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Margaret Elizabeth Batchelor

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**The Dissertation Committee for Margaret Elizabeth Batchelor certifies that this is
the approved version of the following dissertation:**

The Balance between Positive and Negative Interactions in a Savanna

Committee:

Norma Fowler, Supervisor

Randy Linder

Marcy Litvak

Mike Singer

Martha Smith

The Balance between Positive and Negative Interactions in a Savanna

by

Margaret Elizabeth Batchelor, B.A., M.S.Stat.

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The Balance between Positive and Negative Interactions in a Savanna

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Supervisor: Norma L. Fowler

Three separate studies investigated the spatial patterns observed in central Texas savannas and the potential plant interactions (i.e. competition and facilitation) that may be causing them. The first study measured the magnitude and the direction of the spatial association between *Quercus fusiformis* (live oak) and *Juniperus ashei* (Ashe juniper) in several sites on the eastern Edwards Plateau. *J. ashei* individuals occurred in significantly higher than expected frequencies under woody canopies and in significantly lower than expected frequencies in the open grassland. The strength of this pattern decreased with *J. ashei* size, suggesting that facilitation by woody canopy species becomes less strong over the life of a *J. ashei* understory individual.

The second study was a garden experiment testing the hypothesis that whether the effect of shade on *Juniperus ashei* seedlings is negative or positive depends upon water availability. The effects of three watering treatments and two shade treatments upon survival and growth were measured in a full-factorial design. The results of this study

confirmed that the effect of shade upon *Juniperus ashei* seedlings depends upon water availability. Furthermore, instead of the effect gradually changing from negative to positive along a gradient of decreasing water availability, the effect changed abruptly from negative to positive at the point at which seedlings began to die from water shortage.

The third study was a two-year experimental field study of the effects of three overstory types ('*Quercus*' overstory, '*Juniperus*' overstory, and no overstory) and three substrate types (soil and litter from live oak clusters, from juniper clusters, and from open patches) on the germination, survival, and growth of *Juniperus ashei* seedlings in a factorial design. The presence of an adult *Juniperus ashei* facilitated *J. ashei* seedling germination and survival, but decreased growth rates. Evidently, facilitation of seedlings contributes to the positive spatial association between *Juniperus ashei* adults and *J. ashei* seedlings. However, the positive spatial association between adult oaks and *J. ashei* seedlings is evidently not due to facilitation.

Table of Contents

List of Tables.....	xi
List of Figures.....	xii
Chapter 1: Introduction.....	1
Chapter 2: Spatial association between two woody plants in a savanna system: evidence for facilitation?.....	5
Abstract.....	5
Introduction.....	6
Methods.....	7
Species.....	7
Study sites.....	8
Data collection.....	8
Comparisons with external expectations.....	10
Comparisons with internal expectations.....	13
Results.....	14
Is the distribution of <i>Juniperus</i> individuals consistent with external expectations?.....	14
Is the distribution of <i>Juniperus</i> individuals consistent with internal expectations?.....	16
Discussion.....	16
Literature cited.....	31
Chapter 3: Shifts in the balance between positive and negative effects along an environmental stress gradient in a controlled experiment.....	34
Abstract.....	34
Introduction.....	36
Methods.....	38
Study system and organism.....	38
Experiment 1.....	39

Experiment 2.....	41
Results.....	44
Experiment 1.....	44
Experiment 2.....	44
Discussion.....	45
Mechanism of positive effect.....	46
Mechanism of negative effect.....	47
Potential interactions among factors.....	48
Interaction between light and water on growth rates.....	49
Limits of this study.....	50
Extension of results to field.....	51
Literature cited.....	62
Chapter 4: Intraspecific facilitation of <i>Juniperus ashei</i> in Texas savannas.....	67
Abstract.....	67
Introduction.....	68
Methods.....	70
Organisms and study site.....	70
Materials.....	72
Experimental design.....	73
Statistical analyses.....	74
Summary data.....	74
Treatment effects.....	75
Survival analysis.....	76
Results.....	77
Summary data.....	77
Treatment effects.....	78
Survival analysis.....	80
Discussion.....	81
Life history of <i>J. ashei</i>	81

Seed dispersal.....	83
Treatment effects on germination.....	84
Treatment effects on survival.....	85
Treatment effects on growth rates.....	86
Treatment effects on the number of seedlings alive at the end of the experiment.....	87
Facilitation of seedlings by adult <i>Juniperus ashei</i>	87
Competition with seedlings by adult <i>Juniperus ashei</i>	88
The balance between competition and facilitation.....	89
What this says about spatial pattern.....	90
What this says about woody encroachment.....	91
Literature cited.....	111
References.....	118
Vita.....	128

List of Tables

Table 2.1:	Study sites.....	20
Table 2.2:	Two measures of the strength of the association with each habitat type...	21
Table 2.3:	Full log-linear model maximum likelihood analysis of variance.....	22
Table 3.1:	Results of the ANOVA of mean total biomass.....	52
Table 3.2:	Results of the ANOVA of mean root/shoot ratio.....	52
Table 3.3:	Results of the ANOVA of above-ground height.....	53
Table 3.4:	Results of the ANOVA of belowground height.....	53
Table 4.1:	Contingency table analysis of germination date and survival.....	93
Table 4.2:	Number of naturally dispersed (not planted) seeds in each habitat type by block.....	93
Table 4.3:	Results of the ANOVA of mean germination date.....	93
Table 4.4:	Results of the ANOVA of the mean number of germinants.....	94
Table 4.5:	Results of the ANOVA of the mean number of surviving individuals.....	94
Table 4.6:	Results of the ANOVA of mean biomass of surviving individuals.....	94
Table 4.7:	Summary of logistic regression results of the effects of germination date on survival to end of experiment.....	94
Table 4.8:	Results of the ANOVA of mean difference between predicted and observed survival.....	95
Table 4.9:	Climate data for study site.....	95

List of Figures

Figure 2.1:	Comparison of the total number of observed and expected <i>J. ashei</i> individuals at all three sites. Expected numbers calculated from null model A.....	23
Figure 2.2:	Comparison of the total number of observed and expected <i>J. ashei</i> individuals at all three sites. Expected numbers calculated from null model B.....	24
Figure 2.3:	Comparison of the number of observed and expected <i>J. ashei</i> individuals at all three sites. Expected numbers calculated from null model C.....	25
Figure 2.4:	Comparison of the number of observed and expected <i>J. ashei</i> individuals by size class at the National Wildlife Refuge. Expected numbers calculated from null model D.....	26
Figure 2.5:	Comparison of the number of observed and expected <i>J. ashei</i> individuals by size class at the Freeman Ranch. Expected numbers calculated from null model D.....	27
Figure 2.6:	Comparison of the number of observed and expected <i>J. ashei</i> individuals by size class at Pedernales Falls State Park. Expected numbers calculated from null model D.....	28
Figure 2.7:	The average value of the strength of association (observed-expected/expected) by size class and habitat type.....	29
Figure 2.8:	Size distribution of <i>J. ashei</i> individuals within each habitat type for each site.....	30
Figure 3.2:	The effect of water on the percent survival of transplanted <i>J. ashei</i> plants in experiment 1.....	55
Figure 3.3:	The effect of shade on the mean total biomass of <i>J. ashei</i> individuals....	56
Figure 3.4:	Effect of watering treatment on mean total biomass of <i>J. ashei</i> individuals.....	57
Figure 3.5:	Total biomass of <i>J. ashei</i> plants by shade treatment and water treatment.	58
Figure 3.6:	The effect of shade on mean root/shoot ratio of <i>J. ashei</i> individuals.....	59

Figure 3.7:	The effect of shade on mean above-ground height of <i>J. ashei</i> individuals.....	60
Figure 3.8:	Effect of watering treatment on the mean above-ground height of <i>J. ashei</i> individuals.....	61
Figure 4.1:	Number of <i>J. ashei</i> germinants by month.....	96
Figure 4.2:	Per capita germination rate of <i>J. ashei</i> by month.....	97
Figure 4.3:	Number of <i>J. ashei</i> deaths reported by month.....	98
Figure 4.4:	Per capita death rate (i.e. deaths per seedling alive at the beginning of the month) of <i>J. ashei</i> germinants by month.....	99
Figure 4.5:	Number of <i>J. ashei</i> germinants alive at the end of the experiment by cohort.....	100
Figure 4.6:	Proportion of <i>J. ashei</i> cohort that died before the end of the experiment.....	101
Figure 4.7:	Mean germination date of <i>J. ashei</i> seeds in different habitat types and different soil types.....	102
Figure 4.8:	Mean number of <i>J. ashei</i> germinants by habitat type and soil type.....	103
Figure 4.9:	Mean number of surviving <i>J. ashei</i> individuals by habitat type.....	104
Figure 4.10:	Mean number of surviving <i>J. ashei</i> individuals by soil type.....	105
Figure 4.11:	Mean biomass of <i>J. ashei</i> individuals by habitat type.....	106
Figure 4.12:	The effect of habitat type on the residual between the mean observed survival and the predicted survival from the mean germination date.....	107
Figure 4.13:	The effect of habitat type and soil type on the residual between the mean observed survival and the predicted survival from the mean germination date.....	108
Figure 4.14:	Hazard function of <i>J. ashei</i> individuals by habitat type.....	109
Figure 4.15:	Cumulative survival of <i>J. ashei</i> individuals by habitat type.....	110

Chapter 1: Introduction

Plant community ecologists have been describing non-random spatial patterns in natural plant communities and inferring their causes for almost a century (McIntosh 1985). Typically, negative associations are ascribed to competition, while positive ones have sometimes been ascribed to facilitation, that is, the positive effects of one plant on another (Begon et al. 1990). Plant interactions are thought to be important in structuring community-level patterns and processes (Tilman 1982, Fowler 1986, and Goldberg and Barton 1992). Classic ecological studies acknowledged the role of both negative and positive interactions in natural systems (e.g. Clements 1916). The importance of negative interactions has been widely explored with many observational, theoretical, and empirical studies (Connell 1983, Keddy 1989, and Goldberg and Barton 1992). Recently, more effort has focused on the role of positive interactions (see review in Callaway 1995, special feature in Ecology October 1997, Menge 2000, Stachowicz 2001), although the importance of negative interactions is not disputed.

Although experiments are needed to test hypotheses about facilitation and competition, a descriptive study of the spatial association generates these hypotheses, identifies critical factors for further study, and forms a foundation for future experiments. Positive spatial associations between small plants of *Juniperus ashei* (Ashe juniper, locally known as ‘cedar’) and adults of *Quercus fusiformis*, *Prosopis glandulosa*, and conspecific adults have been previously reported (Fowler 1988a, Jackson and Van Auken 1997, Anderson et al. 2001). However no previous study had measured the strength and

the direction of the association at multiple sites for multiple size classes with substantial sample sizes. In chapter 2, I measure the magnitude and the direction of the spatial association between *J. ashei* plants and adult woody plants, for three size classes of target *J. ashei* plants and two species of adult neighboring plants (*Juniperus ashei* and *Quercus fusiformis*) at three different savanna sites in central Texas.

There appears to be broad agreement in the literature that the balance between positive and negative interactions (1) may shift within a system and (2) may depend on the severity of abiotic stress in the system (Holmgren et al 1997, Callaway and Walker 1997, Bertness and Leonard 1997, Tielborger and Kadmon 2000, Tewksbury and Lloyd 2001). It has been proposed that facilitation (or positive interactions) is more common in environments that are more stressful (Bertness and Callaway 1994, Brooker and Callaghan 1998, Pugnaire and Luque 2000, Callaway et al. 2002,). A majority of the studies that report finding facilitation have been done in arid, saline, or otherwise abiotically stressed environments (Callaway 1995), although facilitation has occasionally been found in less stressful environments (Berkowitz et al. 1995, Holmgren 2000, Holl 2002, Ganade and Brown 2002, Pages et al. 2003). However, the apparent tendency for facilitation to be more common in high-stress environments may be due in part to its being tested in such environments more often.

Authors who report finding facilitation in arid systems often suggest that the positive effects of shading by a neighboring plant on the water status of a target plant have outweighed the negative effects of competition for light and water with the same neighboring plant (Callaway 1992, Greenlee and Callaway 1996, Weltzin and McPherson

1999, Hastwell and Facelli 2003). However, very few studies have directly tested the interaction between the effects of soil moisture and light reduction in this context, that is, the balance between their positive and negative effects on plants (but see Canham et al. 1996, Holmgren 2000, Hastwell and Facelli 2003). In Chapter 3, I examine the relationship between positive and negative effects along a gradient of water stress. The experiment was conducted in a garden, which allowed me to control other potential factors and isolate the direct effects of shade on *Juniperus ashei* plants along a gradient of water availability.

The balance between positive and negative interactions between plant species can differ across space and time at many scales. For example, microclimate and micro-site conditions can shift a relationship from positive to negative within a single site (Pugnaire and Luque 2001), as can differences in precipitation between years (Aguiar and Sala 1994). Whether a plant experiences a net negative or positive impact from a neighboring plant can also depend upon the age and developmental stage of the focal plant (Greenlee & Callaway 1996, Pugnaire et al. 1996, Callaway 1998, Rousset and Lepart 2000). Therefore studies that only examine a single trait of a species may miss important shifts from positive to negative and vice versa in that species' interactions with other plant species (Howard and Goldberg 2001).

In chapter 4, I test whether the most common canopy species of savannas on the Edwards Plateau, *Quercus fusiformis* and *Juniperus ashei*, have a net effect of facilitation or net effect of competition on the germination, survival, and growth of young *J. ashei*. To provide a definitive test of this hypothesis, a randomized full-factorial field

experiment was done. Unlike an observational study, an experimental study can determine which factors are direct causes of the phenomenon (the spatial association, in this case) and which are not. Unfortunately much of the existing literature about ‘nurse plants’ is limited to observational studies of spatial patterns (but see Barnes and Archer 1999, Holl 2002, Martinez 2003, Franks 2003, Tirado and Pugnaire 2003).

Chapter 2: Spatial association between two woody plants in a savanna system: evidence for facilitation?

ABSTRACT

Facilitation (the positive effects of one species on another), in theory, can lead to positive spatial associations between species. Competition (the negative effects of one species on another) can lead to negative spatial associations. Therefore the magnitude and the direction of the spatial association between *Quercus fusiformis* and *Juniperus ashei* were measured in multiple savanna sites on the Edwards Plateau in central Texas. Stratified random sampling was used to determine the number of *Juniperus ashei* individuals in each of three size classes found in each of three types of habitat (under *Quercus fusiformis* canopy, under *Juniperus ashei* canopy, and in open grassy areas). This observed spatial distribution was compared with the distribution generated by a null model that assumed no interaction between *J. ashei* individuals and habitat type. *J. ashei* individuals were found in significantly higher than expected frequencies under woody canopies and in significantly lower than expected frequencies in the open grassland. The positive association with *Quercus fusiformis* and *Juniperus ashei* canopies was significant for all size classes of target *J. ashei* individuals, but the strength of the pattern decreased with size. Mechanisms other than facilitation could explain the spatial distribution of *J. ashei* on the Edwards Plateau (e.g. seed dispersal). This study suggests that if facilitation exists in this system, it probably occurs between woody canopy and *J. ashei* during the early stages of its life history.

INTRODUCTION

Plant community ecologists have been describing non-random spatial patterns in natural plant communities and inferring their causes for almost a century (McIntosh 1985). Typically, negative associations are ascribed to competition, while positive ones have sometimes been ascribed to facilitation, that is, the positive effects of one plant on another (Begon et al. 1990). Although experiments are needed to test hypotheses about facilitation and competition, a descriptive study of the spatial association generates these hypotheses, identifies critical factors for further study, and forms a foundation for future experiments. Accordingly, I report here the results of such a descriptive study.

A positive spatial association between small plants of *Juniperus ashei* (Ashe juniper, locally known as ‘cedar’) and adults of *Quercus fusiformis*, and *Prosopis glandulosa* as well as conspecific adults had been previously reported (Fowler 1988, Jackson and Van Auken 1997, Anderson et al. 2001). However no previous study had measured the strength and the direction of the association at multiple sites for multiple size classes with substantial sample sizes. I therefore measured the magnitude and the direction of the spatial association between *J. ashei* plants and adult woody plants, for three size classes of target *J. ashei* plants and two species of adult neighboring plants (*Juniperus ashei* and *Quercus fusiformis*) at three different savanna sites in central Texas.

The observed spatial pattern of the study species was compared to the spatial pattern predicted by a simple null model that did not require the use of specialized spatial statistics. There are many methods for analyzing spatial pattern in plant communities, many of which are quite complex (Liebhold and Gurevitch 2002). The relatively simple

methods used here may be generally useful, since they provide an approachable, straightforward alternative for studying spatial patterns in plant communities. The choice of an appropriate null model is always a critical step (Harvey et al. 1983); I used a null model that assumed that individual *J. ashei* plants are found within the different habitat types in a site in proportion to the relative abundance of each of those habitat types in that site, thus avoiding a bias towards more abundant habitat types.

METHODS

Species

Juniperus ashei is a multi-trunked ‘tree’ up to 6 m tall (Correll and Johnston 1970) native to central Texas and common throughout this region. Its seeds are dispersed by cedar waxwings, mockingbirds and robins (Chavez-Ramirez and Slack 1994).

Quercus fusiformis (Plateau liveoak) is common in the savannas of the eastern Edwards Plateau of central Texas. Both species are evergreen. *Q. fusiformis* is true tree (i.e., single-trunked), reaching 8 m in height (Correll and Johnston 1970). Unlike *J. ashei*, *Q. fusiformis* can resprout after being cut or burned. *Q. fusiformis* trees commonly have root sprouts, although presently these very rarely grow more than 0.5 m tall, due to deer browsing (Russell and Fowler 1999). Perhaps due to past vegetative regrowth after fires at times when deer were less abundant, *Q. fusiformis* trees often occur in clusters.

Juniperus ashei is a ubiquitous invader of *Quercus fusiformis* savannas in central Texas. It may once have been controlled by summer fires, but now is routinely removed by land managers by various mechanical methods. If not removed, a near mono-specific

stand of *J. ashei* will form, containing the remaining adult *Q. fusiformis* but few other woody or herbaceous species.

Study sites

The study was conducted at three sites, all on the eastern Edwards Plateau of central Texas (Table 2.1). All three sites were in an intermediate stage of *Juniperus ashei* encroachment; they each had *Juniperus ashei* individuals of all sizes, from seedling to adult 'tree', but also had a substantial amount (between 50% and 65% cover) of open grassy area not under the canopy of any woody species. None of the sites had woody canopy species other than *Q. fusiformis* and *J. ashei*. Recent aerial photographs were available for each site (TNRIS 1997). In each site a square survey area of 1.5 ha or less was selected that was easily defined on the ground and in the aerial photographs. The identity of canopy species in the aerial photograph and any changes in cover since the photograph was taken were noted at the same time.

Data collection

Three size classes of *Juniperus ashei* were used: < 0.5m tall, 0.5 - 1.5 m tall, and > 1.5 m tall. These size classes were used because they represent three important transitions in the life history of *J. ashei*. Individuals less than 0.5 m tall are almost never reproductively mature. Individuals in this size class also appear to have a relatively high rate of mortality (Noel unpublished data). Individuals in the next size class, 0.5-1.5m tall, may be reproductively mature, have a relatively low rate of mortality, but are still

susceptible to fire-induced mortality (Noel unpublished data). Individuals in the largest size class, >1.5m tall, are almost always reproductively mature, have a very low rate of mortality, and are likely to have escaped fire induced mortality (Noel unpublished data). In the survey area of each site, the number of *Juniperus ashei* individuals in each size class was estimated. Since the goal was to census 100 individuals in each size class, a sampling intensity was calculated by dividing 100 by the estimated number in the size class in a given site. Then, walking through the survey area, each *Juniperus ashei* individual was included or discarded depending upon whether a separately drawn random number was or was not less than the sampling intensity. For example, if the estimated number of individuals in size class 1 in site A was 200, the sampling intensity was 0.5, and each individual had a 50% chance of being included in the sample, independent of whether its neighbors had been included.

Each sampled individual *J. ashei* was classified as (1) being in the open, that is, not under a tree canopy, hereafter called ‘open’, or (2) being under the canopy of *Q. fusiformis*, hereafter called ‘*Quercus*’, or (3) being under the canopy of *J. ashei*, hereafter called ‘*Juniperus*’. If a *J. ashei* individual was under both a *J. ashei* tree and a *Q. fusiformis* tree, it was classified as being under *Q. fusiformis*, because in all cases the overstory species was *Q. fusiformis*. A canopy tree was defined as being > 1.5 m; a small *J. ashei* individual under another small individual of either species was considered to be in the open. The location of the central stem of a *J. ashei* individual was used to define its location if the individual grew at the edge of a canopy. This operational definition of ‘under’ introduces a potential bias because the area of the intersection of two circles is

actually less than half the area of the smaller circle. Therefore if the central stem of a small *J. ashei* was found to be under the canopy of a tree, it was considered to be ‘under’ even though less than half of its area was actually under the canopy of a tree. The magnitude of the bias introduced by using this definition of being under a canopy was investigated with a simulation and found to be very small as long as the *Juniperus ashei* individuals were mostly small and the canopies were large, as was the case in this study (Fowler and Batchelor unpublished data).

Comparisons with external expectations

Null models that assumed no spatial association were used to calculate the expected number of *Juniperus* individuals in each habitat type. In these null models, the relative abundance of *Juniperus* individuals in each habitat type was assumed to be proportional to the relative abundance of that habitat type. Three sets of null models were calculated:

Null model A: (*Juniperus* habitat/*Quercus* habitat/open habitat). In this model, size classes were ignored and the total number of *Juniperus* individuals under the null model was equal to the total number of individuals of all sizes in a site. A separate null model of this type was calculated for each site, using the observed relative frequencies of habitat types in that site, and generating the expected numbers of individuals in each of the three habitat types in that site. Expected and observed numbers of individuals in each habitat type were compared with a Pearson χ^2 test (3 x 1 contingency table, df = 2) for each site separately.

To explore the significant deviations from the null expectation revealed by null model A, two more null models were constructed (models B and C), comparable to the contrasts one would do in ANOVA after finding a significant treatment effect. A Bonferroni correction was used to adjust the α -level for multiple testing (Sokal and Rohlf 1994). Because two additional models (models B and C) were tested that were hierarchically nested within null model A, an α -level of 0.025 was used for significance testing in models B and C. This adjusted α -level yielded an overall α -level of 0.05 for these tests.

Null model B: (open habitat/woody habitat). This model was used to determine whether the significant departures from the expectations of null model A were due in part to differences between being under a woody canopy (pooling the under *Juniperus* habitat type with the under *Quercus* habitat types) and being in the open. In this model, size classes were ignored, the total expected number of *Juniperus* individuals in the open in a given site was unchanged from model A, and the total expected number of *Juniperus* individuals under woody canopies was equal to the proportion of the site under woody canopies multiplied by the total number of *Juniperus* individuals. Expected and observed numbers of individuals in each of two categories (open and under woody canopy) were compared with a Pearson χ^2 test (2 x 1 contingency table, $df = 1$) for each site separately.

Null model C: (*Juniperus* habitat/*Quercus* habitat). This model was used to determine whether the significant departures from the expectations of null model A were due in part to differences between being under a *Juniperus ashei* and being under a *Quercus fusiformis* canopy. In this model, size classes were ignored, the total expected

number of *Juniperus* individuals under *Juniperus* canopy in a given site was equal to the product of the total number of *Juniperus* individuals under woody canopy times the proportion of woody canopy area that had a *Juniperus* overstory in that site. The total expected number of *Juniperus* individuals under *Quercus* canopy in a given site was equal to the product of the total number of *Juniperus* individuals under woody canopy times the proportion of woody canopy area that had a *Quercus* overstory in that site. Expected and observed numbers of individuals in each of the two categories (*Juniperus* canopy and *Quercus* canopy) were compared with a Pearson χ^2 test (2 x 1 contingency table, df = 1) for each site separately.

