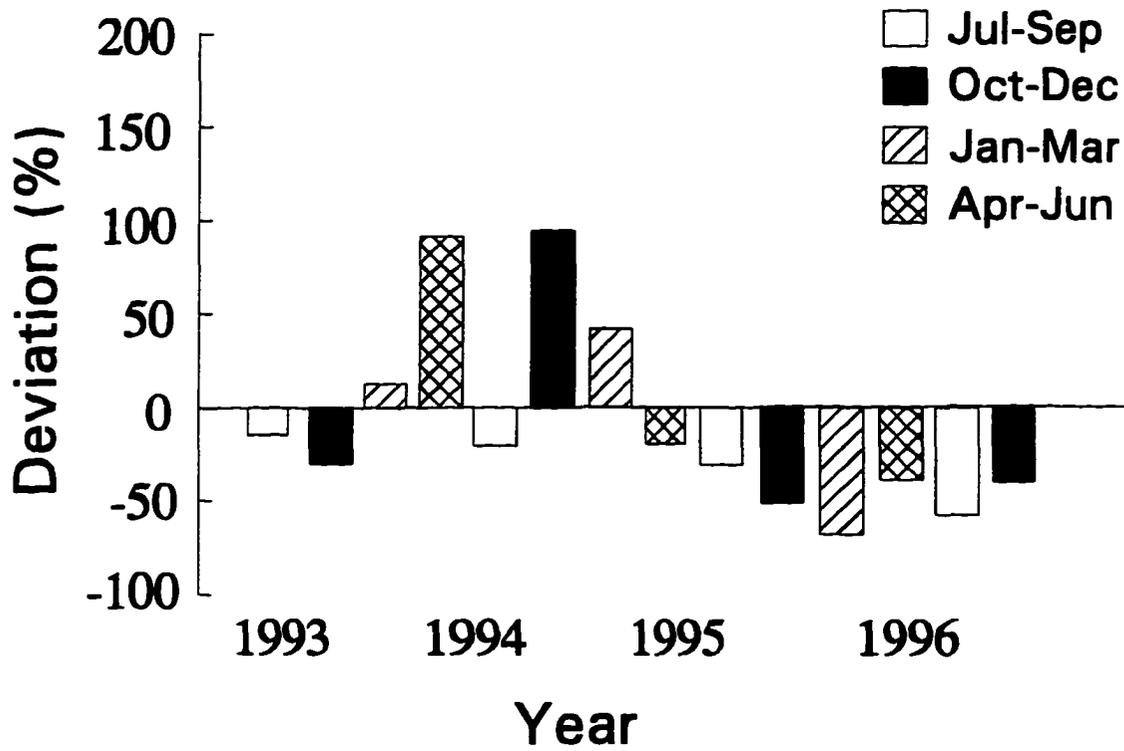


Figure 2.6. Deviation from long-term average precipitation in Blacktail Canyon, Arizona. Adapted from McPherson and Weltzin (in press).

height was greater in vertebrate-excluded plots than in other treatments. Average height of Emory oak seedlings was less than 29.5 cm at 42 months of age in all treatment combinations, which is consistent with the slow aboveground growth of this species observed by McPherson (1993).

Emergence and especially survival of Emory oak seedlings are affected by abiotic factors to a greater extent than by biotic factors. Numerous studies that cite biotic factors as the primary constraints on woody plant recruitment were conducted at relatively short temporal scales (e.g., Myster and McCarthy 1989, Terborgh and Wright 1994, Berkowitz et al. 1995, and Ida and Nakagoshi 1996). Data from the current experiment indicate that although biotic constraints (e.g., vertebrate herbivory) were important for short periods of time, abiotic constraints were the primary factors structuring these communities. Thus, these data illustrate the importance of long-term ecological experiments and highlight the importance of abiotic factors on woody plant recruitment.