Null model D: (*Juniperus* habitat/ *Quercus* habitat /open habitat by size class). This null model was conceptually the same as null model A except size classes were included. A separate null model of this type was calculated for each site, using the observed relative frequencies of habitat types in that site, and generating the expected numbers of individuals in each of the three habitat types within each size class in that site. Expected and observed numbers of individuals in each size class within each habitat type were compared with a Pearson χ^2 test (3 x 3 contingency table, df = 4) for each site separately.

Null model E: (*Juniperus* habitat/ *Quercus* habitat /open habitat within size class). To quantify the degree of association between *Juniperus* individuals and woody canopy for each size class, we calculated a simple measure of the degree of deviation from the expected value, (observed - expected)/(expected). This metric was used in combination with the standard Pearson's χ^2 test statistic. The magnitude of the χ^2 value

provides a second, familiar measure of the strength of the spatial association between *Juniperus* individuals and habitat types, albeit one that also is affected by sample size. The expected values were obtained from a fifth null model. In this model, the total number in each size class was set equal to the actual number of individuals sampled in that size class in the given site. (Recall that sampling intensity was pre-set in the sampling design.) The expected number of *Juniperus* individuals of a given size class in a given habitat type was equal to the total number in that size class times the proportion of the site in that habitat type. Expected and observed numbers of individuals were compared with a Pearson χ^2 test (3 x 1 contingency table, df = 2) for each site x size class combination separately. Multiple testing was taken into account using Bonferroni's correction (Sokal and Rohlf 1994). For each site nine tests were conducted to test for one-tailed deviations from the null hypothesis (i.e. three habitat types * three size classes = nine comparisons). Therefore an adjusted α -level of 0.0053 was used to achieve an overall α -level of 0.05.

Comparisons with internal expectations

To test whether *Juniperus* size classes differed among sites in the degree to which they were disproportionately associated with tree canopies, a log-linear model was used because standard chi-squared analyses do not allow three categories of variables (habitat type, site, and size class). No external expectations were calculated for these statistical tests; instead, a standard multi-way contingency table was constructed and tested. The full model included three main effects (site, habitat type, and size class), all two-way

interactions, and the three-way interaction. Parameter values were calculated using maximum likelihood estimation (Bishop et al. 1975, SAS 1990). Wald tests and likelihood ratio tests were used to determine significance.

Because the three-way interaction (site x habitat type x size class) was significant, a separate two-dimensional contingency table (habitat type x size class) was calculated and tested for each site. For each site, the habitat type x size class contingency table was tested with a Pearson χ^2 test (3 x 3 contingency table, df = 4) with an adjusted α -level of 0.017 for multiple testing.

RESULTS

Is the distribution of *Juniperus* individuals consistent with external expectations?

In each of the three sites, *Juniperus* individuals did not grow in the three different habitat types in proportion to the area occupied by each habitat type in that site (Fig. 2.1). Because the difference between the expectations of null model A (see Methods) and the observed locations of *Juniperus* individuals was significant in each site ($\chi^2 = 285.6$, 296.6, and 156.5, respectively; all $p < 0.001$), additional statistical tests were done. Comparison with the expectations of null model B revealed that significantly more *Juniperus* individuals grew under ‘woody’ canopy (pooled *Quercus* and *Juniperus* canopies), and fewer individuals in the open, than would be expected by chance, in each site ($\chi^2 = 267.9$, 268.0, and 194.6, respectively; all $p < 0.001$) (Fig. 2.2). Comparison with the expectations of null model C revealed that in two of the sites (NWR and Freeman) significantly more *Juniperus* individuals were found under *Juniperus* canopy

and fewer under *Quercus* canopy than expected by chance (NWR: $\chi^2 = 51.2$, $p < 0.001$; Freeman: $\chi^2 = 9.18$, $p = 0.002$) (Fig. 2.3). At PF there was a non-significant trend in the opposite direction.

When the *Juniperus* individuals were separated into size classes, the proportion of individuals in each size class in each habitat type differed from the expectations of null model D (see Methods) in each site ($\chi^2 = 196.8$, 369.4, 333.6, respectively; all $p < 0.001$) (Figs. 2.4-2.6). Therefore separate tests were made of each size class - site combination (null model E); each of these nine tests reached significance (Table 2.2). In other words, the distribution of each size class of *Juniperus* among habitat types differed significantly from the null expectation, at each site. The separate size classes of *Juniperus* each followed the same pattern as the pooled individuals did: fewer than expected in the open and the greatest excess over expectation under *Juniperus* canopy (compare Figs. 2.4-2.6 with Figs. 2.1).

However, there was an interesting trend for the strength of the deviation from the null expectation to decrease from the size class with the smallest individuals to the size class with the largest individuals. This can also be seen by examining the absolute value of the ratio [(observed - expected)/expected] for each size class (Table 2.2). This trend was strongest for plants under *Juniperus* canopies at NWR, where the ratio dropped from 3.3 in size class 1 to 0.125 in size class 3 (Table 2.2). This trend was most consistent for plants in the open, where the ratio decreased in absolute value from size class 1 to size class 3 at each site. Overall, based upon an average of this ratio for all three sites, the

intensity of the spatial pattern decreased with *Juniperus* size class in two of the three habitat types (Fig. 2.7).

Is the distribution of *Juniperus* individuals consistent with internal expectations?

The three-way interaction (site x habitat type x size class) was significant in the log-linear model ($p < 0.001$): the size distribution within each habitat type varied significantly among sites (Table 2.3 and Fig. 2.8). The habitat type x size class 3x3 contingency table was significant for each site ($\chi^2 = 36.5, 55.6, 42.3$ all with $p < 0.001$). The size distribution of *Juniperus* individuals was significantly different for each habitat type for each site.

DISCUSSION

Juniperus ashei individuals disproportionately occurred under the canopies of conspecific adults and under the canopies of *Quercus fusiformis* in the savannas of central Texas. They were correspondingly under-represented in open grassy areas in these savannas. Such positive associations are usually interpreted as cases of facilitation, that is, the positive effect of one plant upon another (e.g., McPherson et al. 1988, Kikvidze 1993, Eccles et al. 1999, Schenk et al. 2003). Because the spatial association described in this paper involves seedlings under larger woody plants, it resembles the classic ‘nurse plant’ phenomenon, although the original descriptions of ‘nurse plants’ involved the seedlings of a cactus species associated with adults of other, woody species (Niering et al. 1963; Turner et al. 1969; Steenberg and Lowe 1969). It is also possible,

however, that some or all of the pattern observed in this study could be due to spatial patterns of seed dispersal or the spatial patterns of favorable microsites.

The strength of the positive association between *Juniperus ashei* and larger conspecific plants decreased with the size of the target *J. ashei* plants at most sites (Fig. 2.7). Welden et al. (1990) reported a similar result in pinyon-juniper woodlands in Colorado. He found that small trees, including a *Juniperus* species, were often clumped, while medium and large trees were either randomly or uniformly dispersed. Others have also reported similar decreases in association strength with increasing plant size in other genera (e.g. Skarpe 1991, Martinez 2003). Because *J. ashei* size and age are probably correlated, the positive association probably decreases over the lifespan of a *J. ashei* plant.

The fact that the positive association between target *Juniperus ashei* plants and their much larger neighboring *J. ashei* plants was most pronounced for the smallest target plants suggests that facilitation, if it occurs, occurs early in life and that the interaction shifts from facilitative to competitive as the target *J. ashei* plants grow. In other words, the results of this study indicate that, if a positive effect of neighboring plants is responsible for the non-random spatial distribution of *J. ashei*, it acts only very early in life. This in fact was found to be the case in another study (Batchelor chapter 4). The presence of a canopy overhead may benefit a young *J. ashei* by reducing radiation, transpiration, and water stress, while later in life competition becomes relatively more important and amelioration of the aboveground environment becomes relatively less important. The results of a study of *Prosopis glandulosa* in the same region are

consistent with this hypothesis: Anderson et al. (2001) reported greater *Prosopis glandulosa* seedling density and transplant survival under the canopies of trees than in the open, but larger *Prosopis* plants were more evenly distributed and had lower water potentials under trees than in the open. Comparable results have been reported for other species and regions (e.g., Rykiel and Cook 1986, Skarpe 1991, Berkowitz et al. 1995, Martinez 2003).

The data presented here suggest that facilitation is important, especially when *Juniperus* plants are small and young, but no descriptive study can by itself eliminate other possible causes of positive spatial associations, and so the conclusions reached in this study must be regarded with caution. Callaway's review (1995) of positive interactions reported a total of 169 articles on positive interactions. A little over half of these articles (88 articles) rely solely on a correlative spatial association to infer a positive spatial association. Even many recent studies rely only on positive spatial association to infer positive interactions (e.g., Kikvidze and Nakhutsrishvili 1998; Eccles et al. 1999; Haase 2001; Schenk et al. 2003). In contrast, many, but not all, experimental studies include or were preceded by a descriptive study that documented a positive spatial association.

The majority of the experimental tests of potential facilitation look only at the effects of one or two factors, without measuring the net effect of the neighboring plant on the focal plant (but see, e.g., Callaway 1992, Aguiar and Sala 1994, Berkowitz et al. 1995, Greenlee and Callaway 1996, Rousset and Lepart 2000, Holl 2002, Hastwell and Facelli 2003, Martinez 2003, Tirado and Pugnaire 2003). While it is very valuable to

measure the effects of single factors, on single life-history traits or stages, such studies cannot tell us what the net effect of many different factors, operating at different times in the life-history, on different traits, is. For example, a positive effect upon seedlings survival may be outweighed by a negative effect upon later growth, as was found in another study of *J. ashei* (Batchelor chapter 4). Furthermore, the discovery of a positive effect on one trait at one stage in the life-history does not mean that the factor being studied caused, even in part, the positive spatial association. Conversely, the absence of a positive effect on one trait at one stage in the life-history does not mean that the positive association can be ascribed to a cause other than facilitation (e.g., to differential dispersal). A series of experimental studies is needed to determine the causes of the distribution of *Juniperus ashei* in central Texas savannas described here.

Table 2.1. Study sites

Name and Abbreviation	National Wildlife Refuge (NWR)	Freeman Ranch (FR)	Pedernales (PF)
Full Name	Doeskin Tract, Balcones Canyonlands National Wildlife Refuge	Texas State University Freeman Ranch	Pedernales Falls State Park
County	Burnet	Hays	Blanco
Area surveyed (ha)	1.5	1.1	0.6
Site Size (ha)	18.9	1701.0	2109.2
Latitude & Longitude	30° 37'N 97° 4' W	29° 56'N 98° W	30° 19'N 98° 15' W
Soil Type	Brackett-Purves-Doss Association (shallow loamy and clayey soils underlain with limestone)	Rumple-Comfort Association (relatively shallow, rocky soils that have developed over fractured limestone)	Hensley-Tarpley Association (shallow, reddish brown loam)
Slope	<5%	<5%	<5%
Land Use	Ungrazed for previous 9 years/3 cool season prescribed burns	Most of site is grazed. Area used in study was used for public wilderness trail and had no grazing. No prescribed burns.	Most of site is grazed. Area used in study was used for public wilderness trail and had no grazing. No prescribed burns.

Table 2.2. Two measures of the strength of the association with each habitat type(j = juniper, q = oak, o = grass) for each size class at each site: (observed-expected)/expected and chi-squared. The α -level was adjusted using a Boniferroni correction for multiple comparisons. Sample sizes are also given because the chi-squared statistic is sensitive to sample size.

	-----National Wildlife Refuge -----			-----Freeman Ranch-----			--Pedernales State Park-----		
	(observed- expected) expected j/q/o	Number of obs. j/q/o	χ^2 df=2 $\alpha_{.005}=\text{---}$ 7.77	(observed- expected) expected j/q/o	Number of obs. j/q/o	χ^2 df=2 $\alpha_{.005}=\text{---}$ 7.77	(observed- expected) expected j/q/o	Number of obs. j/q/o	χ^2 df=2 $\alpha_{.005}=\text{---}$ 7.77
Size class 1	3.3 0.76 -1.0	43 60 0	182.4	0.71 1.47 -0.99	41 106 1	184.8	1.37 0.63 -0.93	69 44 4	118.0
Size class 2	1.7 0.94 -0.85	27 60 8	97.7	2.39 0.03 -0.70	61 34 19	130.7	0.17 1.23 -0.64	24 47 17	52.7
Size class 3	0.125 1.111 -0.66	9 57 16	53.4	2.00 0.41 -0.75	27 24 8	53.7	-0.11 1.06 -0.42	17 35 22	26.2

Table 2.3. Full log-linear model maximum likelihood analysis of variance

Source	DF	Chi-Square	P-value
Site	2	3.88	0.1434
Habitat type	2	76.23	<.0001
Size class	2	13.02	0.0015
Site x Habitat	4	26.58	<.0001
Site x size class	4	7.15	0.1280
Habitat x size class	4	24.95	<.0001
Site x size class x habitat	7	60.64	<.0001

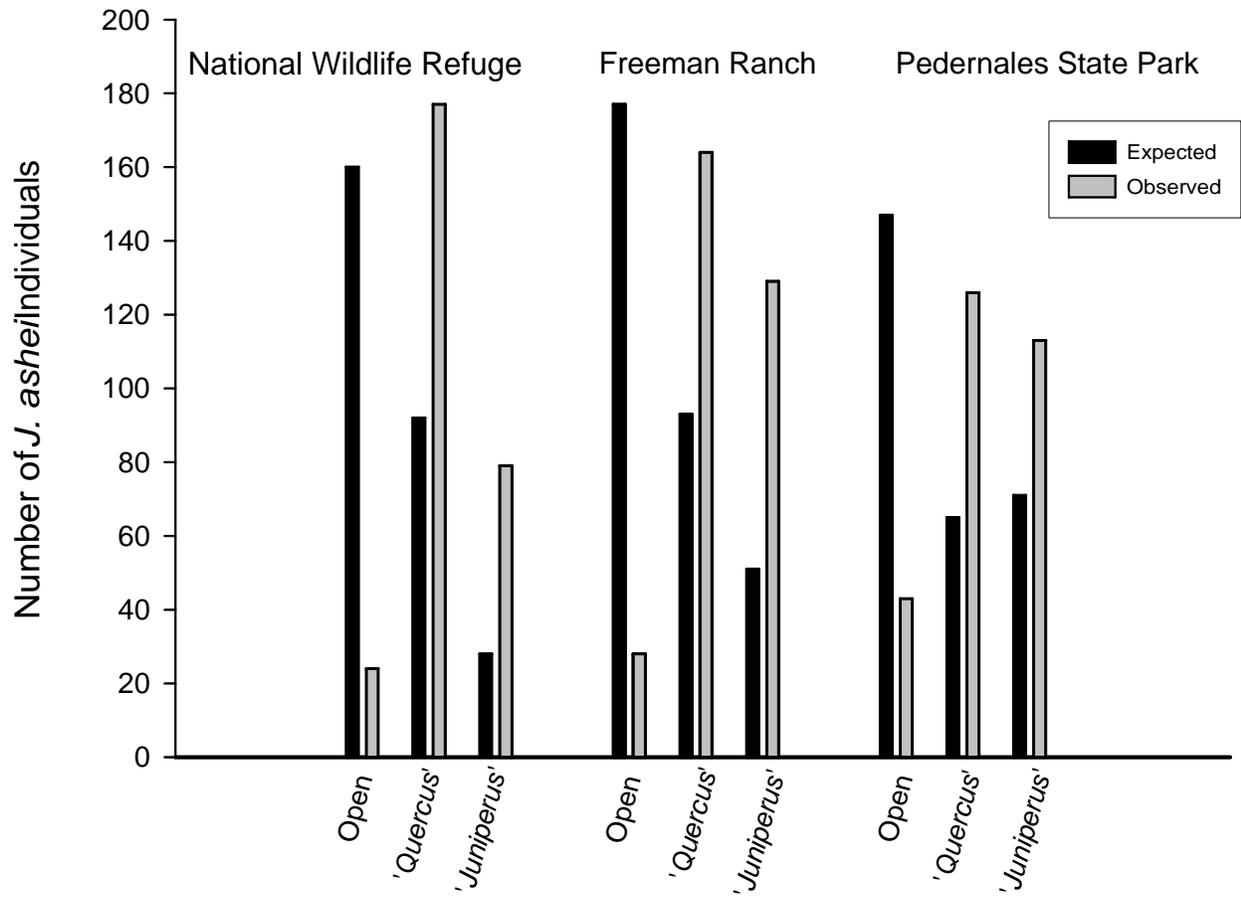


Figure 2.1. Comparison of the total number of observed and expected *J. ashei* individuals at all three sites. Expected numbers calculated from null model A.

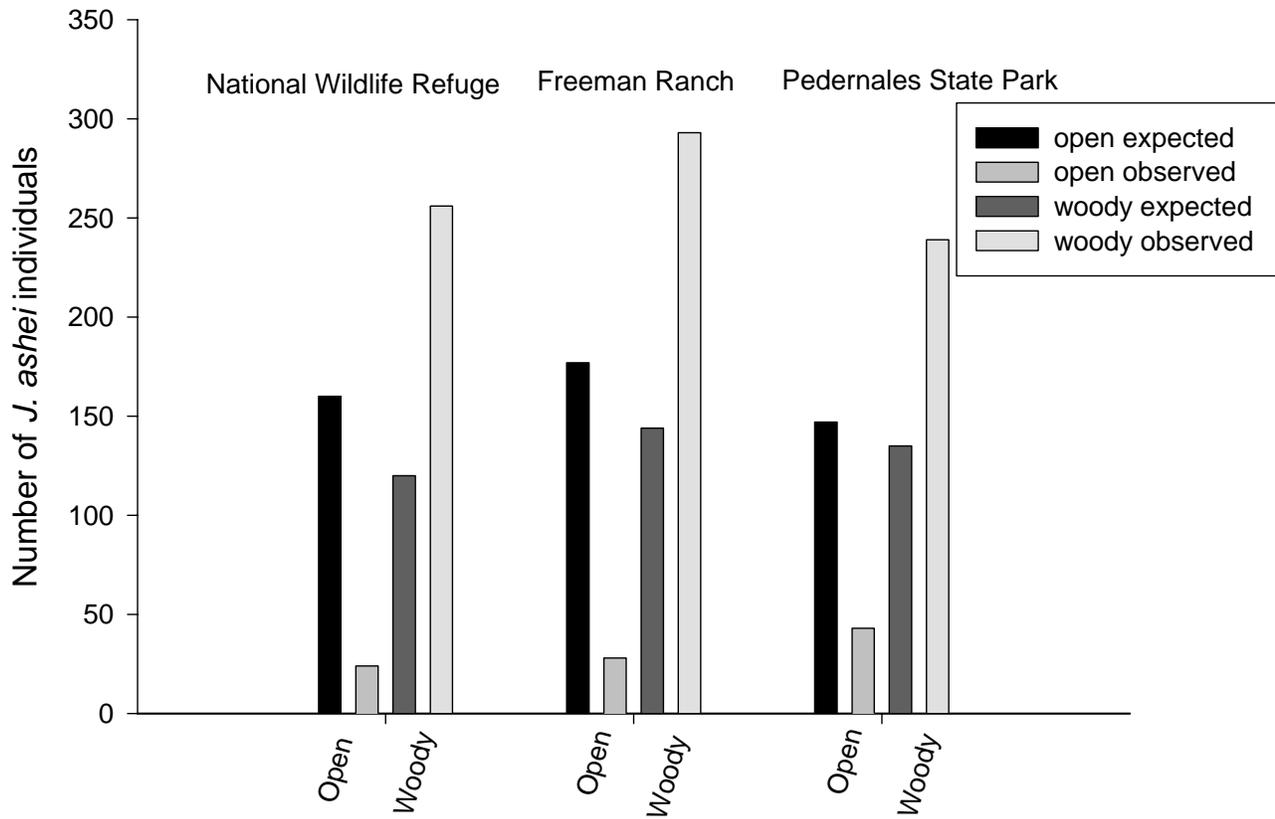


Figure 2.2. Comparison of the total number of observed and expected *J. ashei* individuals at all three sites. Expected numbers calculated from null model B.

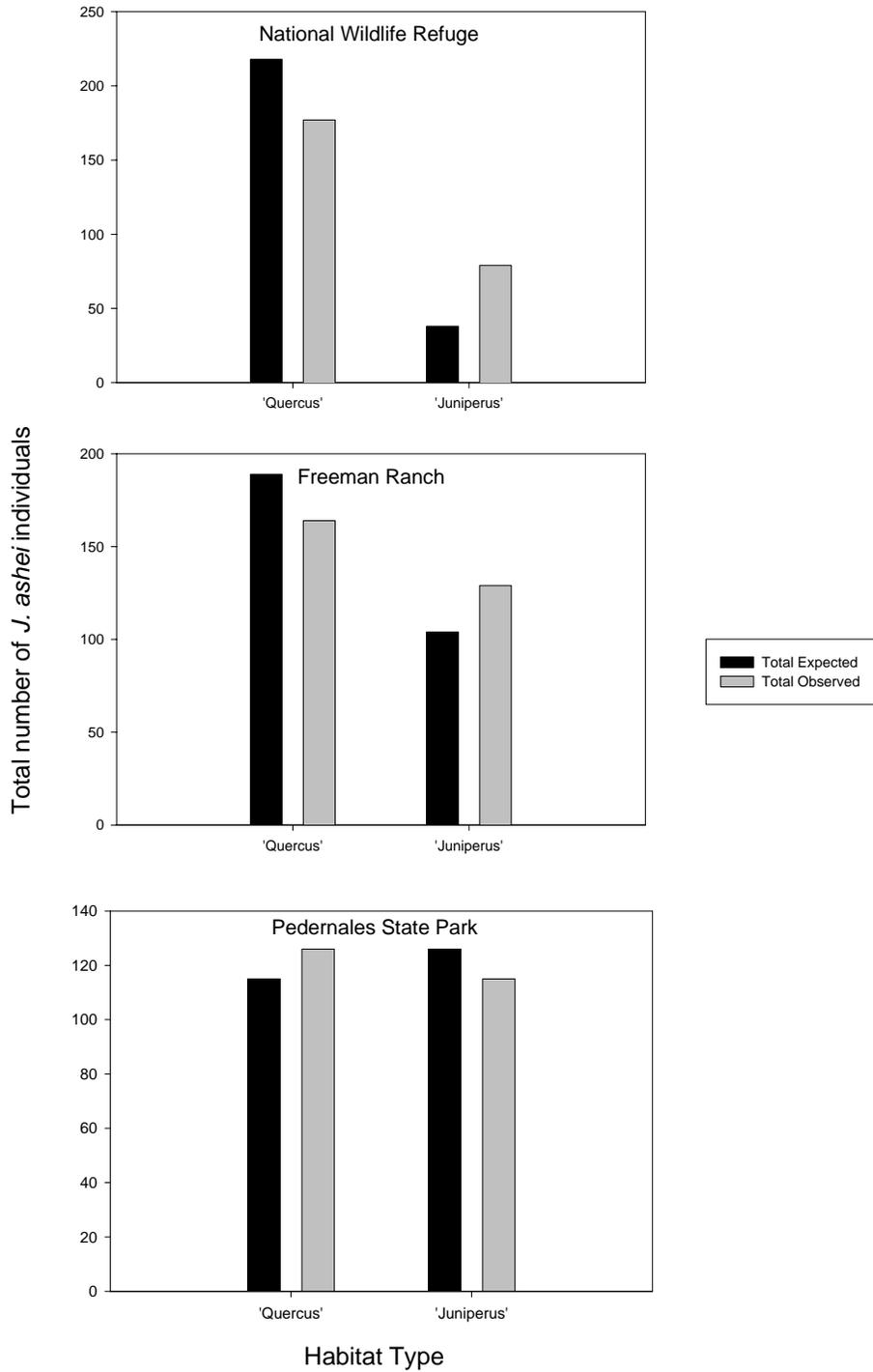


Figure 2.3. Comparison of the number of observed and expected *J. ashei* individuals at all three sites. Expected numbers calculated from null model C.