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**CHAPTER 3**  
**EFFECTS OF MONITORING FREQUENCY ON DEMOGRAPHIC RESULTS**  
**IN WOODY PLANT STUDIES**

**Abstract**

There is little consistency regarding frequency of monitoring in demographic research. Therefore, the objective of this study was to examine how different monitoring frequencies affect the results of demographic studies with woody plants. Data collected from the interference/herbivory study described in chapter 2 were used to produce 4 different data sets that represented 4 different monitoring frequencies (thrice-weekly, weekly, monthly, and annually). Emergence and survival were under- and over-estimated, respectively, with annual monitoring. Thus, woody plants should be monitored at least monthly to evaluate emergence and survival after 1 year. Confidence in determination of the date of emergence and the cause of mortality increases at higher frequencies of monitoring. Information gained with different monitoring frequencies should be considered as seriously as other elements of the study design when research is planned and implemented.

Demography is a central focus of study in ecology. However, examination of recent ecological literature indicates that there is little consistency regarding frequency of monitoring in demographic research. Even studies with similar objectives and intended audiences exhibit considerable variability in monitoring frequency (Table 3.1). Some of this variability may result from differing life histories of species under study, but I suspect that convenience, convention, or available resources play a large role. This may be due in part to the relative paucity of knowledge regarding the relationship between monitoring frequency and demographic information (e.g., date of emergence, survival, cause of mortality). Therefore my objective was to examine how different monitoring frequencies affect the results of demographic studies with woody plants.

This study was conducted at Blacktail Canyon in the Huachuca mountains of southeastern Arizona. The site is at the oak woodland/semi-desert grassland boundary at 1565 m elevation. A more detailed description is provided in chapter 2. Several hundred *Quercus emoryi* Torr. (Emory oak) seedlings were monitored as frequently as three times a week during the first few months after acorns were planted. Dates of emergence and mortality were recorded and cause of

Table 3.1. Monitoring frequencies of field studies that investigated woody plant emergence, survival, or cause of mortality in Ecology, 1986 to 1995.

Citation	Monitoring Objective	Monitoring Frequency
Berkowitz et al. 1995	Survival	Twice Yearly
Shibata and Nakashizuka 1995	Emergence & Survival	2 weeks (Apr-Aug) Monthly (Sept-Oct)
Sipe and Bazzaz 1995	Survival	Yearly
Facelli 1994 (thereafter)	Emergence	6 days (1st month) Monthly
Terborgh and Wright 1994	Survival	Yearly
Ostfeld and Canham 1993	Survival & Cause of Mortality	Monthly
Callaway 1992	Survival & Cause of Mortality	Unclear
Molofsky and Augspurger 1992	Emergence & Survival	Not stated
De Steven 1991a	Survival	6-12 months
De Steven 1991b	Emergence	Weekly (Mar-Apr) 2-3 weeks (thereafter)
Borchert et al. 1989	Emergence Survival	Monthly Yearly
Harmon and Franklin 1989 (2 experiments)	Survival	1=periodically 2=6-8 months
Kitajima and Augspurger 1989	Emergence  Survival  Cause of mortality	2 weeks (1st 2 months) at 7 months, 1 yr, & 2 yr 2 weeks (1st 2 months)

Table 3.1. (continued)

Citation	Monitoring Objective	Monitoring Frequency
Sork 1987	Survival	Monthly

mortality was determined. Using the data collected at this high frequency, data were eliminated in a hierarchical fashion to produce 4 different data sets that represented 4 different monitoring frequencies (thrice-weekly, weekly, monthly, and annually).

Monitoring frequencies were compared with respect to seedling emergence (expressed as a percentage of planted acorns) and survival (expressed as a percentage of emerged seedlings) 1 year after acorns were planted. Emergence after 1 year was 30, 27, 27, and 13% with thrice-weekly, weekly, monthly, and yearly sampling, respectively; survival was 44, 48, 49, and 100% at the same frequencies. Emergence and survival were under- and over-estimated ( $P < 0.05$ ) respectively, with annual monitoring. Seedlings that emerged and died within the year were not detected with annual sampling; therefore, percent survival at the first observation always would be 100%. Consequently, annual monitoring misrepresented actual seedling demography. Conversely, there was no difference ( $P > 0.10$ ) between thrice-weekly, weekly, and monthly regimes with respect to emergence and survival after 1 year.