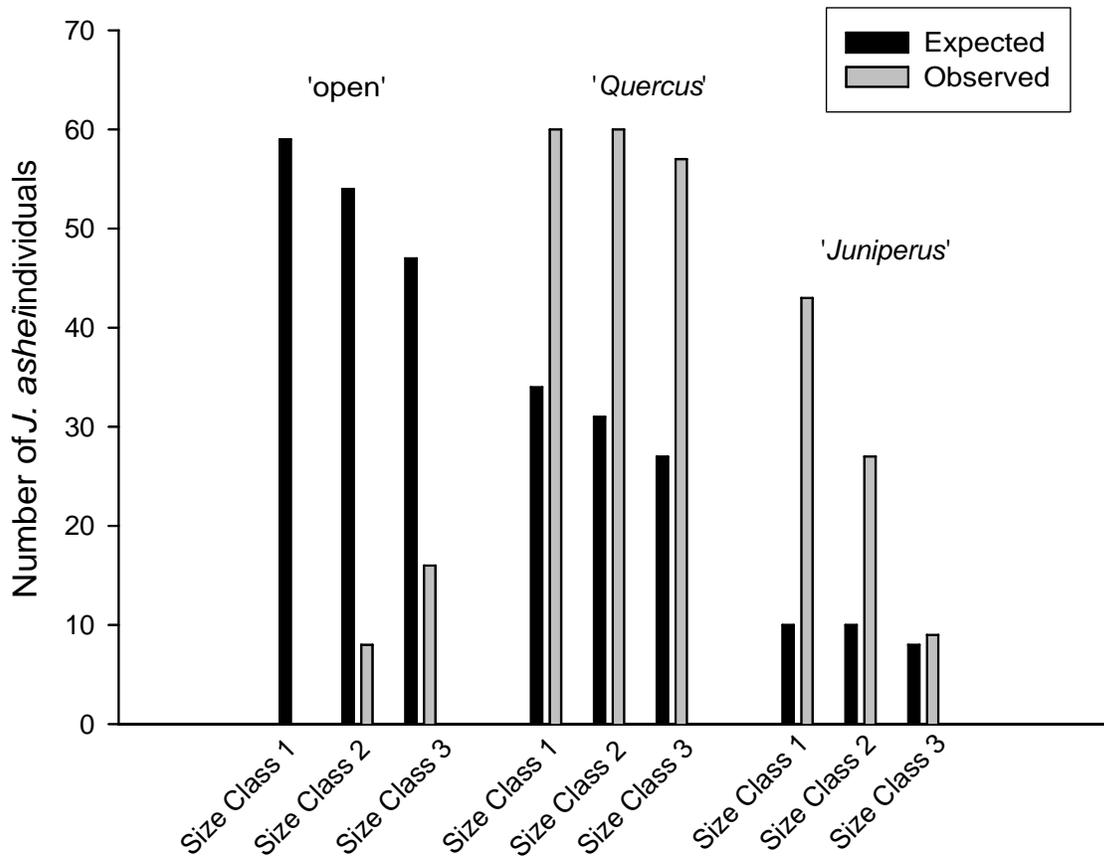


Figure 2.4. Comparison of the number of observed and expected *J. ashei* individuals by size class at the National Wildlife Refuge. Expected numbers calculated from null model D.

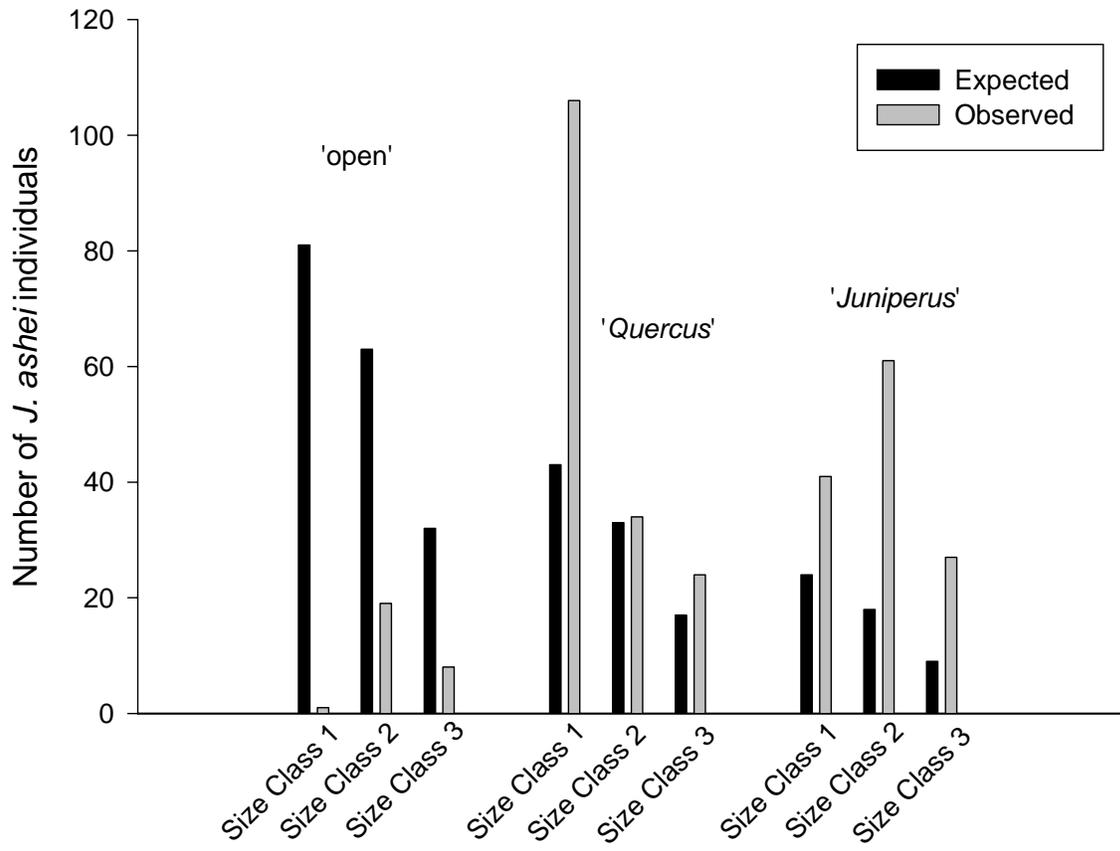


Figure 2.5. Comparison of the number of observed and expected *J. ashei* individuals by size class at the Freeman Ranch. Expected numbers calculated from null model D.

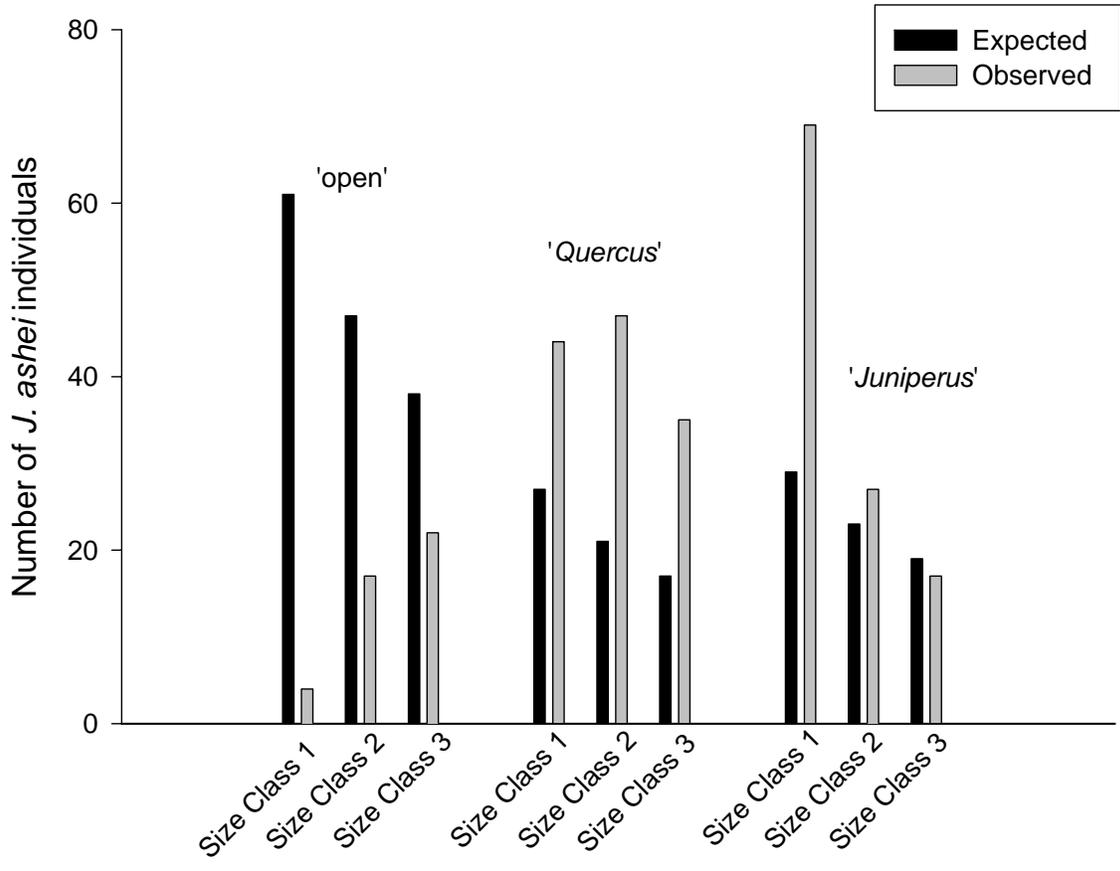


Figure 2.6. Comparison of the number of observed and expected *J. ashei* individuals by size class at Pedernales Falls State Park. Expected numbers calculated from null model D.

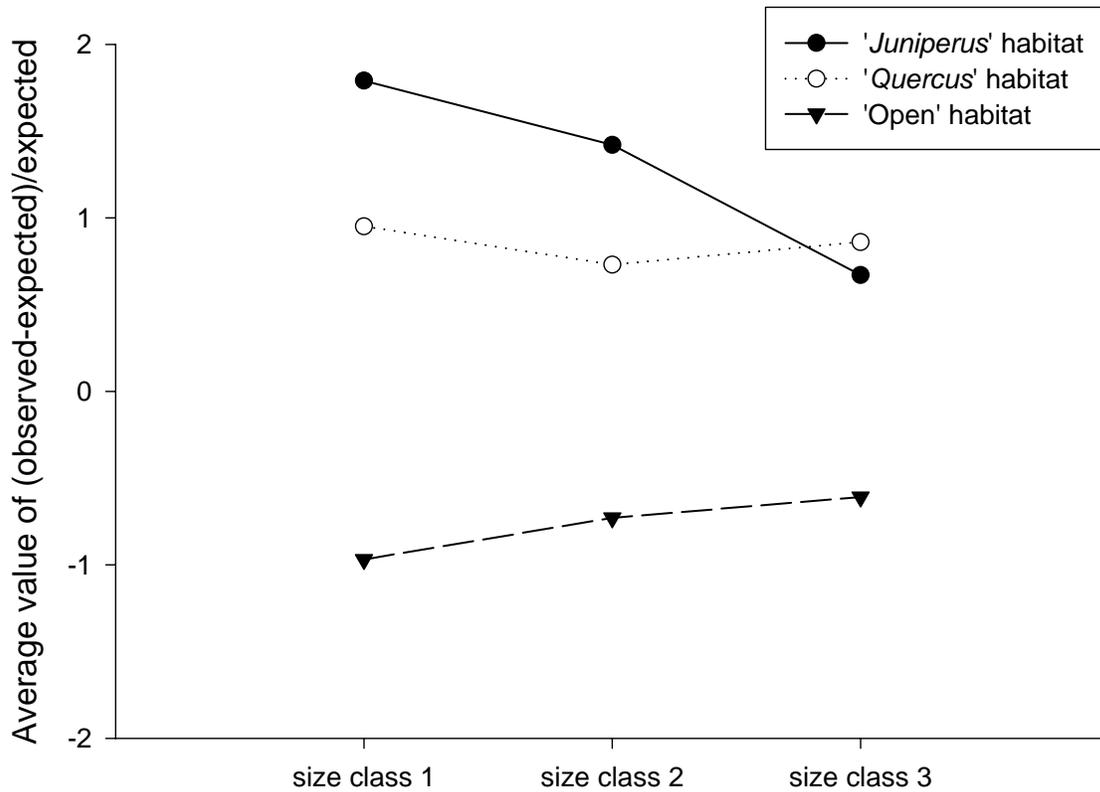


Figure 2.7. The average value of the strength of association (observed-expected/expected) by size class and habitat type. Each point represents the average value for all three sites. Negative values represent an average negative association with *J. ashei* individuals and positive values represent an average positive association with *J. ashei* individuals.

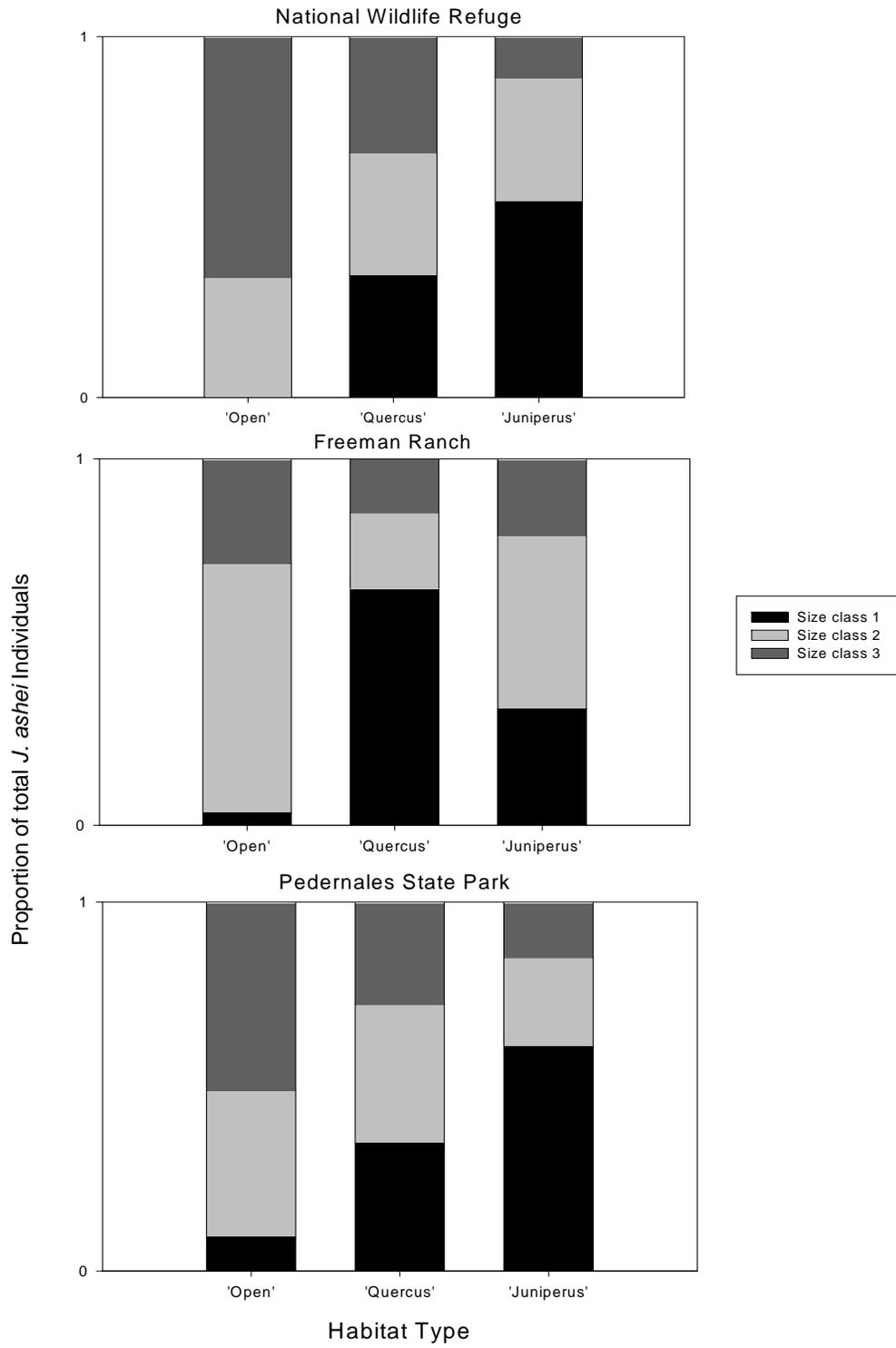


Figure 2.8. Size distribution of *J. ashei* individuals within each habitat type for each site.

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Chapter 3: Shifts in the balance between positive and negative effects along an environmental stress gradient in a controlled experiment.

ABSTRACT

There appears to be broad agreement in the literature that the balance between positive and negative interactions (1) may shift within a system and (2) may depend on the severity of abiotic stress in the system. It has been proposed that facilitation (or positive interactions) is more common in environments that are more stressful. Authors who report finding facilitation in arid systems often suggest that the positive effects of shading by a neighboring plant on the water status of a target plant have outweighed the negative effects of competition for light and water with the same neighboring plant. This study tests, in a controlled experiment, the hypothesis that the effect of shade on *Juniperus ashei* plants can vary from negative to positive depending upon water availability. The effects of three watering treatments and two shade treatments on survival and growth were measured in an experiment with a full-factorial design. Shading and water significantly increased the rate of transplant survival in this experiment. Shade significantly decreased the mean total biomass of *Juniperus ashei* seedlings, regardless of watering treatment. Water significantly increased the mean total biomass of *J. ashei* seedlings, regardless of shade treatment. There was a significant shade x water interaction; the negative effect of shade was not as large in the low watering treatment as it was in the high watering treatment. The results of this study suggest that whether the effect of shade upon *Juniperus ashei* seedlings is negative or positive depends upon water availability. Furthermore, instead of the effect gradually

changing from negative to positive along a gradient of decreasing water availability, it appears that the effect changes abruptly from negative to positive at the point at which seedlings begin to die from water shortage. To understand the net effect of canopy trees on the seedlings under them, we need both garden experiments and companion field experiments, the former to measure the effects on individual factors and the latter to measure the net effect of the many different factors involved.

INTRODUCTION

Plant interactions are thought to be important in structuring community-level patterns and processes (Tilman 1982, Fowler 1986, and Goldberg and Barton 1992). Classic ecological studies acknowledged the role of both negative and positive interactions in natural systems (e.g. Clements 1916). The importance of negative interactions has been widely explored with many observational, theoretical, and empirical studies (Connell 1983, Keddy 1989, and Goldberg and Barton 1992). Recently, more effort has focused on the role of positive interactions (see review in Callaway 1995, special feature in *Ecology* October 1997, Menge 2000, Stachowicz 2001), although the importance of negative interactions is not disputed. There appears to be broad agreement in the literature that the balance between positive and negative interactions (1) may shift within a system and (2) may depend on the severity of abiotic stress in the system (Holmgren et al 1997, Callaway and Walker 1997, Bertness and Leonard 1997, Tielborger and Kadmon 2000, Tewksbury and Lloyd 2001). It has been proposed that facilitation (or positive interactions) is more common in environments that are more stressful (Bertness and Callaway 1994, Brooker and Callaghan 1998, Pugnaire and Luque 2000, Callaway et al. 2002,). A majority of the studies that report finding facilitation have been done in arid, saline, or otherwise abiotically stressed environments (Callaway 1995), although facilitation has occasionally been found in less stressful environments (Berkowitz et al. 1995, Holmgren 2000, Holl 2002, Ganade and Brown 2002, Pages et al. 2003). However, the apparent tendency for facilitation to be more common in high-stress environments may be due in part to its being tested in such environments more often.

Authors who report finding facilitation in arid systems often suggest that the positive effects of shading by a neighboring plant on the water status of a target plant have outweighed the negative effects of competition for light and water with the same neighboring plant (Callaway 1992, Greenlee and Callaway 1996, Weltzin and McPherson 1999, Hastwell and Facelli 2003). However, very few studies have directly tested the interaction between the effects of soil moisture and light reduction in this context, that is, the balance between their positive and negative effects on plants (but see Canham et al. 1996, Holmgren 2000, Hastwell and Facelli 2003).

Combining the hypothesis that facilitation is due to the positive effects of shading on plant water status with the hypothesis that facilitation is more common in drier systems yields another question: why should the positive effects of shading be more likely to outweigh competition in more arid systems? Holmgren et al. (1997), building upon the model of Smith and Huston (1989) and the observation that there is an apparent tradeoff between drought tolerance and shade tolerance among plant species, modeled a shifting balance of positive and negative interactions along moisture gradients.

Previous studies have shown that *Juniperus ashei* (Ashe juniper) individuals are more common under woody plant canopies than they are in open grassy patches (Batchelor chapter 2, Fowler 1988a, Jackson and Van Auken 1997, Anderson et al. 2001). A strong spatial association between junipers and woody plant canopy suggested that the woody plants that form the canopy might serve as ‘nurse plants’ for the junipers, although other explanations also exist (e.g. seed dispersal, differences in the physical microhabitat due to the spatial pattern of soil nutrients or water availability). These

spatial associations are strongest for the smallest size classes of juniper (Batchelor chapter 2), which are probably also the most vulnerable to drought and other stresses. This spatial pattern is what one would expect if facilitation were most likely or strongest when target plants are most vulnerable. This study tests, in a controlled experiment, the hypothesis that the effect of shade on these small plants can vary from negative to positive depending upon water availability.

METHODS

Study System and Organism

The Edwards Plateau of central Texas covers approximately 93,240 square kilometers. Soils are commonly shallow, over limestone bedrock. There is a steep precipitation gradient, from 85 cm/yr on the eastern edge of the Plateau to 35 cm/yr on its western edge (Fowler and Dunlap 1986). Because the precipitation is highly variable from month to month and year to year, with no strong seasonal pattern, and temperatures are high (annual average 19° C; average August maximum 36° C; average December minimum 16° C), the climate is effectively semi-arid even on the ‘wettest’ eastern edge of the Plateau. The potential evaporation exceeds precipitation by an average of 75 cm/yr on the eastern Edwards Plateau (Riskind and Diamond 1988).

The vegetation of the area is primarily a mosaic of woodlands and savannas. On the eastern Plateau, the savannas are usually dominated by *Quercus fusiformis* and a number of species of perennial grasses. However, *Juniperus ashei* is now a ubiquitous invader of these *Q. fusiformis* savannas. *Juniperus ashei* cover has increased from less

than 1% canopy cover in 1948 to more than 20% canopy cover currently at the Texas A&M University Research Station in Sonora, Texas (Smeins et al. 1997).

J. ashei is an evergreen multi-trunked ‘tree’ up to 6m tall (Correll and Johnston 1970) native to central Texas savannas and common throughout the region. Its seeds are dispersed by cedar waxwings, mockingbirds and robins (Chavez-Ramirez and Slack 1994). It may once have been controlled by summer fires, but now is routinely removed by land managers by various mechanical methods. If not removed, a near mono-specific stand of *J. ashei* will eventually form, containing remnant adult *Q. fusiformis* but few other woody or herbaceous species. However, *J. ashei* removal by land managers presently keeps much of the region in *Q. fusiformis* / *J. ashei* savannas.

Experiment 1

In May of 2000 one-year-old *Juniperus ashei* seedlings were collected under a single maternal tree at the University of Texas Brackenridge Field Laboratory in Austin, TX. Seedlings were dug up in May because it is easy to identify newly emerged seedlings by their two cotyledons at that time of year. As a seedling matures, it often loses its cotyledons, which makes it difficult to tell whether such a seedling is in the current year’s cohort or the previous year’s cohort. Two hundred seedlings were extracted, together with a core of soil surrounding the seedling approximately 8cm in diameter by 15cm deep. Because mortality of seedlings transplanted directly into the ground was very high (Batchelor pers. obs), seedlings were grown for three months in a greenhouse before being planted in the experimental garden. Furthermore, immediate

transplanting into the garden would have meant planting them outdoors when temperatures were already very high ($> 32^{\circ} \text{C}$ during the day) and the soil was dry. Because the greenhouse ‘pots’ were 10 cm deeper than the cores, additional native soil was added to them.

Ninety-six holes, each 70cm deep and at least 1m from the next hole, were excavated in an experimental garden at the University of Texas Brackenridge Field Laboratory in Austin, TX. In early September 2000, 96 seedlings were randomly selected from the greenhouse-grown transplants and transplanted into 10 cm diameter by 75 cm tall PVC tubes which were then placed into the holes in the experimental garden. The seedlings were planted with a soil mixture of equal parts of sand and sandy loam, similar to the soils in which *J. ashei* typically grows, and to the surrounding garden soil. Each tube had a porous cloth at the bottom that allowed drainage but prevented roots from growing through it. The tubes minimized competition from other plants. To prevent mortality from transplant shock, all plants were watered daily and shaded with 60% shade cloth for 1 month. Nevertheless many plants died immediately after being planted in the garden, probably because September 2000 was unusually warm (with a record high of 44°C). Dead plants were replaced immediately with additional seedlings from the greenhouse during the first month.

In mid-October 2000 experimental treatments began. A complete randomized block design was used; each block had one randomly positioned replicate of each treatment combination. There were two treatments: watering with three levels (low water, medium water, and high water) and shade with two levels (shade cloth 60% or no

shade). The intensity of shade was used to mimic the natural conditions of light found under healthy *Quercus fusiformis* trees (Anderson et al. 2001). Work on previous studies in the garden suggested that water addition was necessary to maintain the plants in pots. All plants were watered three times per week, in addition to natural rainfall if any. Each tube received either 100 ml of water (i.e., 300 ml/wk) or 200 ml (600 ml/wk) or 400 ml (1200 ml/wk). Plants were given equal amounts of a water soluble (15-30-15) fertilizer approximately bi-weekly. Sixteen blocks were planted in a 2 by 8 arrangement. Despite the additional water of the watering treatments, by the end of December about half the plants had died and the experiment was terminated. The experiment had been designed to test the effects of the treatments on growth, but the high mortality rate between mid-October and mid-December made this impossible.

Survival rates were analyzed by a linear categorical model (see Fowler 1988b for a detailed description of this type of analysis applied to survival rates). Shade and water treatments were independent variables and survival rate was the dependent variable. To obtain sufficient sample sizes to test the effects of the treatments on survival, blocks were omitted from the analysis. This, however, limited the analysis to testing the main effects of the two treatments, omitting the interaction effect.

Experiment 2

In May of 2001 two hundred one year old *Juniperus ashei* seedlings were again collected under a single maternal tree at the University of Texas Brackenridge Field

Laboratory in Austin, TX. Seedlings were collected and transplanted into containers following the same protocol as experiment 1.

Because of the high mortality rates observed in experiment 1, three changes to the protocol were made to increase survival. (a) Seedlings were not transplanted in the garden until the first week of November of 2001, when temperatures are substantially lower than they are in September and October. (b) All plants were watered daily and shaded with 60% shade cloth for 2.5 months, instead of 1 month. (c) An irrigation system replaced hand watering. Automatically-timed irrigation delivered specified amounts of water several times each day. Each tube had its own pressure compensating dripper to insure that each tube received water at the designated rate. Compared to the first experiment, the soil around the transplants in this experiment never dried out as completely as it did in the first experiment (i.e., the temporal variability in soil moisture was less) and the average amount of water delivered to each tube was greater (i.e., the 'low' water treatment of this experiment added more water to each tube than the 'low' water treatment of experiment 1, and so forth).

The experimental treatments began in February 2002. A complete randomized block design was used; each block had one randomly positioned replicate of each treatment combination. There were two treatments: watering with three levels (low water, medium water, and high water) and shade with two levels (shade cloth 60% or no shade). The three levels of watering treatment were low water (30 seconds at 1 gallon per hour), medium water (30 seconds at 2 gallons per hour), and high water (30 seconds at 4 gallons per hour). These rates were determined by the availability of the irrigation

equipment, but three watering treatments consisting of a baseline, two times the baseline, and four times the baseline seemed to be a plausible spread in the water availability gradient. The actual amount of water for the watering treatments could be manipulated by controlling the number of waterings per day; these varied from 1 to 3 depending on the season. The intent of the watering schedule was to cause water stress in the lowest watering treatment without causing mortality. As in experiment 1, these watering treatments were in addition to whatever rain fell. Plants were given equal amounts of a water soluble (15-30-15) fertilizer approximately bi-weekly. Sixteen blocks were planted, but one was lost early in the experiment due to an accidental interruption in the watering treatment and four blocks were lost at the end of the experiment to herbivory by attine ants (*Atta texana*). These blocks were discarded from the experiment and from all analyses. Each tube was protected from small mammal disturbance by a round wire cage 40 cm in diameter. Shade cloth was put on top of these cages if the tube received the shade treatment.

Experimental treatments were imposed from February 2002 until the first week in March 2003 (53 weeks). The plants were harvested by lifting the tubes out of the ground and pouring the contents onto a wire screen. A pressure hose was used to wash away the soil from the roots. The height of the aboveground biomass was recorded for each plant and then clipped and collected in a brown paper bag. The length of the longest root for each plant was recorded before all roots were collected in a brown paper bag. Both below- and above-ground biomass were dried, weighed and recorded for each plant. Analysis of variance was used to analyze the results. All analyses were performed in

SAS using the GLM procedure, LSMEANS option (1990).. Block, shade, and water were all treated as fixed effects. Each F-ratio was calculated using the MS of the three-way interaction as its denominator. The MS of the three-way interaction also serves as the MS_{error} because there was only one replicate of each treatment combination per block.

RESULTS

Experiment 1

Shading significantly increased the rate of transplant survival in this experiment (Fig. 3.1, $\chi^2 = 3.76$, $p = 0.0525$). Additional water also significantly increased survival rate (Fig. 3.2, $\chi^2 = 6.32$, $p = 0.0425$). Plants that received the high watering treatment had a survival rate twice as large as plants that received the low watering treatment. There was not a significant difference between the high and medium watering treatments.

Experiment 2

Shade significantly decreased the mean total biomass of *Juniperus ashei* seedlings, regardless of watering treatment (Table 3.1). Shaded plants were on average half the size of non-shaded plants (Fig. 3.3). Water significantly increased the mean total biomass of *J. ashei* seedlings (Table 3.1), regardless of shade treatment. Plants in the highest watering treatment were on average more than twice as large as the plants in the lowest watering treatment and significantly larger than plants in the medium watering treatment (Fig. 3.4). Plants in the medium watering treatment were also significantly larger than plants in the lowest watering treatment. There was a significant shade x water

interaction (Table 3.1). The negative effect of shade was not as large in the low watering treatment as it was in the high watering treatment (Fig. 3.5).

Shade significantly increased the mean root/shoot ratio (Table 3.2, Fig. 3.6), although the difference was not large. Block, water, and all interactions were not significant. Shade significantly decreased above ground height (Table 3.3). Non-shaded plants were on average just over 25% taller than shaded plants (Fig. 3.7). Water significantly increased plant height (Table 3.3). Plants that received the highest watering treatment were on average 36% taller than plants that received the lowest watering treatment (Fig. 3.8). The block*shade interaction was significant. In most blocks the mean height for plants with shade was smaller than the mean height for plants without shade. In two blocks the reverse was true. There were no other significant interactions in the analysis of above-ground height. Somewhat surprisingly, no significant effects were found in the analysis of below-ground length (Table 3.4).

DISCUSSION

The results of these two experiments suggest that whether the effect of shade upon *Juniperus ashei* seedlings is negative or positive depends upon water availability. Furthermore, instead of the effect gradually changing from negative to positive along a gradient of decreasing water availability, it appears that the effect changes abruptly from negative to positive at the point at which seedlings begin to die from water shortage.

In other words, if there was enough water for the seedlings to survive (the second experiment), then the effects of shade were negative; there was no evidence that shade

facilitated plant growth. But when water availability was so low that it reduced survival rates (the first experiment), the effects of shade were positive.

Although the seedlings in these experiments were not more than two years old at harvest, they were somewhat larger than plants of the same age that germinate and grow naturally, because the experimental plants were raised in a greenhouse for several months and received extra water. Therefore the results of these experiments might be more applicable to 12-16 month old plants (experiment 1) or to 2-4 year old plants (experiment 2) (pers. obs, M. Batchelor).

Mechanism of positive effect

The positive effect of shade on survival rate was plausibly due to the more favorable water status in the shaded seedlings. The precise mechanism or mechanisms by which shade improved plant water status, however, were not determined. Studies have documented increased humidity, lower soil and air temperature, and lower wind velocity under the canopies of trees (Breshears et al., 1998, Larcher 1983, Chen et al. 1995). The lower temperatures and wind speeds probably improved plant water status by decreasing transpiration rates (Larcher 1983, Kramer 1983).

Lower temperatures and wind speeds under tree canopies may also improve plant water status by reducing soil evaporation rates and thus increasing available soil moisture (Kramer 1983). However, at the same time the canopy plants are presumably reducing soil moisture by their own transpiration. Whether the net effect on soil moisture is positive or negative is unclear; the literature is not consistent on this point. For example,

Breshears et al. (1997) measured drier soils under *J. monosperma* canopies while Ko and Reich (1993) measured wetter soils under various species of *Quercus* canopies. On the Edwards Plateau, Wayne and Van Auken (2004) measured higher mean soil water content under *J. ashei* canopies than between the tree clusters. However, Anderson et al. (2001) reported that plants under *Quercus fusiformis* trees were more water stressed than plants in open areas. The difference may be due to the difference in canopy species, or it may be due to the difference in soil depth between the two studies: Wayne and Van Auken took soil samples from 2cm-40cm cm, while Anderson et al. measured water potential on established plants that were certainly rooted more deeply than 40 cm.

Mechanism of negative effect

The negative effect of shade on plant growth rates in this experiment was due to the direct effect of reduction in light levels, because potential indirect effects (such as effects on large herbivores) were prevented. I conclude that tree canopies have a negative effect on *Juniperus ashei* seedlings via competition for light.

This experiment isolated the effect of shade from the many other potential effects of canopy trees on *J. ashei* seedlings, including indirect effects via herbivores, pathogens, and herbaceous plants; soil properties other than soil evaporation rate; and the physical damage done by falling branches. A few other studies have also found that shade alone, independent of all other factors, can increase seedling survival rates of savanna species. Callaway (1992) reported higher survival rates of *Quercus douglasii* seedlings, compared to unshaded seedlings, as did Valiente-Banuet and Ezcurra (1991) for cactus

(*Neobuxbaumia tetetzo*) seedlings. However the difficulty of isolating the effects of shade from all other factors has meant that there are very few such studies, especially in the field. The great advantage of garden experiments such as the present study is that the individual factors can more readily be isolated.

Potential interactions among factors

There have been many studies that have compared survival rates or growth rates of seedlings under canopies with those in the open in savannas. In general, survival is higher under canopies (e.g., Callaway 1992, Berkowitz et al. 1995, Holzapfel and Mahall 1999, Weltzin and McPherson 1999, Franks 2003, Martinez 2003). Similarly, in a companion field study, I found that *Juniperus ashei* seedlings had higher survival rates under conspecific canopies (Batchelor chapter 4). However, it is very difficult in any field study to isolate the effect of a single factor such as shade. There are so many ways in which a canopy species can affect a seedling that the number of factors that would have to be included in a definitive experiment, bearing in mind that each additional factor multiplies the size of a factorial design, is logistically prohibitive. However there are some field experiments that have separated some of the possible mechanisms involved. For example, Callaway (1992) tested the effects of shade and of herbivory (and their interaction) and found that *Salvia* and *Artemisia* shrubs facilitated *Quercus douglasii* survival by both the direct effects of shade and by the protection from herbivory. Weltzin and McPherson (1999) examined the effects of soil nutrients and shade on *Quercus emoryi* seedlings and found that shade was the primary reason for higher survival under

woody canopy. Soil nutrient addition to open sites had little effect on seedling survival. In a companion field study to the present one, I found that soil properties other than soil moisture did not have a direct effect on survival (Batchelor chapter 4).

Interaction between light and water on growth rates

Higher levels of water and of light each led to greater final plant biomass. Plants in the different treatments did not differ in average initial size; this means that more water and more light each increased plant growth rates. These two factors interacted in their effects: their effects were multiplicative rather than additive (Fig. 3.5). Multiplicative effects between factors affecting plant size are common, e.g., between herbivory and competition (Gurevitch et al. 2000), between disease and competition (Clay 1990).

The fact that additional water produces larger plants at all light levels, and vice versa, implies that water and light are substitutable resources (Tilman 1988). Clearly, however, they are not directly substitutable the way different nitrogen sources (nitrate versus ammonium) are. In general, lower light levels tend to produce plants with lower root:shoot ratios, and vice versa (Larcher 1983, Yin et al. 2004). Holmgren et al. (1997) state that, given this relationship, light and water can be to some degree substitutive resources, because shaded plants, with lower root:shoot ratios, need higher levels of available soil moisture.

The hypothesis of Holmgren et al. (1997) is critically dependent upon a change in root:shoot ratio in a particular direction. However, in this experiment, root:shoot ratios shifted in the opposite direction; shaded plants had higher root:shoot ratios. I suggest that

this is primarily due to the levels of water availability used in experiment 2. The plants were not sufficiently water stressed to threaten survival, so it is plausible that even plants receiving the lowest watering treatment did not experience enough water stress to cause the expected shift in resource allocation from above-ground to below ground. There were not significant differences in the below-ground biomass and shaded plants had significantly less above-ground biomass. Therefore, the most parsimonious explanation for the lower root/shoot ratio observed in the non-shaded plants is that they grew taller thereby decreasing their root/shoot ratio. It is also possible that these seedlings were adding woody stem tissue as well as leaf tissue as they grew. Larger plants may have had the same ratio of root surface area to leaf surface area as smaller plants, but larger plants had relatively more stem tissue, which lowered their root:shoot ratios. Because on average the non-shaded plants were larger (and taller), a greater proportion of their biomass was stem tissue than was the case for the smaller, shaded plants.

Limits of this study

This experiment was originally designed to test the effects of shade on plant growth, which experiment 2 did. Soil moisture levels in experiment 1 were so low that that experiment became a test of the effects of shade on survival, not growth. However, there is presumably a range of water availability between the two experiments that was not studied, where both survival and growth are affected. Within that range, any experiment that would measure the effects of shade and water on both survival and

growth would have to be prohibitively large, to insure enough survivors to measure effects on growth.

Data are not available to compare the 51% survival rate of seedlings in experiment 1 with wild seedlings directly. Natural recruitment was very low that year (P. Batchelor, pers. obs.). Seedling survival was higher than 51% in a natural field setting the following year (Batchelor chapter 4). It is probable that the extra water the experimental plants all received increased the survival rate, even in the low water treatment. Unfortunately to manipulate precipitation around natural levels would require a movable 'rainout shelter', an irrigation system, and much larger sample sizes (the latter to provide good estimates of low survival rates).

Extension of results to field

I have shown that shade per se increases *Juniperus ashei* seedling survival rates in the garden, presumably through its effect on seedling water status. The direct effect of shade on seedling temperature and therefore on seedling transpiration rate should be similar in the field and in the garden. However, in the field, uptake of water from the soil by the canopy tree may outweigh the reduction in soil evaporation rate due to its shade. And of course there are many other potential effects of canopy trees on seedlings, not related to shading. To understand the effects, both positive and negative, of canopy trees on the seedlings under them, we need both garden experiments and companion field experiments, the former to measure the effects on individual factors and the later to measure the net effect of the many different factors involved.

Table 3.1. Results of the ANOVA of mean total biomass. Block, shade, and water were all treated as fixed effects. Each F-ratio was calculated using the MS of the three-way interaction as its denominator. The MS of the three-way interaction also serves as the MS_{error} because there was only one replicate of each treatment combination per block.

Source of Variation	df	Type III SS	MS	F	p
block	10	629.3211	62.9321	3.68	0.0063
shade	1	2053.6634	2053.6634	120.15	<0.0001
water	2	1688.4246	844.2123	49.39	<0.0001
block*shade	10	300.6749	30.0675	1.76	0.1355
block*water	20	274.8145	13.7407	0.80	0.6849
shade*water	2	296.9591	148.4795	8.69	0.0019
block*water*shade	20	341.8505	17.0925	-----	-----
total	65				

Table 3.2. Results of the ANOVA of mean root/shoot ratio. Block, shade, and water were all treated as fixed effects. Each F-ratio was calculated using the MS of the three-way interaction as its denominator. The MS of the three-way interaction also serves as the MS_{error} because there was only one replicate of each treatment combination per block.

Source of Variation	df	Type III SS	MS	F	p
block	10	0.3966	0.0397	1.42	0.2396
shade	1	0.2341	0.2341	8.41	0.0089
water	2	0.0136	0.0068	0.24	0.7854
block*shade	10	0.2238	0.0224	0.80	0.6275
block*water	20	0.7426	0.0371	1.33	0.2627
shade*water	2	0.0468	0.0234	0.84	0.4464
block*water*shade	20	0.5567	0.0278	-----	-----
total	65				

Table 3.3. Results of the ANOVA of above-ground height. Block, shade, and water were all treated as fixed effects. Each F-ratio was calculated using the MS of the three-way interaction as its denominator. The MS of the three-way interaction also serves as the MS_{error} because there was only one replicate of each treatment combination per block.

Source of Variation	df	Type III SS	MS	F	p
block	10	276.8436	27.6844	0.96	0.5030
shade	1	809.2001	809.2001	28.13	<.0001
water	2	901.8664	450.9332	15.67	<.0001
block*shade	10	856.6448	85.6644	2.98	0.0181
block*water	20	885.6436	44.2822	1.54	0.1714
shade*water	2	132.6439	66.3220	2.31	0.1256
block*water*shade	20	575.4061	28.7703	-----	-----
total	65				

Table 3.4. Results of the ANOVA of belowground height. Block, shade, and water were all treated as fixed effects. Each F-ratio was calculated using the MS of the three-way interaction as its denominator. The MS of the three-way interaction also serves as the MS_{error} because there was only one replicate of each treatment combination per block.

Source of Variation	df	Type III SS	MS	F	p
block	10	1242.2279	124.2228	0.77	0.6524
shade	1	422.0547	422.0547	2.63	0.1206
water	2	574.0839	287.0420	1.79	0.1930
block*shade	10	2002.2236	200.2224	1.25	0.3220
block*water	20	2488.6893	124.4345	0.78	0.7129
shade*water	2	134.2494	67.1247	0.42	0.6639
block*water*shade	20	3211.0373	160.5519	-----	-----
total	65				

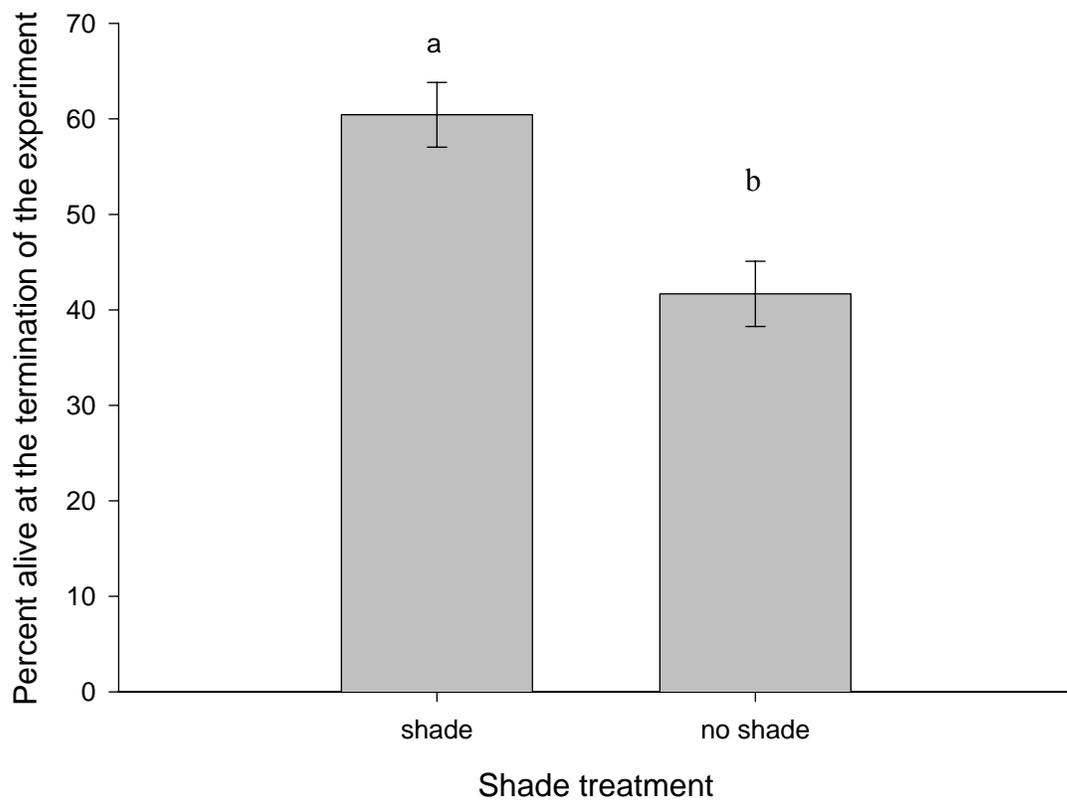


Figure 3.1. The effect of shade on the percent survival of transplanted *J. ashei* plants in experiment 1. Error bars show the standard deviation calculated from the binomial distribution.