Although total emergence and survival after 1 year were estimated accurately with monthly or more frequent sampling, the timing of demographic events (e.g., date of emergence or

mortality) was portrayed most accurately at the highest frequencies of monitoring (Fig. 3.1). On the first day of monitoring, monthly monitoring had already under-estimated actual emergence by about 30% compared to thrice-weekly monitoring. Interpolation within the first month revealed that monthly monitoring over-estimated actual emergence in the first 2 weeks after planting by at least 5-fold. Furthermore, monthly monitoring prohibited precise determination of emergence dates: errors of  $\pm 15$  days could be expected (vs.  $\pm 3$  days or  $\pm 1$  day with weekly and thrice-weekly regimes, respectively). Thus, monitoring at least weekly during the first month of seedling emergence allows considerable precision in estimates of emergence dates.

Just as annual monitoring showed survival as 100% after 1 year, monthly sampling indicated that survival after 1 month was 100%. However, nearly 20% of the emerged seedlings had died by this time (Fig. 3.2). Interpolation of monthly monitoring for survival revealed that actual survival was under-estimated by half relative to weekly and thrice-weekly monitoring in the first 2 weeks after planting.

Some investigators are interested in determining cause(s) of mortality. In this study, considerable biological activity, including emergence, desiccation,

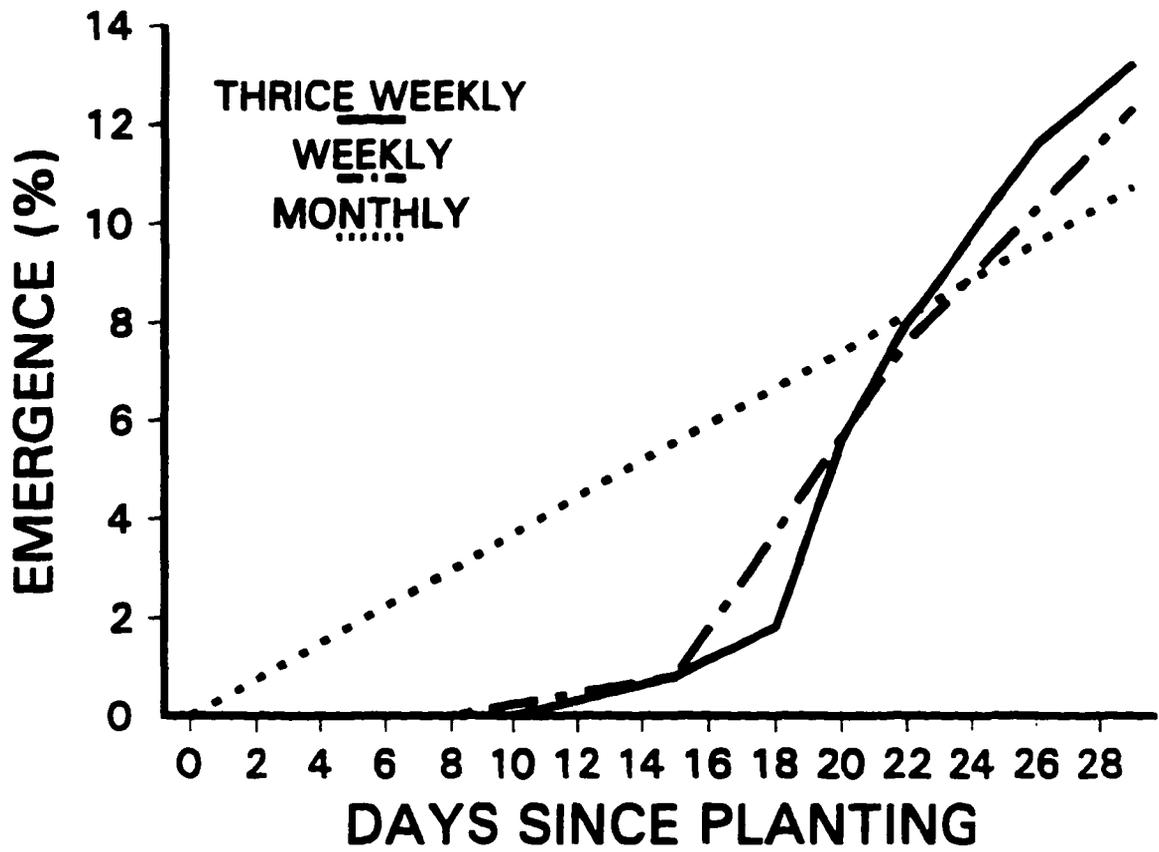


Figure 3.1. Percentage of Emory oak seedlings that emerged during the first month as determined by monitoring thrice-weekly, weekly, and monthly.