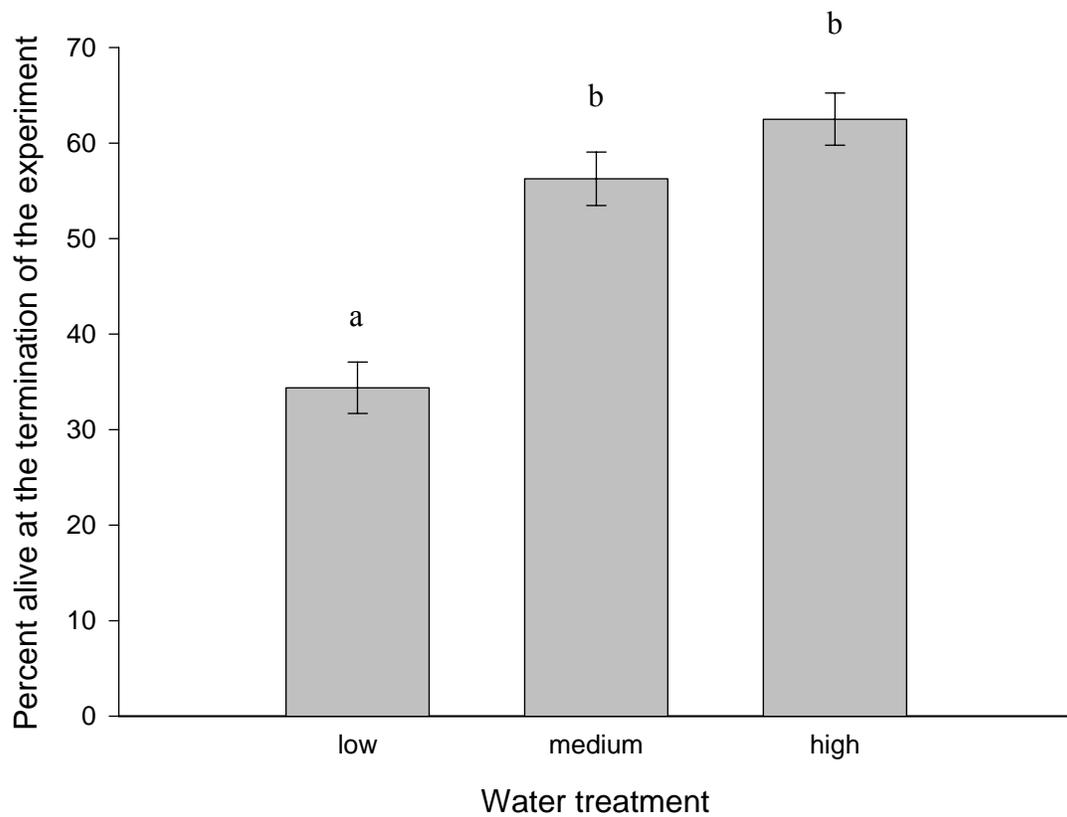


Figure 3.2. The effect of water on the percent survival of transplanted *J. ashei* plants in experiment 1. Error bars show the standard deviation calculated from the binomial distribution.

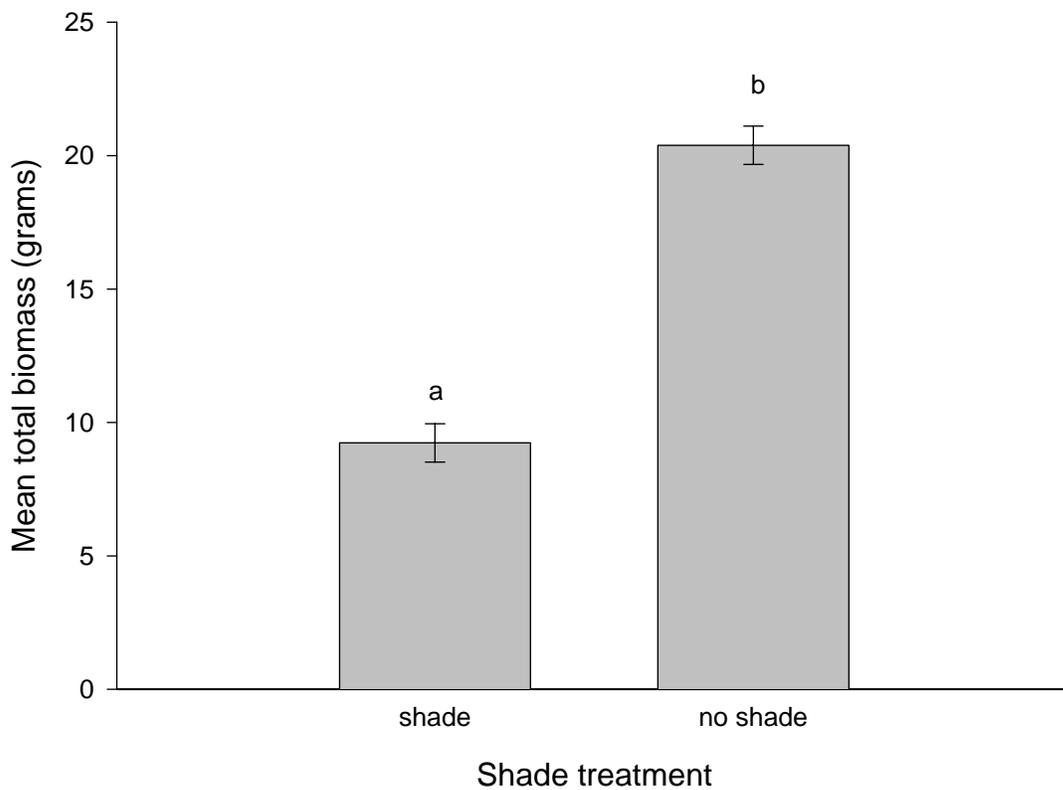


Figure 3.3. The effect of shade on the mean total biomass of *J. ashei* individuals. Bars sharing letters are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (1990).

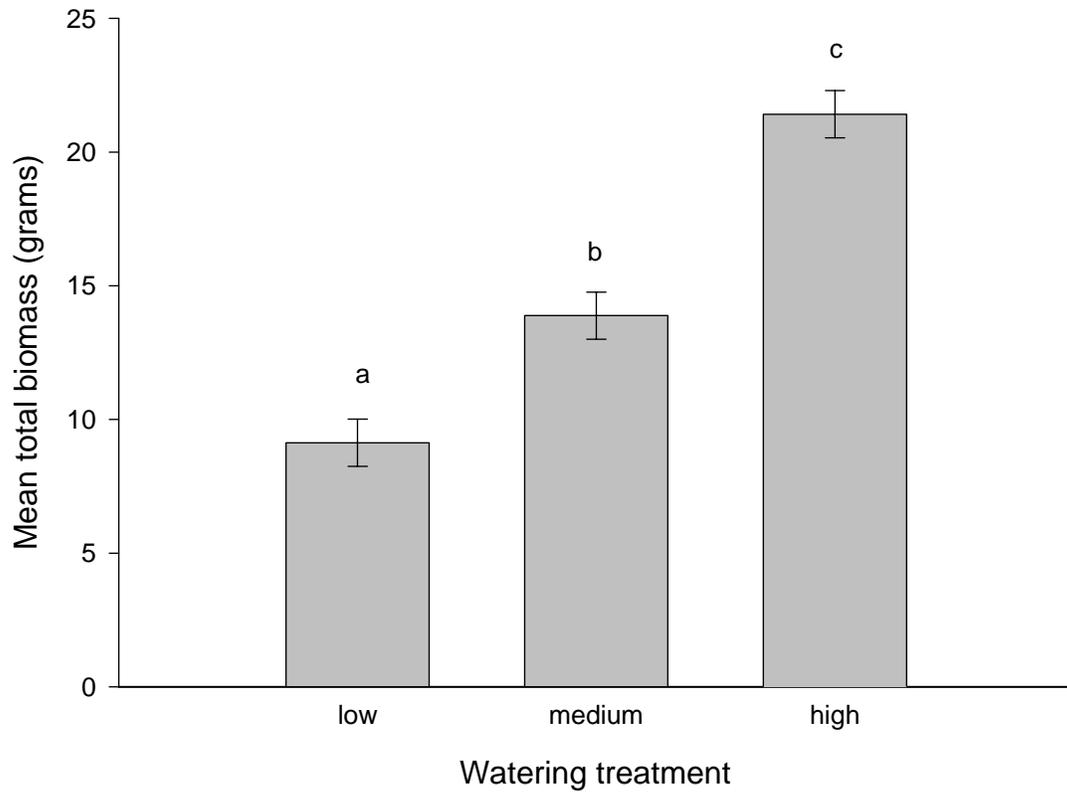


Figure 3.4. Effect of watering treatment on mean total biomass of *J. ashei* individuals. Bars sharing letters are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (1990).

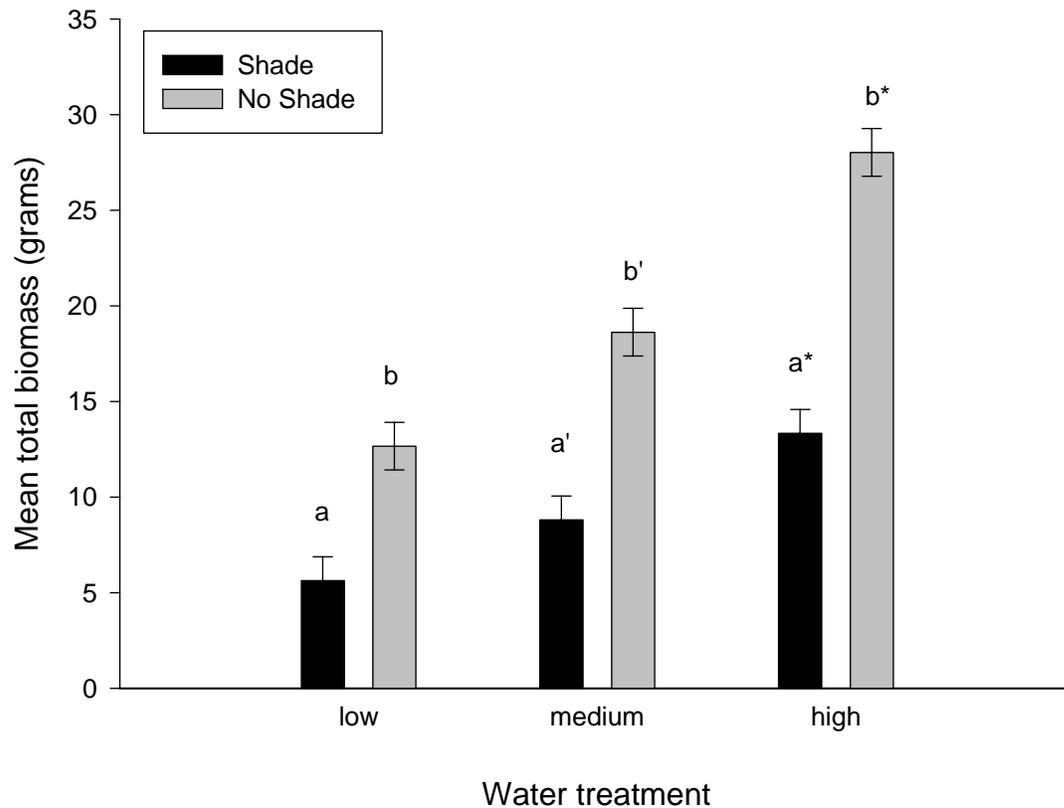


Figure 3.5. Total biomass of *J. ashei* plants by shade treatment and water treatment. Bars sharing labels are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Comparisons were made between shade levels within a watering treatment. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (1990).

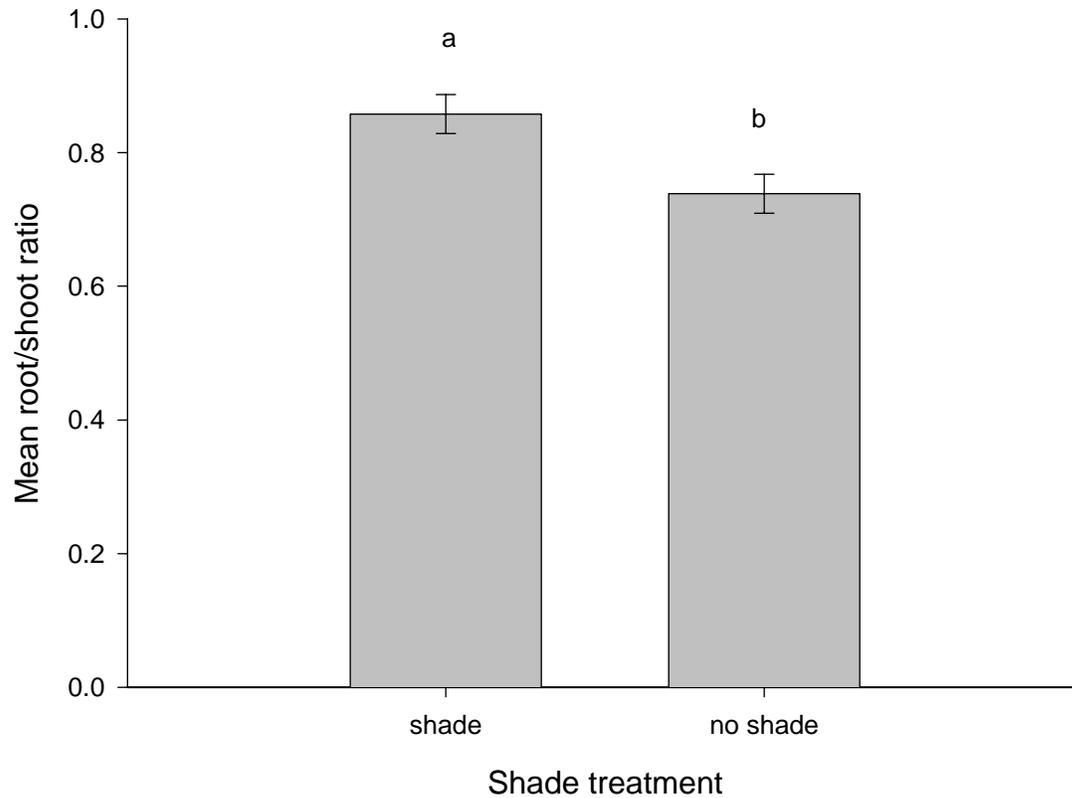


Figure 3.6. The effect of shade on mean root/shoot ratio of *J. ashei* individuals. Bars sharing letters are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (1990).

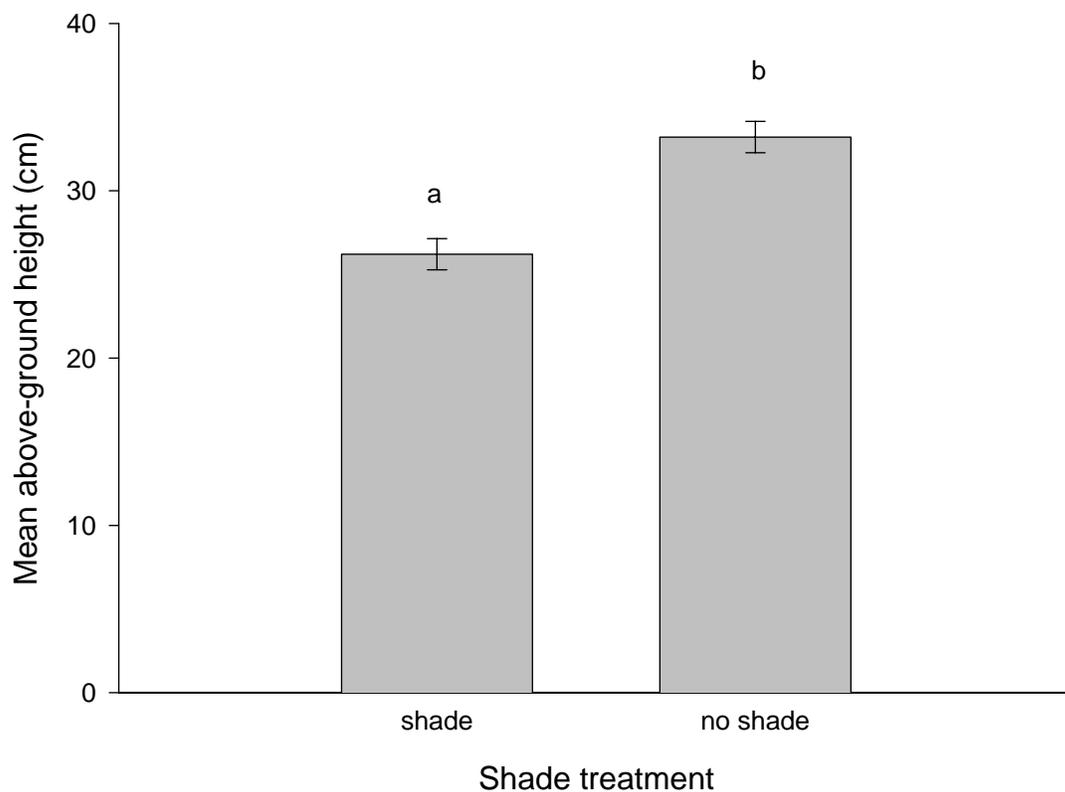


Figure 3.7. The effect of shade on mean above-ground height of *J. ashei* individuals. Bars sharing letters are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (1990).

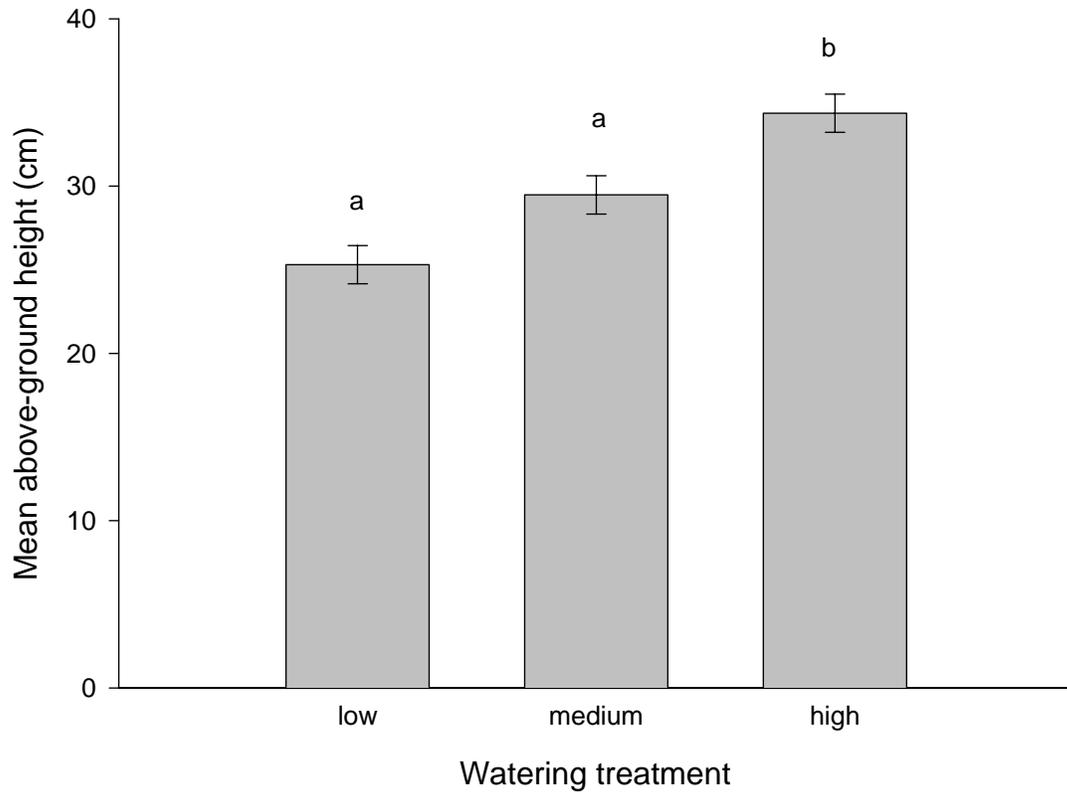


Figure 3.8. Effect of watering treatment on the mean above-ground height of *J. ashei* individuals. Bars sharing letters are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (1990).

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Chapter 4: Intraspecific facilitation of *Juniperus ashei* in Texas savannas

ABSTRACT

Previous studies have shown that *Juniperus ashei* seedlings are more common under woody plant canopies than in open grassy patches. I tested the hypothesis that this spatial pattern is due to facilitation (i.e., positive effects of canopy species on *J. ashei* seedlings). A field study was conducted to test two potential mechanisms of facilitation. The effects of three overstory types ('*Quercus*' overstory, '*Juniperus*' overstory, and no overstory, i.e., 'open' grassy patch) and three substrate types (soil and litter from live oak clusters, soil and litter from juniper clusters, and soil and litter from open patches) on the germination, survival, and growth of *Juniperus ashei* seedlings in a factorial design were measured for two years. Substrate type had no effect on germination, survival, or growth. Germination and survival rates were higher under '*Juniperus*' overstory than under '*Quercus*' overstory or in the open. '*Quercus*' overstory and no overstory were not significantly different from each other. Total biomass was significantly higher in the 'open' than under '*Juniperus*' or '*Quercus*' overstory. These data indicate that the presence of an adult *Juniperus ashei* facilitated *J. ashei* seedling germination and survival, but decreased growth rates. Furthermore, these data suggest that the mechanism of facilitation did not involve semi-permanent soil and litter characteristics. (The most likely mechanism of facilitation is reduction of water stress via shading.) Evidently, facilitation of seedlings contributes to the positive spatial association between *Juniperus ashei* adults and *J. ashei* seedlings, but it cannot explain the positive spatial association between adult oaks and *J. ashei* seedlings.

INTRODUCTION

Plant-plant interactions are known to be very important in structuring community-level patterns and processes (Tilman 1982, Fowler 1986, and Goldberg and Barton 1992). While the majority of plant-plant interactions are probably negative, or at least no better than neutral, for both partners, ecologists have long acknowledged the role of positive interactions as well (e.g., Clements 1916). However, the majority of studies have been of negative interactions, especially of competition for resources (Connell 1983, Keddy 1989, and Goldberg and Barton 1992). Recently, more effort has focused on the role of positive interactions, especially of direct positive interactions (i.e., the facilitation of one plant by another, not involving a third species) (Callaway 1995, see special feature in Ecology October 1997, Menge 2000, Stachowicz 2001). In this study, I measured both the positive and negative effects of other plant species upon *Juniperus ashei*.

The balance between positive and negative interactions between plant species can differ across space and time at many scales. For example, microclimate and micro-site conditions can shift a relationship from positive to negative within a single site (Pugnaire and Luque 2001), as can differences in precipitation between years (Aguilar and Sala 1994). Whether a plant experiences a net negative or positive impact from a neighboring plant can also depend upon the age and developmental stage of the focal plant (Greenlee & Callaway 1996, Pugnaire et al. 1996, Callaway 1998, Rousset and Lepart 2000). Therefore studies that only examine a single trait of a species may miss important shifts from positive to negative and vice versa in that species' interactions with other plant species (Howard and Goldberg 2001). Accordingly, in this study I measured several

different traits, including germination, survival and growth, of the focal species, *Juniperus ashei*.

Juniperus ashei individuals, especially plants in the smallest size classes, are more common under woody plant canopies than they are in open grassy patches (Batchelor chapter 2, Fowler 1988a, Jackson and Van Auken 1997, Anderson et al. 2001). This spatial association suggested that these canopy species might be serving as ‘nurse plants’ for the junipers. I hypothesized that the commonest canopy species, *Quercus fusiformis* and *Juniperus ashei* itself, facilitated the germination, survival, and growth of young *J. ashei*.

To provide a test of this hypothesis, a randomized full-factorial field experiment was done. Unlike an observational study, an experimental study can determine which factors are direct causes of the phenomenon (the spatial association, in this case) and which are not. For example, the spatial association of small *J. ashei* and larger woody plants could be due to differential seed dispersal, in which case the facilitation hypothesis would be wrong. An experimental study is also the only way to separate the direct effects of each factor of interest, in this case, to separate the effects of soil and litter from the direct effects of the canopy overhead, for each of the canopy species. Unfortunately much of the existing literature about ‘nurse plants’ is limited to observational studies of spatial patterns (but see Holl 2002, Martinez 2003, Franks 2003, Tirado and Pugnaire 2003).

METHODS

Organisms and Study Site

Juniperus ashei is a multi-trunked ‘tree’ up to 6m tall (Correll and Johnston 1970) native to central Texas and common throughout the region. Its seeds are dispersed by cedar waxwings, mockingbirds and robins (Chavez-Ramirez and Slack 1994). *Quercus fusiformis* (Plateau live oak) is common in the savannas of the eastern Edwards Plateau of central Texas. *Q. fusiformis* can be either a large rhizomatous shrub or a large true tree (i.e., single-trunked)(Correll and Johnston 1970). Both *J. ashei* and *Q. fusiformis* are evergreen. Unlike *J. ashei*, *Q. fusiformis* can resprout after being cut or burned. *Q. fusiformis* trees commonly have root sprouts, although presently these very rarely grow more than 0.5 m tall, due to deer browsing (Russell and Fowler 1999). Past vegetative regrowth after fires when deer were less abundant, may account for the clusters of *Q. fusiformis* trees often observed in savannas. Typically the other dominant plant species of these savannas are various perennial grasses and *J. ashei*.

Juniperus ashei is a ubiquitous invader of *Quercus fusiformis* savannas in central Texas. It may once have been controlled by summer fires, but now is routinely removed by land managers by various mechanical methods. If not removed, a near mono-specific stand of *J. ashei* will eventually form, containing the remaining adult *Q. fusiformis* but few other woody or herbaceous species. However, *J. ashei* removal by land managers presently keeps much of the region in *Q. fusiformis* / *J. ashei* savannas.

I defined the following three types of habitat patches within *J. ashei*/*Q. fusiformis* savannas: ‘*Juniperus*’, ‘*Quercus*’ and ‘open’. A substantial portion of the area of the

study site fit the definition of one of the three habitat types defined above; there were also some bare rocky patches and prickly pear (*Opuntia spp.*) patches.

(1) 'Juniperus' patches were under the canopy of one or more *J. ashei* trees that were at least 2.5 m tall. Many 'Juniperus' patches also had *J. ashei* plants less than 2.5 m in them. No 'Juniperus' patch had any other woody species that were taller than 0.5m.

(2) 'Quercus' patches were under the canopy of one or more *Q. fusiformis* trees that were at least 2.5 m tall. Some 'Quercus' patches also had *J. ashei* plants in them that were more than 2.5 m tall, but in all of the 'Quercus' patches the canopy species was *Q. fusiformis*. No 'Quercus' patch had any woody species other than *J. ashei* that were taller than 0/5m.

(3) 'Open' patches had no woody species in them. Herbaceous cover (living and dead) was at least 75% in the 'grass' patches. These patches were dominated by various mixtures of the grasses *Nassella leucotricha*, *Bothriochloa ischaemum*, and *Aristida purpurea var. longiseta*.

The study was conducted at the Texas State University Freeman Ranch on the Edwards Plateau in central Texas at approximately 29° 56' N 98° W. The Freeman Ranch is a 1701 ha tract of land that is thought to have been managed as a cattle or sheep ranch since the early to mid 1800's (Barnes et al. 2000). Experimental plots were established in the 'nature trail' area of the ranch, which was not grazed during this experiment. Most of the Freeman Ranch, including the area used in this study, has soils in the Ruple-Comfort association and the Comfort-Rock complex. These soils are relatively shallow and rocky and have developed over fractured limestone (Barnes et al.

2000). The vegetation of the study site was typical of savannas in this region. It had clusters of woody plants, primarily *J. ashei* and *Q. fusiformis*, scattered in a matrix of herbaceous vegetation.

Materials

In the fall and early winter of 2001 seeds of *J. ashei* were collected from the University of Texas Brackenridge Field Laboratory in Austin, Texas. These seeds were stored in brown paper bags and cold-stratified at 2° C until planting (approximately 2 months). Seeds were mixed thoroughly before planting and counted into 45 sets of 500 seeds. Only seeds without obvious blemishes or insect infestation were included in the 45 sets.

In the early fall of 2001 the covering layer of litter and the first 12 cm of the soil in the experimental plots were collected and stored in plastic containers. The litter layers collected from *J. ashei* habitat and *Q. fusiformis* habitat were kept separately from the soil layers. Each soil type and litter type was sterilized using steam sterilization for 4 hours at 100° C. To test whether the sterilization killed all *J. ashei* seeds that existed in the soil and litter, a plot of each soil/litter type was established in the open and monitored for seedling emergence. No seedlings were observed; I concluded that the sterilization had succeeded in removing all viable seeds from the collected soil and litter. The soil sterilization was necessary to remove bias in the results due to pre-existing differences in the seedbank of each soil type. Soil sterilization obviously removes any potential

biological effect of the soil. Thus this study focused simply on the potential physical effects of the three different soil/litter types.

Experimental Design

In January of 2002 I randomly selected five out of nine possible experimental blocks in a 1.5 ha area of the study site. Each block contained one plot in each of the three habitat types defined above. Within a block, all the plots were oriented in the same direction (e.g., north-south). Each plot was 1.5 m X 0.5 m in area and contained 3 subplots. Each subplot was 0.5 X 0.5 m in area and had a 'wall' 0.5 m high around it, constructed out of plywood.

Any pre-existing plants rooted in the plots and the existing litter down to the soil surface were removed from each plot; then the top 12 cm of soil were removed from each plot. Within each plot, each of the subplots was randomly assigned to one of three soil/litter types (hereafter referred to as soil type): '*Quercus* soil', '*Juniperus* soil', or 'open soil'. Sterilized soil of the appropriate type, as described above, was put into each subplot to a depth of 12 cm. After the soil was added, the corresponding type of litter was added to each subplot, to a depth of 6 cm.

Five hundred *J. ashei* seeds were placed in each subplot. These seeds were evenly distributed 2-3 cm below the surface of the added soil. A cage made of 2 cm mesh chicken wire was then placed over each plot to keep out rodents, deer, and armadillos. During the winter of 2002-2003 seeds that fell into the plot were counted and removed. After 1 January 2002 each subplot was visited weekly because I expected

germination to begin immediately; however, germination did not begin in any subplot until October 2002. Each *J. ashei* seedling was marked with a labeled toothpick for future identification. Its week of germination was recorded and its presence or absence in each subsequent week until it died or until harvest in October 2003. In October 2003 all surviving seedlings were harvested, dried, and individually weighed. Plots were visited approximately every month after October of 2003 to check for additional germination, but none occurred.

The plots were weeded until germination ended to aid in the identification of new germinants. Weeding was stopped to allow for the natural competitors of each habitat type to invade. Very few plants grew in any of the experimental plots in any of the habitat types even after weeding was stopped, because by then it was too late in the season for most species to establish.

Statistical Analyses

Summary Data

Numbers of germinants and numbers of deaths were examined by month and by germination cohort; all the treatments were pooled in this analysis.

Per capita germination rate was calculated by dividing the number of germinants in a month by the estimated number of planted seeds still ungerminated at the beginning of the month. The number of ungerminated seeds was estimated by subtracting the cumulative number of germinants in prior months from the total number of seeds planted.

This of course does not attempt to estimate the number of unviable seeds planted or take into account the rate at which seeds died in the soil.

Per capita death rate was calculated by dividing the number of deaths in a month by the number of germinants alive at the beginning of the month. The number of seeds that fell into each plot are reported but not analyzed.

Treatment effects

Each germinant had a germination date with a value from 1 to 28, since there were 28 consecutive weeks in which germination occurred. A germination date value of 1 was assigned to plants that were first observed in the census of 20 October 2002, a germination date value of 2 was assigned to plants that were first observed in the census of 26 October 2002, and so on.

The effects of habitat type, soil type, and block on germination date, final mass, the number of germinants per subplot, and the number of seedlings alive at the end of the study were analyzed. For each of these variables a single value was calculated for each subplot. These were the mean germination date of all germinants in the subplot, the total number of germinants in the subplot, the total number of survivors in the subplot, and the mean final biomass of all survivors in the subplot. Because the experiment had a split-plot design, each of these four variables was analyzed with an ANOVA in which the habitat type x block term (which is also the plot term) was the denominator of the F tests of habitat type and of block. The denominator of the F tests of soil type, soil type x

habitat type, and soil type x block was the habitat type x block x soil type term (which is also the subplot term).

There is potentially a fifth variable of interest, the survival rate to the end of the experiment of the germinants in a subplot. However, the ratio of the number of survivors to the number of germinants was not analyzed directly because the ratio of two standardized normally distributed variables is a cauchy distribution, which has no mean or variance. A direct analysis of survival rate would also be problematic because germination date had such a strong effect on survival rate when all treatments were pooled and germination dates were grouped into three categories: pre-peak germination (October, November, and December), peak germination (January and February), and post-peak germination (March and April) (Table 4.1). Therefore, I used a logistic regression to fit a function to the relationship between germination date and survival rate, pooling all the germinants from all the subplots. Using this function and the mean germination date of a subplot, I calculated an expected survival rate for that subplot. I then subtracted this expected survival rate from the actual survival rate in that subplot. These differences became the values of the dependent variable in a fifth ANOVA.

Survival Analysis

In these analyses all individuals within a habitat type were pooled. I calculated a hazard function (Fox 2001) for each habitat type (. This shows the instantaneous probability of mortality for each habitat type through time. A cumulative survival function was also calculated for each habitat type. This allowed new individuals to enter

the accounting of the population as they germinated and allowed individuals to leave the accounting of the population as they died. Thus, it gives an adjusted weekly estimate of cumulative survival through time for each habitat type.

RESULTS

Summary data

Germination began in October of 2002; this was a full 8 months after the seeds were planted. The number of seeds germinating per month increased each month through February 2003 (Fig. 4.1). The per capita germination rate (i.e., number of new seedlings per remaining seed) also peaked in February 2003 (Fig. 4.2). After February 2003 the number of seeds germinating each month and the per capita germination rate dropped rapidly. There was no germination after April 2003, which is consistent with the finding of Smeins and Fuhlendorf (1997) that *J. ashei* does not have a persistent seed bank.

The first deaths of germinants occurred in October 2002, shortly after germination began (Fig. 4.3, Fig. 4.4). The number of deaths per month was greatest in March 2003, just after the February peak in germination (Fig. 4.3). The per capita death rate (i.e., deaths per surviving seedling) had a less pronounced peak. The per capita death rate was highest in June 2003, in the beginning of the summer, and was quite low during the rest of the summer (Fig. 4.4).

Plants were separated into cohorts by their week of germination. Not surprisingly, in view of the germination peak in February, the February cohorts contributed the largest numbers of plants still alive at the end of the experiment (Fig. 4.5).

However, the proportion of germinants that survived to the end of the experiment was much more similar among cohorts (Fig. 4.6). Even though the earlier germinating cohorts were at risk longer, they were almost as likely to be alive at the end of the experiment as were the February cohorts.

The greatest number of *J. ashei* berries fell into the ‘*Juniperus*’ plots (Table 4.2). No *J. ashei* berries fell into any of the ‘grass’ plots. Some *J. ashei* berries fell into ‘*Quercus*’ plots, presumably from nearby female *J. ashei* trees. Coyote scat containing 41 *J. ashei* seeds was found once in one ‘*Quercus*’ plot.

Treatment effects

There was no significant effect of habitat type on mean germination date of *J. ashei* seeds (Fig. 4.7, Table 4.3). Soil type did not significantly affect mean germination date (Table 4.3). Neither block nor any of the two-way interactions significantly affected the mean germination date. Because neither soil type nor habitat type had an effect on germination date, one can conclude that any other effect these treatments may have is not through their effects on timing of germination. In other words, if habitat type significantly affects the survival of germinants, it does so through a mechanism other than affecting when seeds germinate.

Figure 4.8 strongly suggests a trend for habitat type to affect the mean number of germinants per subplot, although it was not significant (Table 4.4): ‘*Juniperus* habitat’ plots had the highest mean number of germinants and ‘*Quercus* habitat’ plots the least. There was no significant effect of soil type or block on the number of germinants.

Habitat type had a significant effect on the mean number of seedlings alive at the end of the study (Table 4.5). There were, on average, twice as many surviving seedlings of *J. ashei* in ‘*Juniperus* habitat’ as in ‘*Quercus*’ or ‘open’ habitat (Fig. 4.9). The mean number of surviving individuals was not significantly different between ‘*Quercus* habitat’ and ‘open habitat’. There were no significant differences among soil types or blocks in the mean number of surviving individuals (Fig. 4.10).

Habitat type had a strong significant effect on the mean biomass of seedlings alive at the end of the study (Table 4.6). The direction of the effect on biomass was different, however, from the effects on survival. Surviving *J. ashei* seedlings in ‘open’ habitat were on average more than twice as large as surviving seedlings in the ‘*Juniperus*’ or ‘*Quercus* habitat’ types (Fig. 4.11). Block was not a significant factor in the analysis of mean biomass. Because of the low survival in the ‘open’ and ‘*Quercus* habitat’ types, several of the blocks did not contain all treatment combinations. Thus, it was difficult to estimate the three-way interaction term and therefore soil type and its interactions were not tested. An inspection of the mean biomass by soil type did not reveal any trends.

The relationship between germination date and survival to the end of the experimental was negative: the earlier a plant germinated, the more likely it was to be alive at the end of the experiment, even though it had been at risk longer (Table 4.7). I used this relationship to remove the effect of germination date from survival (see Methods), in order to increase the power of the analysis to detect treatment effects (Table 4.8). The values reported in Fig. 4.12 are therefore means of residual values from a logistic regression; these residuals are differences between the actual rate of survival and

the rate predicted from germination date. '*Juniperus*' plots had a significantly higher mean residual value than the other two habitat types. There was also a significant soil x habitat type interaction effect (Table 4.8). In particular, the residual value is highest in '*Juniperus* soil' in '*Juniperus* habitat' and lowest in '*Juniperus* soil' in 'open habitat' (Fig. 4.13). The effect of soil type thus differs among habitat types. It has no effect in the '*Quercus* habitat', and except for 'open soil' soil type has opposite effects in the other two habitats.

Survival Analysis

The hazard function showed differences in the instantaneous mortality among habitat types (Fig. 4.14). Thus, it appears that the effect of seasons on mortality differed among habitat types. In general, '*Juniperus* habitat' always had a lower value of the hazard function than the other two habitat types. Open grassland and '*Quercus* habitat' had high mortality early in the experiment. '*Quercus* habitat' had a period in the middle of the experiment, which corresponds to the months of March and April, when it had higher mortality than the other two habitats. There was a peak in the mortality for all three habitat types in June, but the peak was highest for the 'open' habitat type.

The cumulative survival function shows that more individuals survived in the '*Juniperus* habitat' than the other two habitats. '*Quercus*' and 'open' habitats did not appear to differ in cumulative survival at the end of the experiment, but they did differ during the experiment. In the middle of the experiment '*Quercus* habitat' had a faster drop in survival than the 'open' habitat (Fig. 4.15). This corresponds with the peak

observed in the hazard function for ‘*Quercus* habitat’ at the same time of year (Fig. 4.14). All three habitats had decreases in cumulative survival during the late spring (i.e. June), but the “open’ habitat had the greatest decrease. Again, this corresponds with the timing and pattern of the hazard function peak in June. These data suggest that ‘*Juniperus* habitat’ provides the safest environment for *J. ashei* seedlings. ‘*Quercus*’ and ‘open’ habitats did not differ in their overall survival, but did differ in the timing of mortality.

DISCUSSION

Life history of *J. ashei*

Of course this experiment only represents one year in a region whose climate varies dramatically from year to year, and therefore the life history variables measured in this experiment may also vary from year to year. Based on the results of the experiment, we can say that:

- *J. ashei* seeds evidently have some innate dormancy that is not broken by a cold pre-treatment, although it might be broken by passage through a bird’s crop. Under the conditions of this experiment (cold pre-treatment, no cleaning or scarification) the mode of germination occurred approximately one year after seed set. During almost all of that year the seeds were on the ground where fungi and bacteria could break down the seed coat whenever the soil was wet enough for microbial activity. This suggests that *J. ashei* is ‘hard-seeded’, that is, the seed coat has to be mechanically weakened for germination to occur.

- *J. ashei* seeds germinated between October and April in this experiment. Cool-season (October through February in central Texas) germination is thought to increase a seedling's chance of survival because the soil is more likely to be wet then.

- Germination date had little effect on a plant's chance of surviving to the end of the experiment as long as it germinated before March 2003. Earlier germination (i.e., closer to October than March) is thought to be beneficial because it gives a seedling more time to form deep roots that can reach moist soil during the summer (Fowler 1988b). It is likely that in this experiment the benefits of earlier germination canceled the extra months at risk, resulting in the lack of relationship between germination date and survival to the end of the experiment.

- There was a peak in the per capita death rate in June. In 2003 June was the first month with a high mean daily maximum temperatures ($>32^{\circ}$ C daytime maximum), although high temperatures often begin in May in central Texas. It may be that water stress associated with these higher temperatures caused the June peak of seedling deaths. Alternatively, the June seedling deaths may have been caused, all or in part, by the delayed effects of below-average rainfall in April and May 2003 (Table 4.9).

- Surprisingly, the per capita death rate was relatively low in July and August. Other studies have reported these months to have the highest rates of *J. ashei* seedling mortality of the year (Jackson and Van Auken 1997). It may be that in this experiment the deaths in June removed most of the poorly rooted seedlings then, so that only well-established seedlings were left by July.

- The per capita death rate in this experiment increased again in October. These deaths may have been due to delayed effects of water stress in prior months.

Seed dispersal

The greatest number of seeds fell onto ‘*Juniperus* habitat’ plots. Seeds were also observed in ‘*Quercus* habitat’ plots in blocks that also had female *J. ashei* trees within 3m. The density of naturally dispersed seeds in ‘*Juniperus* habitat’ plots was about 67 seeds/m².

This density probably represents the low end of natural variation, as the number of seeds collected under female *J. ashei* trees have previously been reported to be as high as 16,600 seeds/m² (Blomquist 1990) but only as low as 1472 seeds/m² (Owens and Schliesing 1995). It is widely accepted that there is a large amount of variation in the number of *J. ashei* seeds produced each year, in part associated with year-to-year differences in precipitation (Smeins and Fuhlendorf 1997). Casual observations in the study site in other years indicate that *J. ashei* seed set in 2003 was particularly low.

Despite the overall low number of seeds, there was a clear, strong pattern of non-random distribution of seeds on the ground. Not surprisingly, more seeds were found under woody canopies that contained at least one female *J. ashei* tree. Chavez-Ramirez and Slack (1994) reported that birds can produce patches with high densities of seeds under post-foraging perching sites. Perching sites of American robins (*Turdus migratorius*) had a post-foraging mean seed density of 30/m² while perching sites of cedar waxwings (*Bombycilla cedrorum*) had a mean seed density as high as 22,250/m².

Chavez-Ramirez and Slack (1994) also reported that open sites had a mean seed density of $5/m^2$, while I found no naturally dispersed seeds in ‘open habitat’ plots. Thus, the clumped distribution of *J. ashei* individuals is partially explained by the clumped dispersal of *J. ashei* seeds.

Treatment effects on germination

Neither habitat type nor soil type affected the mean germination date. There was a strong, but non-significant, tendency for ‘*Juniperus* habitat’ to have the most seedlings arising from the 500 seeds sown in each plot, and for ‘open habitat’ to have the fewest. In other words, being under an adult of the same species apparently facilitated *J. ashei* germination, with the caveat that ‘germination’ actually includes emergence and survival up to 7 days (to a seedling’s first weekly census) as well as seed germination *sensu stricto*. Because this hypothesized facilitation of germination by adult trees will tend to produce the same clustering of juvenile *J. ashei* under adult *J. ashei* as seed dispersal does (see above), the tendency for *J. ashei* seedlings to be more common under adult *J. ashei* than elsewhere (Batchelor chapter 2, Fowler 1988a, Jackson and Van Auken 1997, Anderson et al. 2001, Noel pers. obs.) is not definitive evidence for either hypothesis.

There was no evidence that the soil type treatment, which included litter as well as the top 10 cm of soil, affected the number of seedlings arising from sown seeds. Thus if there were any negative effects of litter on seedlings (cf. Barton 1993, Barritt and Facelli 2001), these negative effects were evidently counteracted by other soil factors such as infiltration rate. This was counter to my expectation that the leaves of *Q.*

fusiformis, which are stiff, sclerophyllous, water-repellant, and slow to break down, would inhibit germination in the ‘*Quercus* soil’ treatment.

Treatment effects on survival

Habitat type affected survival rates above and beyond any effect it had on germination date: survival rates were higher in ‘*Juniperus* habitat’ than in ‘*Quercus* habitat’ or in ‘open habitat’. It seems most likely that the primary beneficial effect of ‘*Juniperus* habitat’ was the shade it provided, because shading has been shown to be beneficial for *J. ashei* seedling survival (Batchelor chapter 3).

The deaths in the ‘open habitat’ plots appeared to be primarily due to water stress. Deaths peaked in June in all three habitat types, but the death rate then was much higher in the ‘open habitat’ plots (Fig. 4.14).

Surprisingly, death rates in the ‘*Quercus* habitat’ plots were as high as those in the ‘open habitat’ plots, despite the beneficial effects of shading on the ‘*Quercus* habitat’ plots. The amount of shade experienced in ‘*Quercus* habitat’ is likely the same amount as in ‘*Juniperus* habitat’. The average summer light level of each habitat type is around $500 \text{ mol s}^{-1} \text{ m}^{-2}$ (Anderson et al. 2001 and Wayne and Van Auken 2004). Why then was ‘*Quercus* habitat’ as poor a habitat for *J. ashei* seedlings as ‘open habitat’? While the *J. ashei* seedlings in the ‘open habitat’ plots appeared to die from water stress, many of the seedling deaths in the ‘*Quercus* habitat’ plots appeared to be due to damage caused by oak leaves, catkins, and branches (with their associated vascular and cryptogamic epiphytes), and ball moss (*Tillandsia recurvata*, an epiphyte) by itself falling on them.

Note that there was a peak of mortality in March in ‘*Quercus* habitat’ plots when *Q. fusiformis* sheds its leaves (Fig 4.14). Some studies in quite different systems have found that mortality from falling plant debris can be substantial (Clark and Clark 1989, Gillman et al. 2003, Peters et al. 2004).

The effects of soil type on survival occurred through the interaction of soil type and habitat type. ‘*Juniperus* soil’ (i.e., juniper litter and the associated top 10 cm of soil) was the most favorable soil type in ‘*Juniperus* habitat’ plots (i.e., under *J. ashei* canopies) but it was the least favorable soil type in the ‘open habitat’ plots. Juniper litter tends to form a finely-textured mat about 5 cm deep that presumably acts as a mulch to retarding soil evaporation (Slaughter 1997), but also perhaps reduces the amount of water that reaches the soil surface because of absorption (Yager 1993); the net effect may be nil (cf. Thurow et al. 1987). Perhaps under *J. ashei* canopies *J. ashei* litter stays moist enough for its beneficial mulching effect to dominate, while in the open it dries out and its effect on infiltration dominates.

Treatment effects on growth rates

Although survival rates were highest in the ‘*Juniperus* habitat’ plots, growth rates were highest in the ‘open habitat’ plots (Fig 4.11). This difference between survival rates and growth rates is consistent with the results of a garden experiment, which showed that shade per se increases *J. ashei* seedling survival but decreases seedling growth (Batchelor chapter 3).

Treatment effects on the number of seedlings alive at the end of the experiment

The number of seedlings alive at the end of the experiment in each plot was the product of the germination rate, the survival rate, and the 500 seeds sown per plot. ‘*Juniperus* habitat’ plots had nearly twice as many germinants alive at the end of the experiment as ‘open habitat’ plots (Fig. 4.9), because both germination rates and survival rates were higher there than in ‘*Quercus* habitat’ and ‘open habitat’ plots. Soil type did not affect the number of surviving individuals, despite the significant soil type X habitat type interaction effect on survival rates.