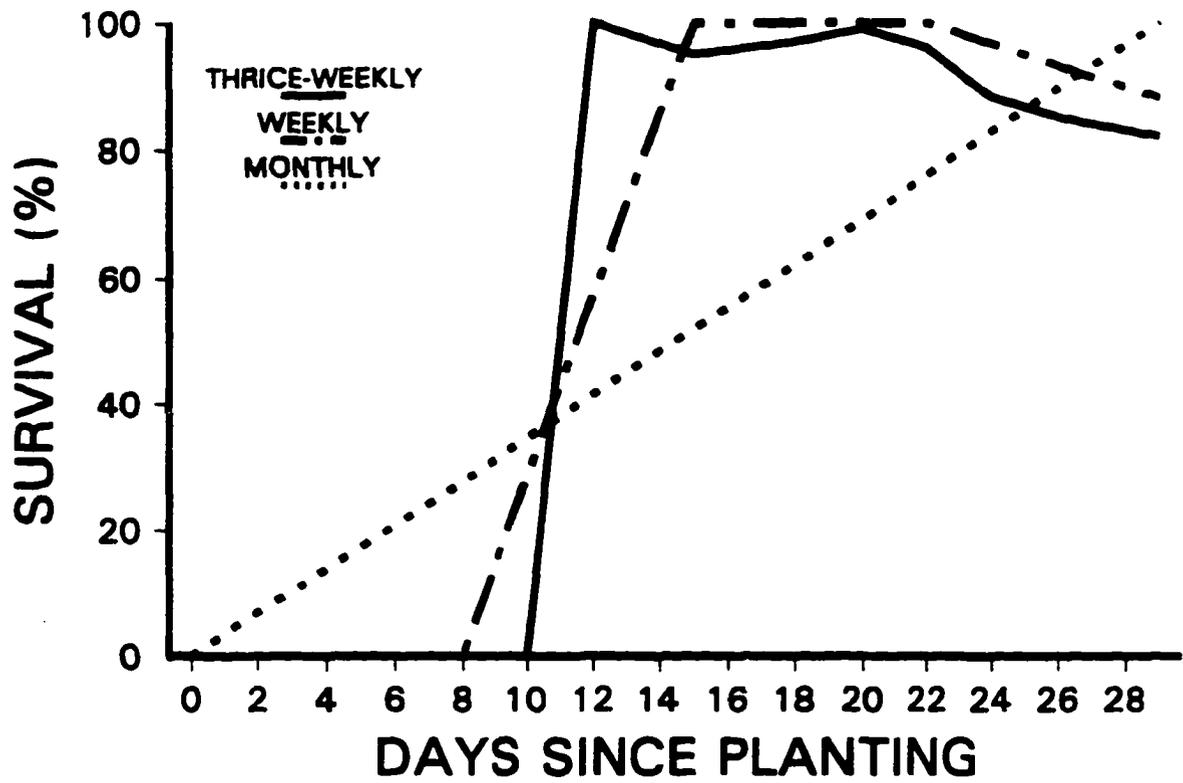


Figure 3.2. Percentage of Emory oak seedlings that survived during the first month as determined by monitoring thrice-weekly, weekly, and monthly.

defoliation by invertebrates and native vertebrates, and resprouting of defoliated seedlings, had occurred within the first month of planting (Fig. 3.2). Consequently, much qualitative information was lost by monitoring monthly. At higher frequencies of monitoring, more diagnostic indicators (e.g., leaf fragments) remained to help confidently determine the cause of mortality. With most Emory oak seedlings, cause of mortality could not be determined at monitoring frequencies greater than once per week.

This investigation of monitoring frequency for woody plants revealed that considerable demographic information may be lost at low frequencies of monitoring. Unless quantification of recruitment into the population after one year is the sole demographic objective, then monitoring yearly is inadequate and potentially misleading. Monitoring should occur at least monthly to evaluate emergence and survival after one year. Confidence in determination of the date of emergence and the cause of mortality increases at higher frequencies of monitoring. The different information gained with different monitoring frequencies should be considered as seriously as other elements of the study design when research is planned and implemented.

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**CHAPTER 4****EFFECTS OF INTRA-ANNUAL TIMING OF PRECIPITATION AND ACORN  
HARVEST DATE ON EMERGENCE OF EMORY OAK****Abstract**

Germination of semi-arid oaks is strongly correlated with the rainy season. However, the timing and amount of summer precipitation in the southwestern United States is extremely variable. Ongoing and impending changes in global and regional climates are likely to increase this variability. Specifically, anthropogenically induced changes in general circulation patterns may alter the seasonal distribution of precipitation in a directional manner. In addition to climatic variability, the inter- and intra-annual variability of Emory oak (*Quercus emoryi* Torr.) acorn maturation also is high. Therefore, in light of existing climatic variability and potential future climate change, we conducted a greenhouse experiment to investigate the effects of acorn maturation date and the timing of the onset of the 'monsoon' on emergence of Emory oak seedlings. Acorns were collected at weekly intervals in July of 1995 and 1996, planted in a greenhouse, and subjected to different watering treatments. Watering treatments were (1) acorns watered the same day as planting, (2) acorns watered

2 weeks after planting, (3) acorns watered 4 weeks after planting. Emergence in 1995 was significantly greater in the last week of acorn maturation and decreased significantly as time to the onset of the 'monsoon' increased. Emergence in 1996 was very low, presumably because of soil moisture contents that were lower than those observed in 1995. Emory oak's dependence on water for emergence has profound implications for oak recruitment in the face of current climatic variability and future climate change. Summers with a delayed 'monsoon' and decreased soil moisture may severely constrain recruitment of Emory oak seedlings.

### Introduction

Germination of semi-arid oaks is strongly correlated with the rainy season (Pase 1969, Griffin 1971, Nyandiga and McPherson 1992). An acorn is most likely to germinate if it falls on or is dispersed to a mesic microsite and is then exposed to adequate precipitation (Pase 1965, 1969). Thus, considerable variability in germination occurs between years or between sites within years (e.g., Sanchini 1981, Borelli et al. 1994, Weltzin and McPherson 1995).

Germination of Emory oak (*Quercus emoryi* Torr.), the dominant tree in southwestern oak savannas, is greatest immediately after acorn maturation (Nyandiga and McPherson 1992). Maturation of Emory oak acorns begins in late June/early July; however, there is considerable variability in the timing of acorn maturation among individuals. Consequently, there is a fairly constant supply of ripe acorns throughout July and August. Little is known about how the timing of acorn maturation affects viability, germination, or emergence.

Summers in the southwestern United States are characterized by a period of intense heavy rainstorms (the 'monsoon') that usually begins in mid-July. However, climatological data reveal that the onset of the 'monsoon' is extremely variable, and may occur as late as the end of

August in some years (NOAA 1900-1994). In addition to the natural variability in the timing of the onset of the 'monsoon,' the amount of precipitation during the summer also is quite variable. Variability in both attributes is likely to increase as a result of ongoing and impending changes in global and regional climates (e.g., Manabe and Weatherald 1986, Balling et al. 1992, Houghton et al. 1996). Specifically, anthropogenically induced changes in general circulation patterns may alter the seasonal distribution of precipitation in a directional manner (e.g., delaying the 'monsoon') (Schneider 1993).

Relationships between acorn maturation, seasonal distribution of precipitation, and seedling emergence are poorly understood, yet these relationships may have important implications for ecology and management of southwestern oak woodlands. For example, understanding relationships between climatic factors and plant life history stages (i.e., emergence, growth, survival) and accurately predicting the response of plants and ecosystems to changes in climate will facilitate proactive resource management (McPherson and Weltzin, in press).

Given the inherent variability of acorn maturation and climate, and in recognition of the potential for climatic changes in the future, we conducted a greenhouse experiment

to further investigate how these 2 factors affect emergence of Emory oak seedlings. The objectives of the experiment were to determine how (1) the timing of acorn maturation, and (2) the timing of the onset of the 'monsoon' affect emergence of Emory oak seedlings.