Facilitation of seedlings by adult *Juniperus ashei*

In this study the net effect of canopy, soil and litter depended on the life history trait being examined. The habitat of ‘*juniperus*’ plots may have increased germination rates and did increase survival rates of seedlings in their first year of life. At the earliest stages of the life history of *J. ashei*, the presence of an adult conspecific had a net positive (i.e., facilitative) effect.

The absence of other plant species from the experimental plots allows one to be sure that this positive effect arose from the direct interaction of seedlings and conspecific adults, not from indirect effects involving other plant species. However, where other plant species are present, *J. ashei* adults might facilitate *J. ashei* seedlings by suppressing competing species. Yager and Smeins (1999) found that removal of *J. ashei* trees resulted in increased survival of transplanted grasses.

Unfortunately most studies have not separated the direct effects of adult plants on seedlings from their indirect effects via competition with other plants. If the only comparison is between seedlings growing under trees or shrubs with seedlings growing in the open, it is not possible to determine whether growing under a larger plant is directly favorable, or is only indirectly favorable due to the suppression of competitors. In the latter case, the most favorable patches would be patches in the open but without competitors, not patches under the trees.

Competition with seedlings by adult *Juniperus ashei*

The presence of adult *J. ashei*, although it increased survival rate, reduced seedling growth rate. Evidence from a garden study (Batchelor Chapter 3) suggests that competition for light was the most likely reason for the slower growth rates measured under trees. Why should survival and growth be affected differently by the presence of an adult tree? Seedling mortality was episodic (Fig. 4.14), suggesting that deaths occurred during or shortly after periods of extreme water stress. The shading provided by an adult may have mitigated water stress during these periods. The effect on growth, however, was probably more continuous, although information on monthly growth rates is not available. Seedlings under the trees had less light, and it may be that light, not water, determined growth rate.

It may be that later in life competition with the large trees for water, especially in the deeper (>10cm) soil layers, may become more important. Anderson et al (2001)

found lower water potentials in sapling *Prosopis glandulosa* under trees, suggesting that competition with the overstory tree may become more important as the seedlings mature.

The balance between competition and facilitation

Survival rates of *J. ashei* increase rapidly as the plants become larger (Noel unpublished data). Therefore the effects of adult *J. ashei* trees may change over the course of the lives of the smaller *J. ashei* plants around them. Early in life, when survival dominates, the adult *J. ashei* has a net positive effect on the smaller plant. Later in life, when survival rates are very high regardless of the proximity of an adult (Noel, unpublished data) and therefore growth rates are the most important, the adult *J. ashei* has a net negative effect.

A few other studies have also found that the balance between positive and negative effects of adult plants depends upon the age of the plant under them (Kellman and Kading 1992, Walker 1994, Greenlee and Callaway 1996, Pugnaire et al. 1996, Callaway 1998). For example, Rousset and Lepart (2000) found that the balance between competition for light and facilitation via protection from herbivores depended on the life stage of the *Quercus humilis*. The hypothesis of a fluctuating net effect of canopy on *J. ashei* is consistent with the tendency of the smallest *J. ashei* to have the strongest spatial association with adult *J. ashei* (Batchelor chapter 2), an association that decreases in strength with the size and therefore presumably with the age of the smaller plants.

What this says about spatial pattern

The spatial association between small and adult *J. ashei* individuals (Batchelor chapter 2), and between small *J. ashei* and adult *Quercus fusiformis*, is likely to be primarily due to non-random seed dispersal by perching birds, as discussed above. It is presumably reinforced, however, by the positive net effect of adult *J. ashei* on *J. ashei* seedling survival and perhaps on *J. ashei* germination rate.

Positive spatial associations between small and large shrubs or trees have been reported from many systems (e.g., Rebertus et al. 1991, Valiente-Banuet et al. 1991, Guevara et al. 1992, Kellman and Kading 1992, Callaway and Bertness 1994, Eccles et al. 1999, Weltzin and McPherson 1999, Schenk et al. 2003), including other species of *Juniperus* (McPherson et al. 1988). Bird dispersal is known to be involved in a few instances (van Ommeren and Whitham 2002), including one involving *Juniperus monosperma*, but is usually not measured. Protection from herbivores was not involved in the present study, because essentially nothing eats *J. ashei* seedlings, but has been shown to cause positive spatial associations in other systems (e.g., Callaway 1992, Louda and Rodman 1996). Reductions in the rate of fire-related deaths have also been hypothesized to cause positive spatial associations (e.g., Fuhlendorf 1992). The experimental site was not burned, but it is known that the presence of an adult tree (*Juniperus ashei* or *Quercus fusiformis*) does not affect the rate of fire-related deaths of small *J. ashei* (Noel unpublished data). Positive spatial associations may also arise in some systems from the positive effects of adult plants upon soil nutrient content, infiltration rate, and other soil properties (e.g., Belsky et al. 1989, Callaway et al. 1991,

Martinez 2003, Tirado and Pugnaire 2003); the present experiment, however, rules out these mechanisms, at least for the top 10cm of soil, in this system. Finally, spatial associations may arise from the positive effects of adults upon plant water status via shading, as I have shown for this system and has also been found in many others (e.g., Callaway 1992, Hoffman 1996, Weltzin and McPherson 1999).

Unfortunately, none of the other studies of *Juniperus* species in Texas separate the effects of these factors (Rykiel and Cook 1986; Fowler 1988a, Jackson and Van Auken 1997, Wayne and Van Auken 2004). However, the presence of a north-facing direction bias in the spatial pattern in all size classes of several woody plant species including *J. ashei* (Phillips and Barnes 2003, but see Gass and Barnes 1998) suggests that microclimate modification may be a persistent mechanism of facilitation.

What this says about woody encroachment

The encroachment of woody plants into former grasslands and the conversion of grasslands and savannas into woodlands have been widely discussed (Scholes and Archer 1997, Van Auken 2000). In the western United States, the primary woody species involved are species of *Juniperus* (Burkhardt and Tisdale 1976, Miller and Wigand 1994, Wangler and Minnich 1996, Briggs et al 2002, Jessup et al. 2003), *Prosopis* (Brown and Archer 1989, Bahre and Shelton 1993, Archer 1995a), and, in desert grasslands, *Larrea tridentata* (Buffington and Herbel 1965, Grover and Musick 1990). Potential causes of the increasing rates at which woody plants are invading grasslands and savannas include fire suppression, overgrazing, changes in temperature and precipitation patterns, and

increases in CO₂ level; the relative importance of each of these is a matter of debate (Boutton et al. 1994, Archer 1995b, Van Auken 2000).

In some systems, encroachment may require facilitation of woody plant seedlings by existing woody plants, so woody plant encroachment becomes a positive feedback process. Weltzin and McPherson (1999) suggest that this is the case at the latitudinal limit of southwestern oak savannas. There may be other systems where woody plant encroachment occurs without any facilitation being involved (Augustine and McNaughton 2004). Finally in other systems, facilitation of woody plant seedlings by existing woody plants may play an important role without being critical. This seems to be the case in, for example, south Texas where *Prosopis* appears to facilitate shrub encroachment (Barnes and Archer 1999). This also appears to be the case in the central Texas savannas of the present study, because *J. ashei* seedlings, while they can be facilitated by adult *J. ashei*, also successfully establish in open areas (Fig. 4.9, Fig. 4.11; see also chapter 2).

Table 4.1. Contingency table analysis of germination date and survival. Pre-peak germination corresponds to germination during October, November, and December. Peak germination corresponds to germination during January and February. Post-peak germination corresponds to germination during March and April.

	pre-peak germination	peak germination	post-peak germination
dead	307	1851	634
alive	200	827	25
percent survival	39%	31%	4%
$X^2 = 238.0948$	$P < 0.0001$		

Table 4.2. Number of naturally dispersed (not planted) seeds in each habitat type by block.

block	'Juniperus habitat'	'Quercus habitat'	'open habitat'	Total
1	184	24	0	208
2	37	2	0	39
3	0	0	0	0
4	0	76	0	76
5	156	0	0	156
Total	377	102	0	479

Table 4.3. Results of the ANOVA of mean germination date.

Source of Variation	df	Type III SS	MS	F	p
block	4	14.1707	3.5427	0.46	0.7604
habitat type	2	34.5693	17.2846	2.27	0.1658
block*habitat type [&plot]	8	60.9561	7.6195	----	----
soil type	2	22.2313	11.1157	2.89	0.0845
block*soil type	8	14.4297	1.8037	0.47	0.8599
soil type * habitat type	4	6.6211	6.6553	1.73	0.1920
block * soil type * habitat type	16	234.4204	14.6513	-----	-----
total	44				

Table 4.4. Results of the ANOVA of the mean number of germinants.

Source of Variation	df	Type III SS	MS	F	p
block	4	16424.5778	4106.1444	1.69	0.2438
habitat type	2	12614.9333	6307.4667	2.60	0.1349
block*habitat type [&plot]	8	19407.2889	2425.9111	----	----
soil type	2	582.9333	291.4667	0.18	0.8394
block * soil type	8	4717.2889	589.6611	0.36	0.9279
soil type * habitat type	4	3435.3333	858.8333	0.52	0.7213
block * soil type * habitat type	16	26346.4444	1646.6528	-----	-----
total	44				

Table 4.5. Results of the ANOVA of the mean number of surviving individuals.

Source of Variation	df	Type III SS	MS	F	p
block	4	2810.9778	702.7444	1.60	0.2071
habitat type	2	10768.3111	5384.1556	12.29	0.0022
block*habitat type [&plot]	8	2987.6889	373.4611	----	----
soil type	2	418.3111	209.1556	0.48	0.6290
block * soil type	8	3396.3556	424.5444	0.97	0.4927
soil type * habitat type	4	3983.9556	995.9889	2.27	0.1066
block * soil type * habitat type	16	7011.3778	438.2111	-----	----
Total	44				

Table 4.6. Results of the ANOVA of mean biomass of surviving individuals.

Source of Variation	df	Type III SS	MS	F	p
block	4	0.0071	0.0018	1.69	0.2433
habitat type	2	0.0392	0.0196	18.67	0.0010
block*habitat type [&plot]	8	0.0084	0.0010	----	----

Table 4.7. Summary of logistic regression results of the effects of germination date on survival to end of experiment.

	df	Estimate	St. error	Wald Chi-Square	p-value
intercept	1	1.2481	0.1575	62.7881	< 0.0001
cohort	1	-0.1188	0.0083	204.1751	< 0.0001

Table 4.8. Results of the ANOVA of mean difference between predicted and observed survival.

Source of Variation	df	Type III SS	MS	F	p
block	4	0.0778	0.0194	0.86	0.5274
habitat type	2	0.7225	0.3612	15.95	0.0016
block*habitat type [plot]	8	0.1811	0.0226	----	----
soil type	2	0.0389	0.1944	1.26	0.3095
block * soil type	8	0.1667	0.0208	1.35	0.2876
soil type * habitat type	4	0.2994	0.0748	4.86	0.0093
block * soil type * habitat type	16	0.2462	0.0154	-----	-----
Total	44				

Table 4.9. Climate data for study site (National Climate Data Center 2004)

Month	Avg. monthly precip. (cm)	2002 monthly precip. (cm)	2003 monthly precip. (cm)	2002 avg. daily max. temp. (°C)	2002 avg. daily max. temp. (°C)
January	5.2	1.6	3.4	18.8	16.4
February	5.6	1.6	7.7	18.1	16.6
March	5.3	2.6	2.9	21.3	21.4
April	7.2	4.2	0.5	28.0	27.5
May	13.5	5.7	0.4	30.7	31.8
June	12.1	15.4	12.1	33.7	33.6
July	5.4	24.0	5.7	31.8	33.4
August	6.7	2.4	2.3	34.5	35.3
September	8.8	10.4	19.1	31.7	30.2
October	10.2	26.0	5.7	26.4	27.9
November	8.1	11.8	4.1	20.8	23.2
December	6.1	11.6	1.4	18.7	19.2
Total	94.3	117.2	65.4	18.8	16.4

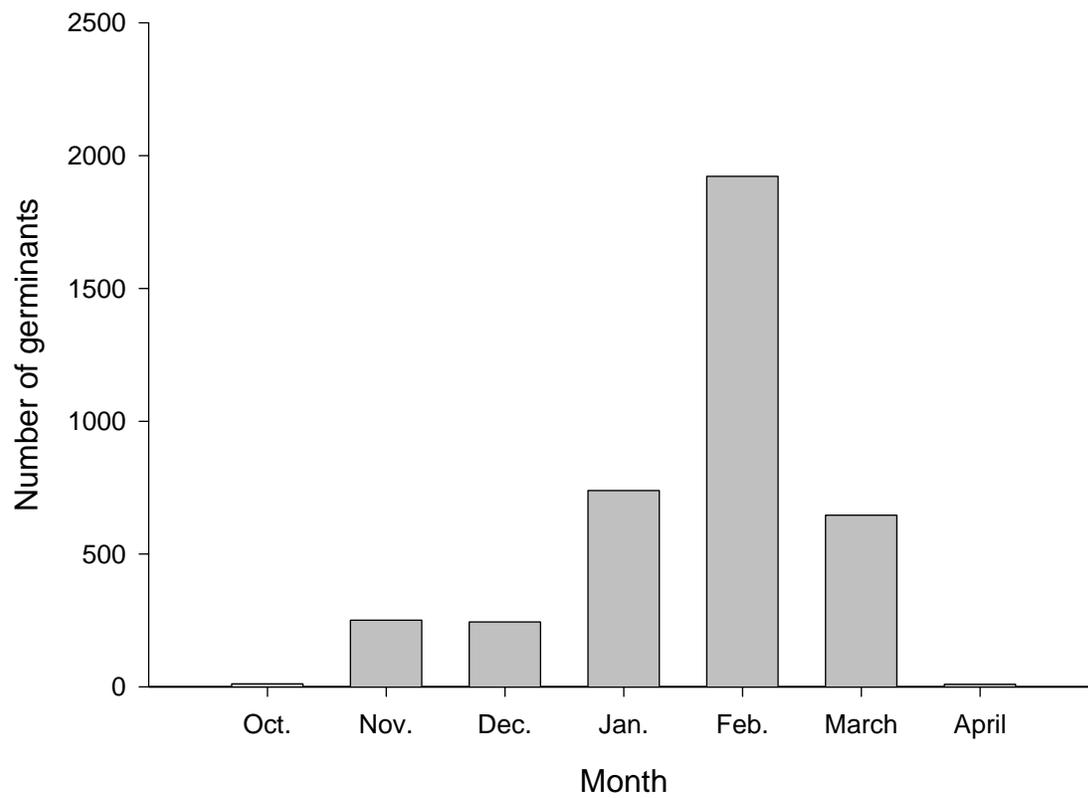


Figure 4.1. Number of *J. ashei* germinants by month.

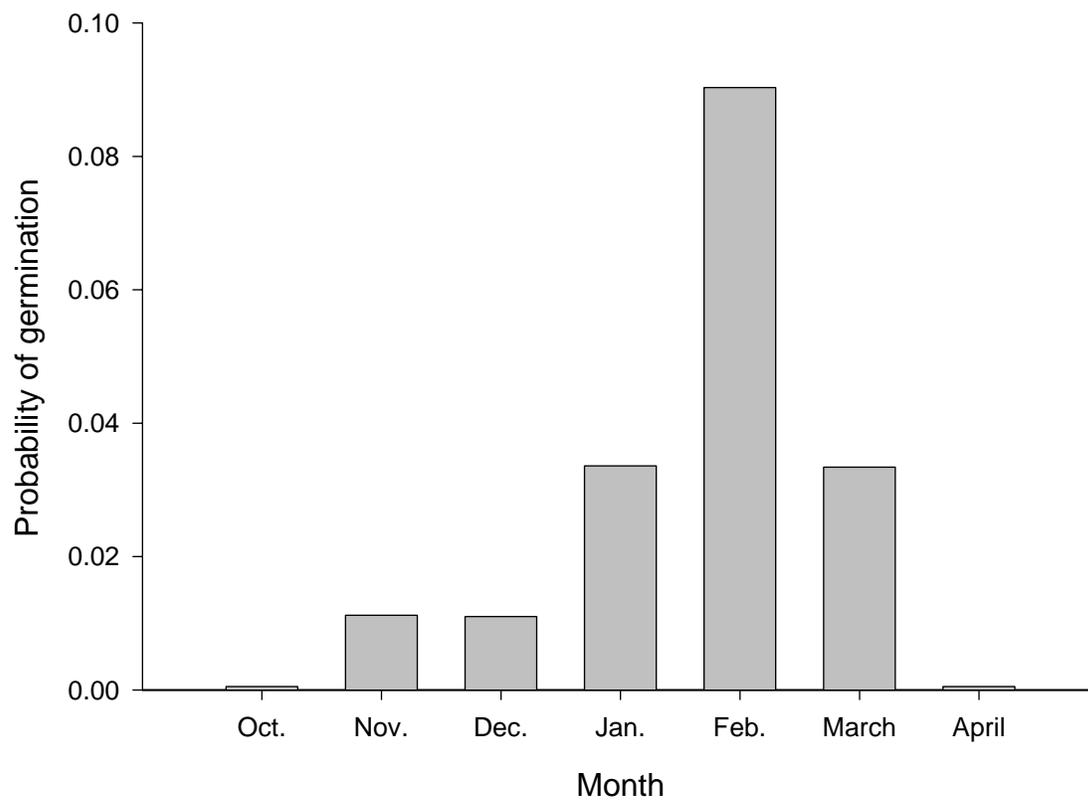


Figure 4.2. Per capita germination rate of *J. ashei* by month.

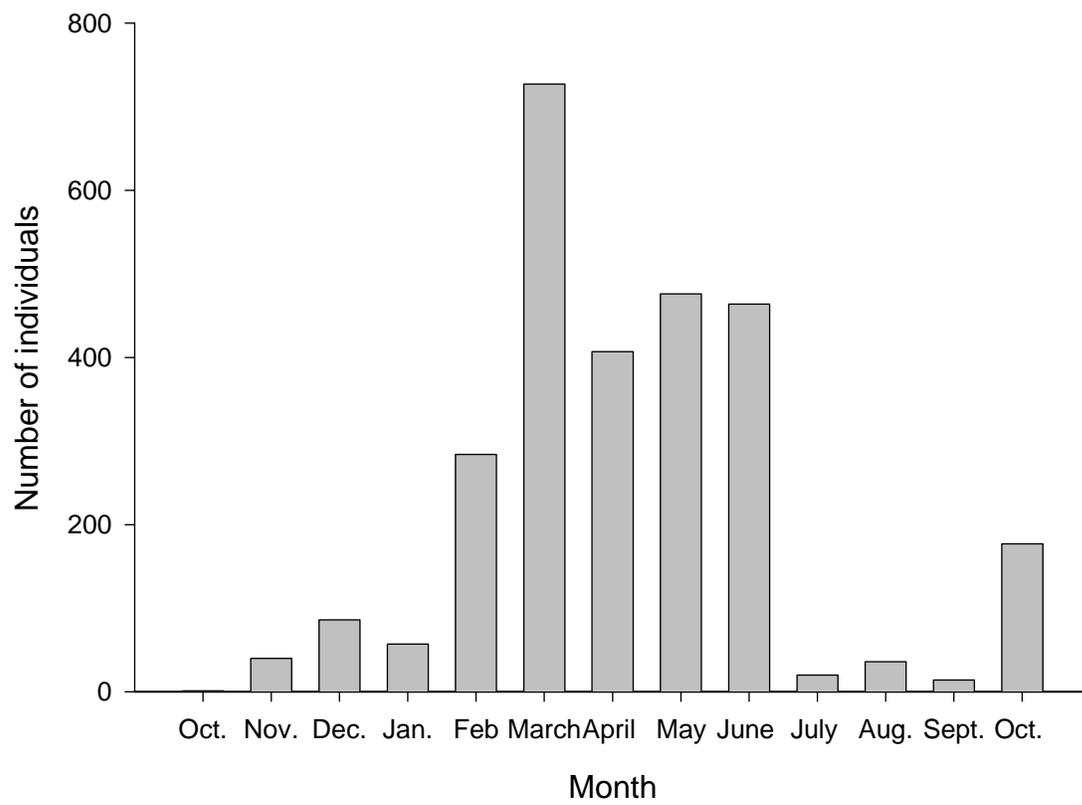


Figure 4.3. Number of *J. ashei* deaths reported by month.