### **Methods**

In June of 1995 and 1996, 100 round (15 cm diameter x 25 cm deep) pots were filled with soil from the upper 20 cm beneath mature Emory oak trees at the mouth of Blacktail Canyon, Huachuca Mountains. A detailed description of the site is provided in Germaine chapter 2. Soil was excavated and placed in pots without disruption of soil horizonation. Pots were taken to a greenhouse in Tucson, Arizona where acorn maturation and watering treatments were assigned to pots in a completely randomized design, as described below. The greenhouse was maintained between 18° and 32° C.

#### *Effects of acorn maturation date*

I collected 350 acorns/week at weekly intervals between 30 June and 21 July 1995, and 28 June and 12 July 1996 (periods of peak acorn ripeness). Acorns were less abundant in 1996 than 1995; consequently, ripe acorns were harvested for 3 weeks in 1996, compared to 4 weeks in 1995. Acorns were selected based on the protocol of Nyandiga and McPherson (1992). Fifty of the 350 acorns were randomly selected for destructive viability testing using 0.1% tetrazolium chloride solution (Nyandiga and McPherson 1992) and length, width, and mass were measured on 20 acorns. The remaining 300 acorns were planted in the greenhouse on the

day they were harvested.

*Effects of timing of 'monsoon' onset*

Three watering treatments were used to simulate differences in the onset of the monsoon: (1) watering that began the day acorns were planted, (2) watering that was delayed for 2 weeks after acorns were planted, and (3) watering that was delayed for 4 weeks after acorns were planted. Each watering treatment had 5 replications (pots), each of which contained 20 acorns planted 1 cm below the soil surface. The 3 watering treatments were applied coincident with each acorn harvesting date (N=60 pots in 1995, 45 pots in 1996).

Amount of precipitation for the experiment was based on the 20-year mean precipitation for July, August, and September (NOAA 1974-1994, Canelo Hills station). Once watering was initiated, each pot received 210 mL of water twice-weekly for 6 weeks. Thus, total amount of water received by the pots in each treatment was held constant throughout the experiment. Soil moisture samples were collected weekly for all 3 watering treatments.

I re-randomized the location of pots weekly and monitored seedling emergence every 2 days for 10 weeks. Emerged seedlings were clipped throughout the experiment to

minimize effects of seedlings on neighboring acorns.

Data were inspected for normality, linearity, and homogeneity of variances by plotting error residuals (Tabachnick and Fidell 1983). Data met all the assumptions of analysis of variance (ANOVA). ANOVA was used to assess main and interactive effects of acorn harvest date, year, and onset of the 'monsoon' on emergence. ANOVA also was used to test for differences in soil moisture between watering treatments and years. Means were compared with Fisher's LSD when appropriate.

### Results

The presence of 2-way interactions ( $P=0.0001$ ) of year by water treatment and water treatment by acorn harvest week precluded discussion of main effects. Within each of the 3 watering treatments in 1995, emergence was greater ( $P<0.0025$ ) for the last week of acorn harvest than the 3 previous weeks, which did not differ ( $P>0.05$ ) (Fig. 4.1). Within each acorn harvest week, mean emergence in 1995 was greater ( $P<0.0001$ ) for the first watering treatment (watered same day as planted) than for the other watering treatments. This pattern was evident ( $P<0.05$ ) only for the first week of acorn harvest in 1996. The first week of acorn harvest and application of water the same day as acorns were planted was the only treatment combination in 1996 for which seedlings emerged.

Soil moisture content was inversely related to watering treatments ( $P<0.05$ ) (Fig. 4.1). In addition, soil moisture content was higher ( $P<0.001$ ) in 1995 than 1996.

Acorn viability did not differ between acorn harvest weeks or years (range=94-98% viable). Similarly, acorn mass did not differ between weeks of harvest or years.

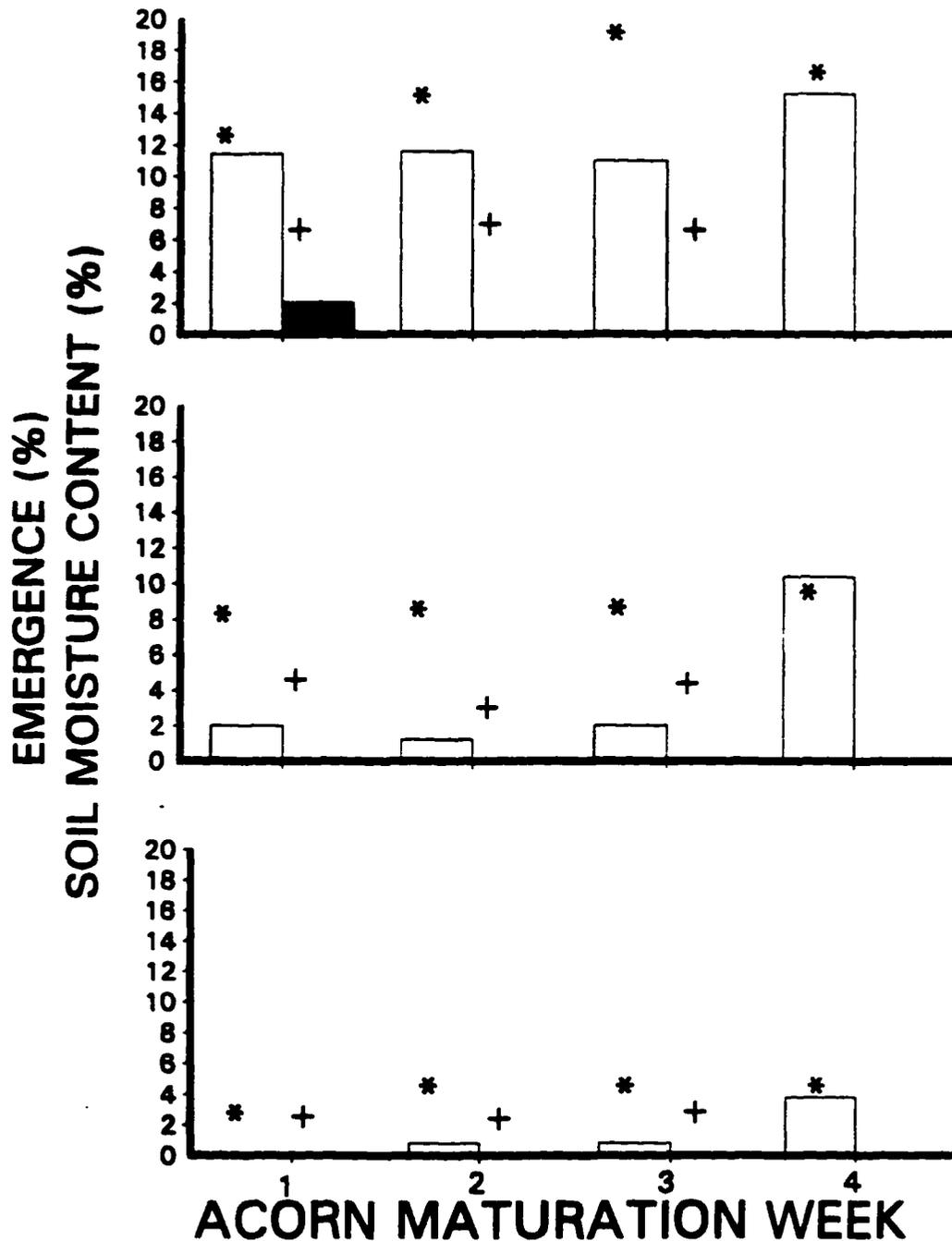


Figure 4.1. Emergence of Emory oak seedlings during 1995 (open bars) and 1996 (solid bars) in a greenhouse in Tucson, Arizona under different watering treatments: (top) initially watered same day planted, (middle) initially watered 2 weeks after planted, (bottom) initially watered 4 weeks after planted. Soil moisture content represented by \* in 1995 and by + in 1996. Acorns were planted coincident with maturation on 4 different weeks in 1995 and on 3 weeks in 1996.

### Discussion

Inter- and intra-annual climatic variability can influence oak emergence. In the current study, emergence decreased as time to the onset of the 'monsoon' was delayed.

Emergence of Emory oak seedlings decreased up to 80% with a 2-week delay in watering and was further reduced with a 4-week delay. Post-maturation delays in precipitation may have profound implications for oak recruitment, especially into relatively xeric grassland sites. If the 'monsoon' does not begin until late August, even acorns produced late in the season (late July) have a low probability of emergence regardless of acorn production.

Emergence and soil moisture content were significantly lower in 1996 than 1995. Acorn viability was high and the same experimental protocol was followed each year (i.e., amount and timing of water application). However, temperatures inside the greenhouse exceeded the desired range in 1996, which caused soil moisture contents to be reduced relative to 1995. Thus, it appears that emergence was low in 1996 because of insufficient soil water. This finding is consistent with the association between emergence and delayed 'monsoon', and has profound implications for oak recruitment in the present and near future. Mean global surface temperatures are expected to increase as a result of

elevated CO<sub>2</sub> levels (Mitchell et al. 1990) which can contribute to decreased soil moisture contents. Reduced soil moisture contents may constrain oak seedling establishment in grassland sites where the ameliorating effects of mature trees are not present.

Data from 1995 revealed that emergence was the greatest in the last week of acorn harvest; however, absence of acorns in 1996 precluded subsequent verification of this pattern. In addition, there are no references in the ecological literature of such a pattern being studied elsewhere. Consequently, I am unable to draw any general conclusions regarding effects of acorn maturation date on emergence.

These data indicate that emergence of Emory oak is significantly limited by post-maturation delays in precipitation and decreased soil moisture content. Inter- and intra-annual climatic variability and the effects of potential future climate change (i.e., delayed monsoon, increased temperature) may exert considerable control over oak recruitment. Further, summers with a late 'monsoon' and decreased soil moisture may severely constrain recruitment of Emory oak seedlings. Elucidation of relationships between timing of precipitation, soil moisture content, acorn maturation, and emergence are fundamental to effective

management in the face of potential redistribution of precipitation and increased temperatures.

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## CHAPTER 5

### CONCLUSIONS

These experiments revealed that abiotic factors affected emergence and survival of Emory oak seedlings to a greater extent than biotic factors. Emergence of Emory oak seedlings was not affected by herbaceous interference but was affected by post-maturation delays in precipitation and decreased soil moisture content (chapters 2 & 4). This finding has broad implications for shifts in lower treeline. Summers characterized by a delayed 'monsoon' and decreased soil moisture may severely constrain recruitment of Emory oak seedlings, especially into relatively xeric grassland sites where emergence, is lower than in the adjacent woodland.

Survival of Emory oak seedlings was affected by interference at 2 levels (understory and overstory) and herbivory (chapter 2). Survival was greatest in plots with all understory vegetation removed. Belowground interference clearly constrained survival of Emory oak seedlings, which suggests that rapid early root growth is crucial for Emory oak seedling survival.

In addition to the negative effects of the understory, the overstory also affected survival. Survival was greatest in plots with complete overstory removal. Thus, the

positive effects of the canopy (e.g., decreased soil temperature, increased soil nutrients) were masked or overridden by negative effects (e.g., shade, decreased soil moisture beneath trees due to interception of precipitation).

Survival also was affected by vertebrate herbivory. However, these results demonstrate that vertebrate-induced mortality is extremely variable from year to year. Even though vertebrates were a major source of mortality during one year and for one cohort of seedlings, they were negligible during the remainder of the study, especially compared to the effects of abiotic factors.

Seedling mortality was almost always attributed to desiccation. Periods of high mortality generally corresponded to periods of low precipitation. The importance of soil moisture on Emory oak recruitment was accentuated by results from the greenhouse experiment (chapter 4).

Data from the frequency of monitoring investigation (Chapter 3) revealed that woody plants should be monitored at least monthly to evaluate emergence and survival after one year. However, confidence in determination of the date of emergence and the cause of mortality increases at higher frequencies of monitoring.

It is clear that identification of the constraints on

woody plant recruitment is crucial to our ability to predict changes in vegetation physiognomy and distribution (e.g., shifts in lower treeline). Results of these experiments highlight the importance of long-term ecological experiments that elucidate mechanisms underlying plant community structure.

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