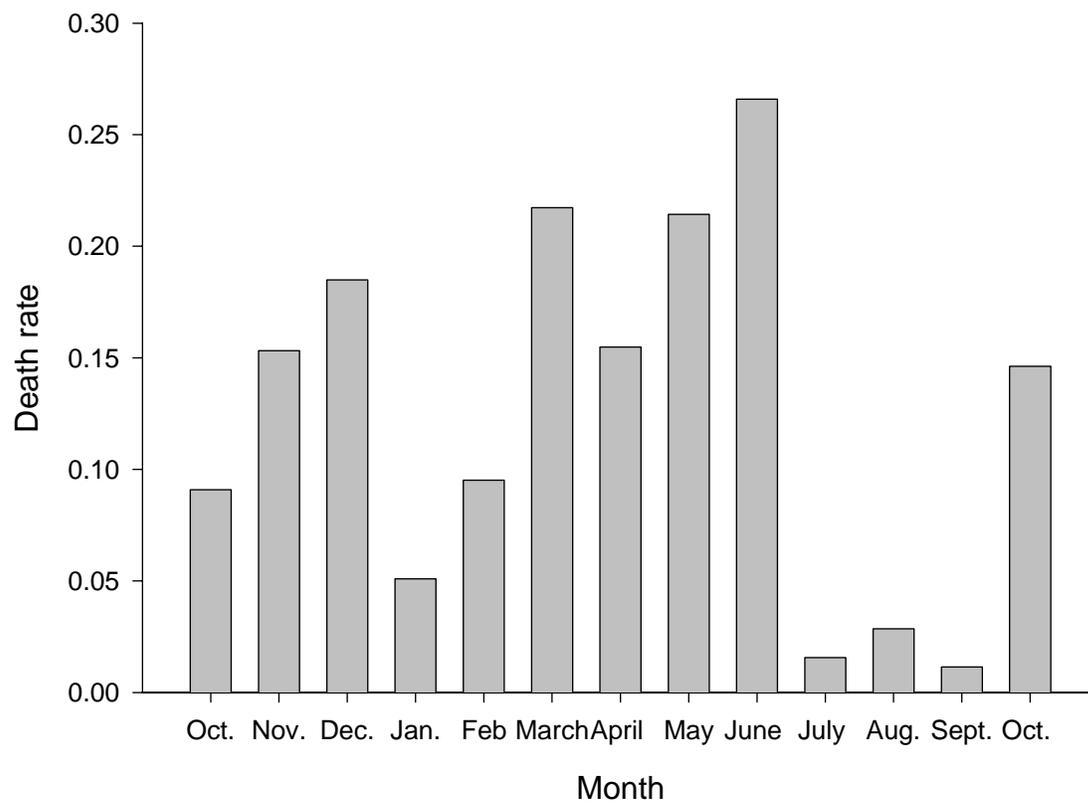


Figure 4.4. Per capita death rate (i.e. deaths per seedling alive at the beginning of the month) of *J. ashei* germinants by month

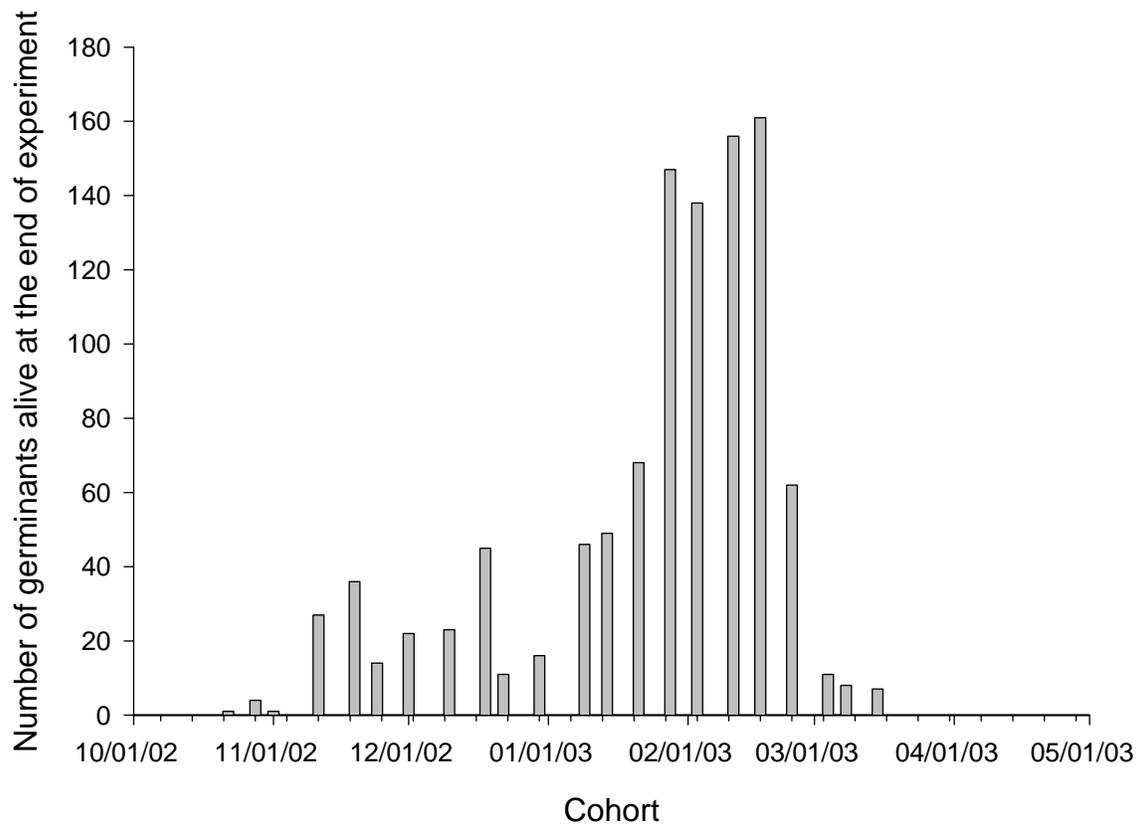


Figure 4.5. Number of *J. ashei* germinants alive at the end of the experiment by cohort

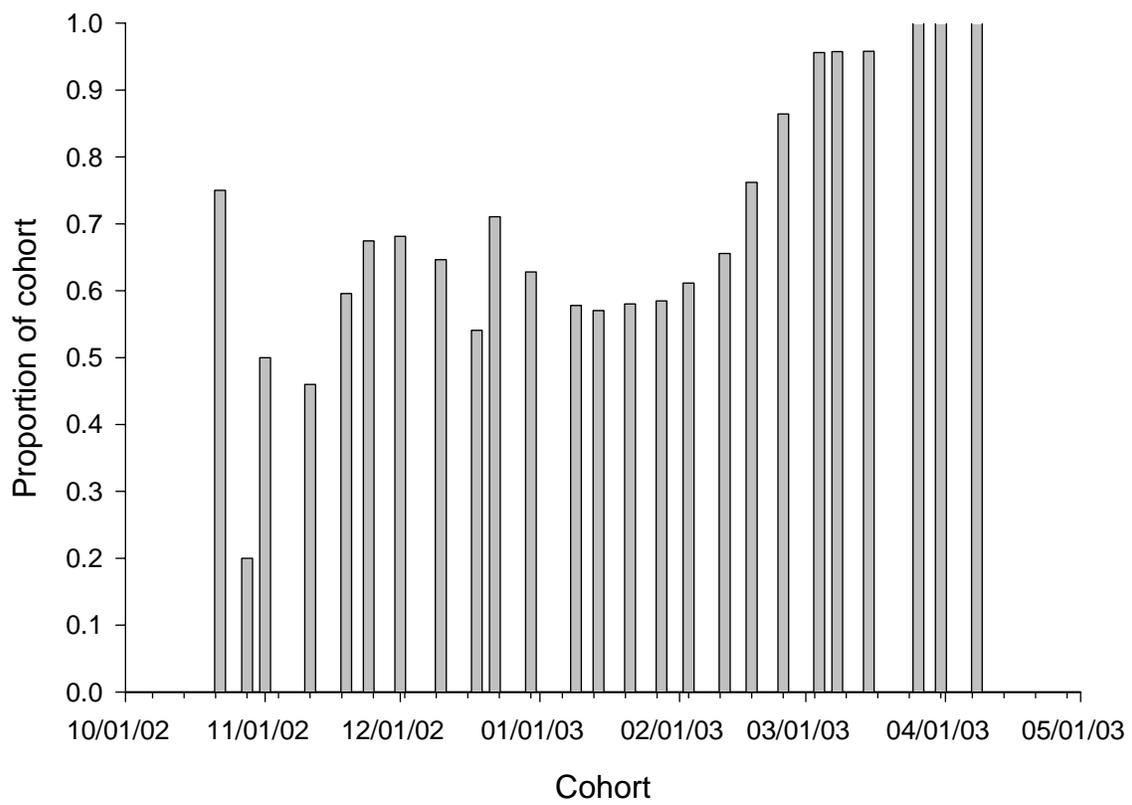


Figure 4.6. Proportion of *J. ashei* cohort that died before the end of the experiment

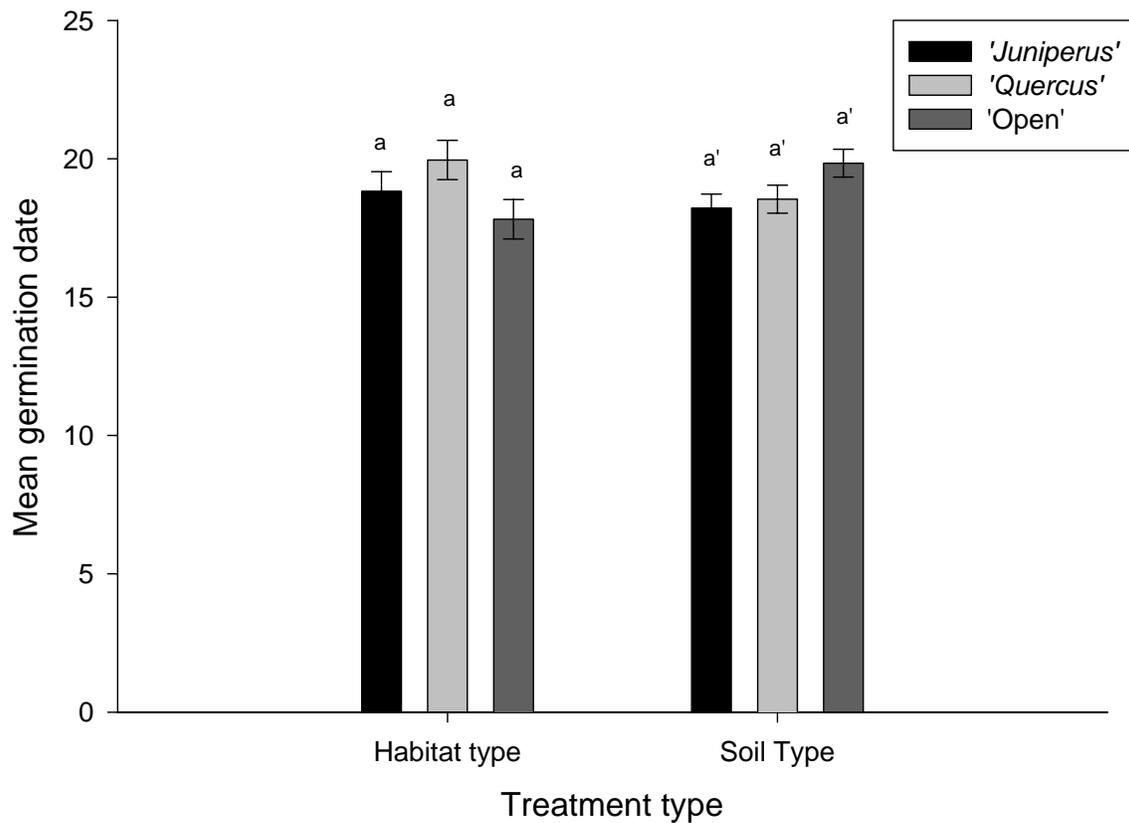


Figure 4.7. Mean germination date of *J. ashei* seeds in different habitat types and different soil types. Bars sharing labels are not significantly different. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (SAS 1990).

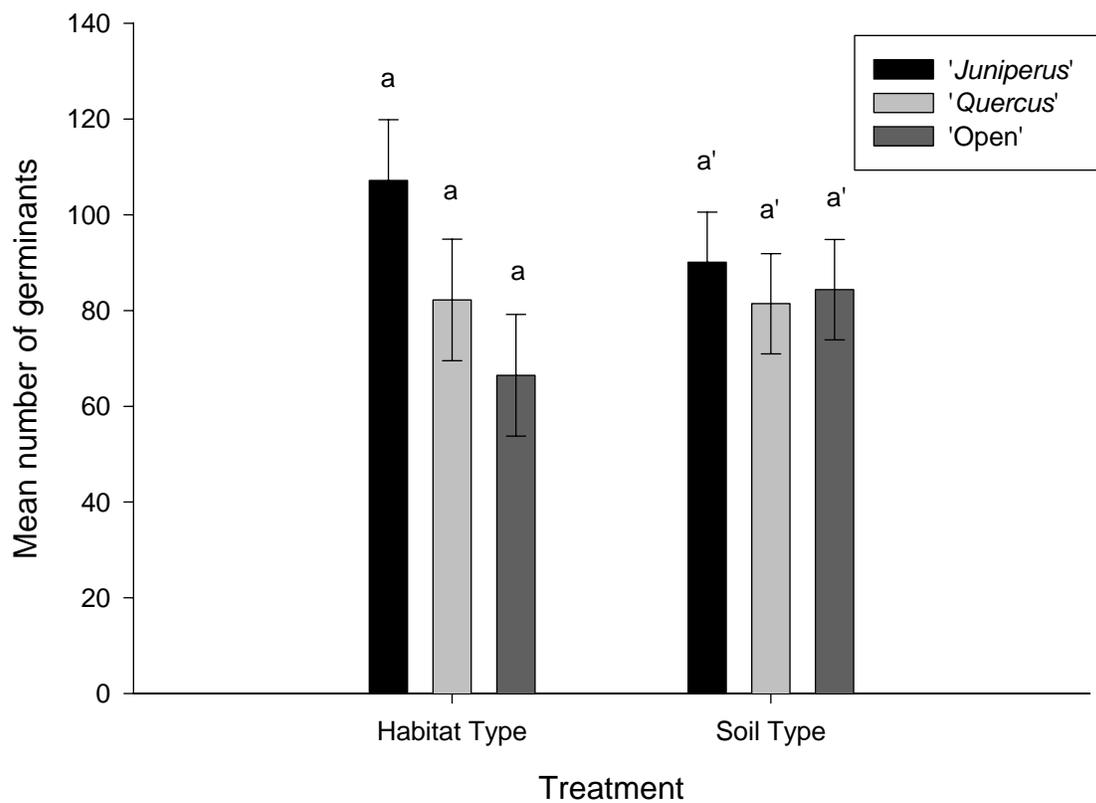


Figure 4.8. Mean number of *J. ashei* germinants by habitat type and soil type. Bars sharing labels are not significantly different. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (SAS 1990).

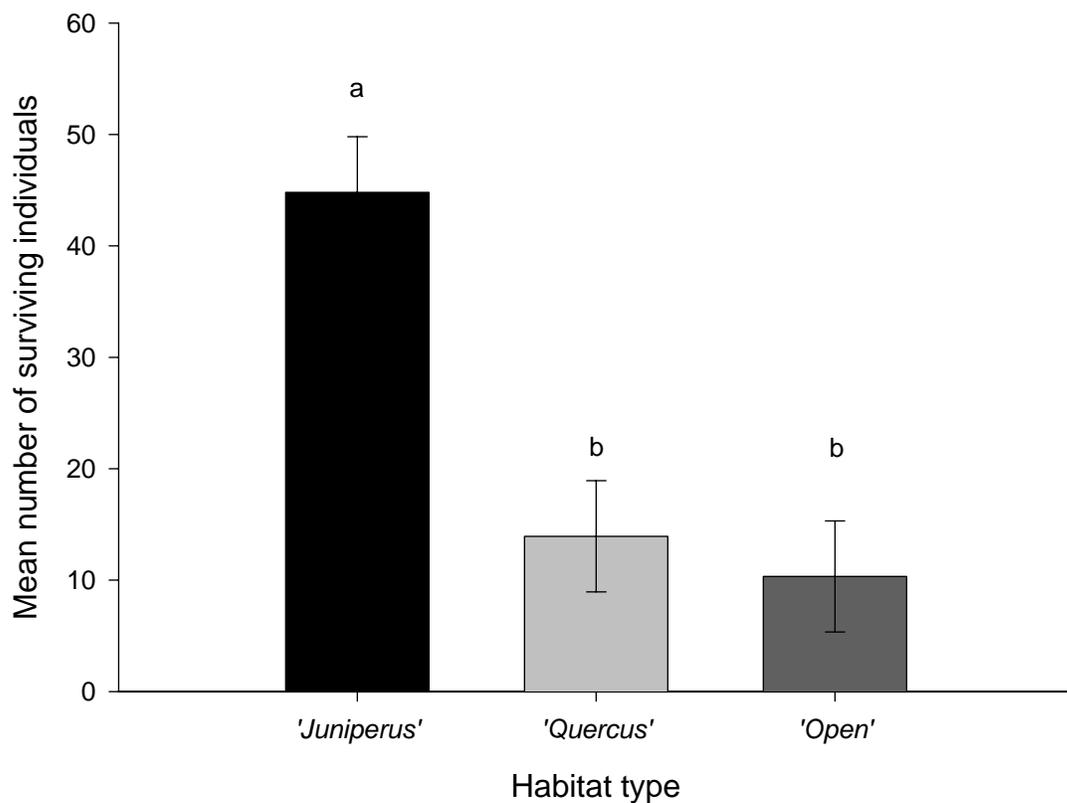


Figure 4.9. Mean number of surviving *J. ashei* individuals by habitat type. Bars sharing letters are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (SAS 1990).

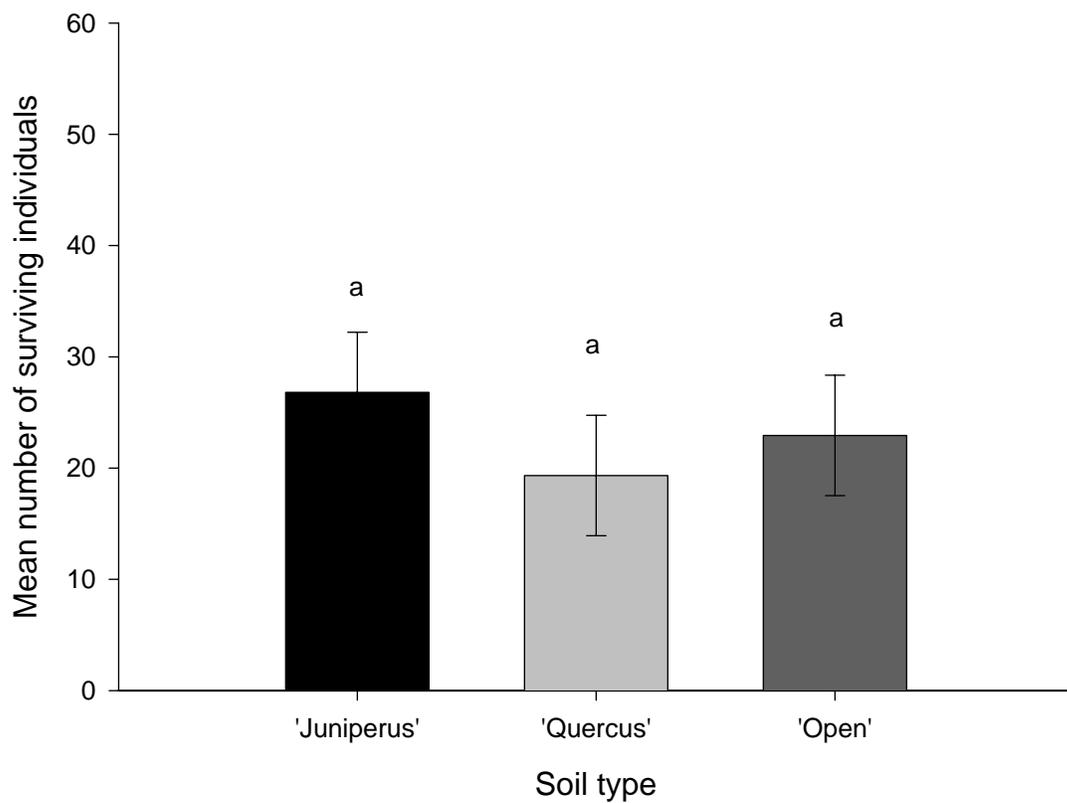


Figure 4.10. Mean number of surviving *J. ashei* individuals by soil type. Bars sharing letters are not significantly different. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (SAS 1990).

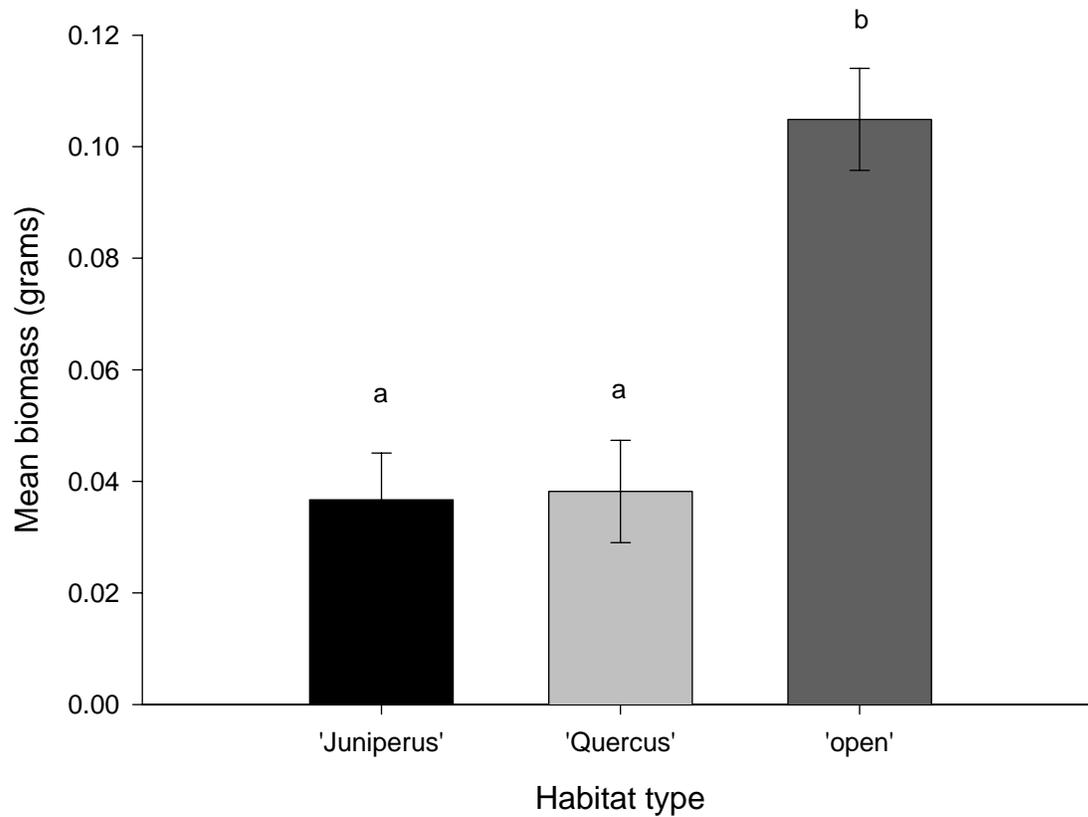


Figure 4.11. Mean biomass of *J. ashei* individuals by habitat type. Bars sharing letters are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (SAS 1990).

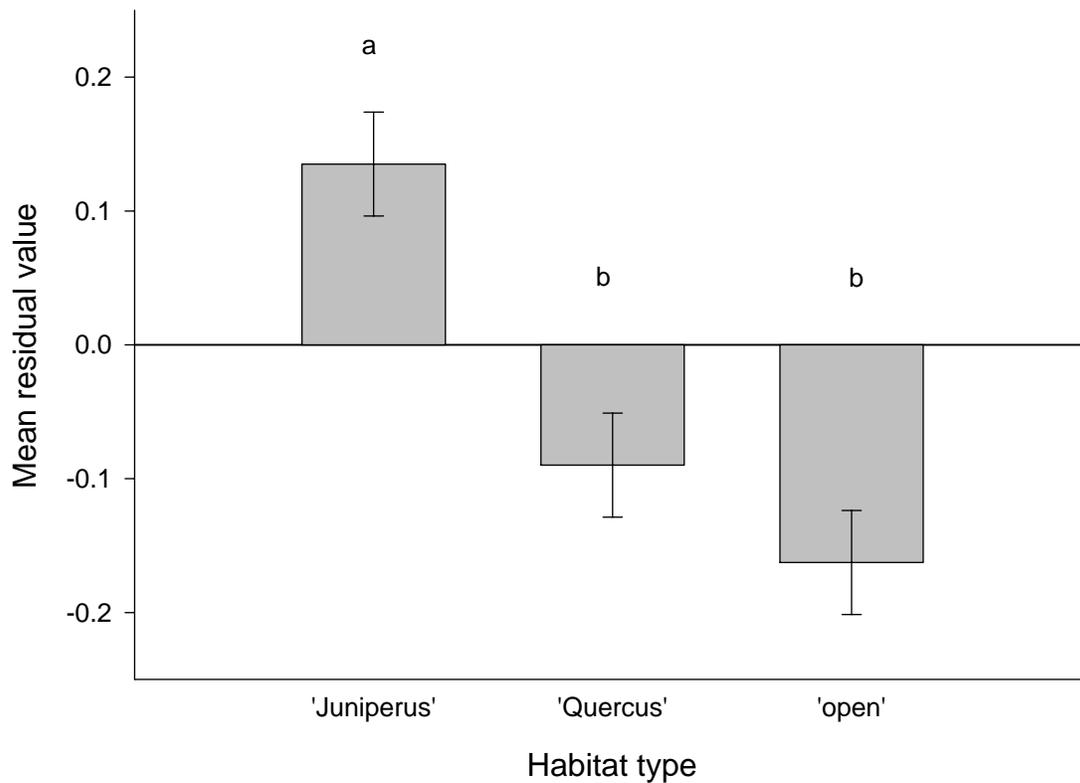


Figure 4.12. The effect of habitat type on the residual between the mean observed survival and the predicted survival from the mean germination date. Bars sharing letters are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (SAS 1990).

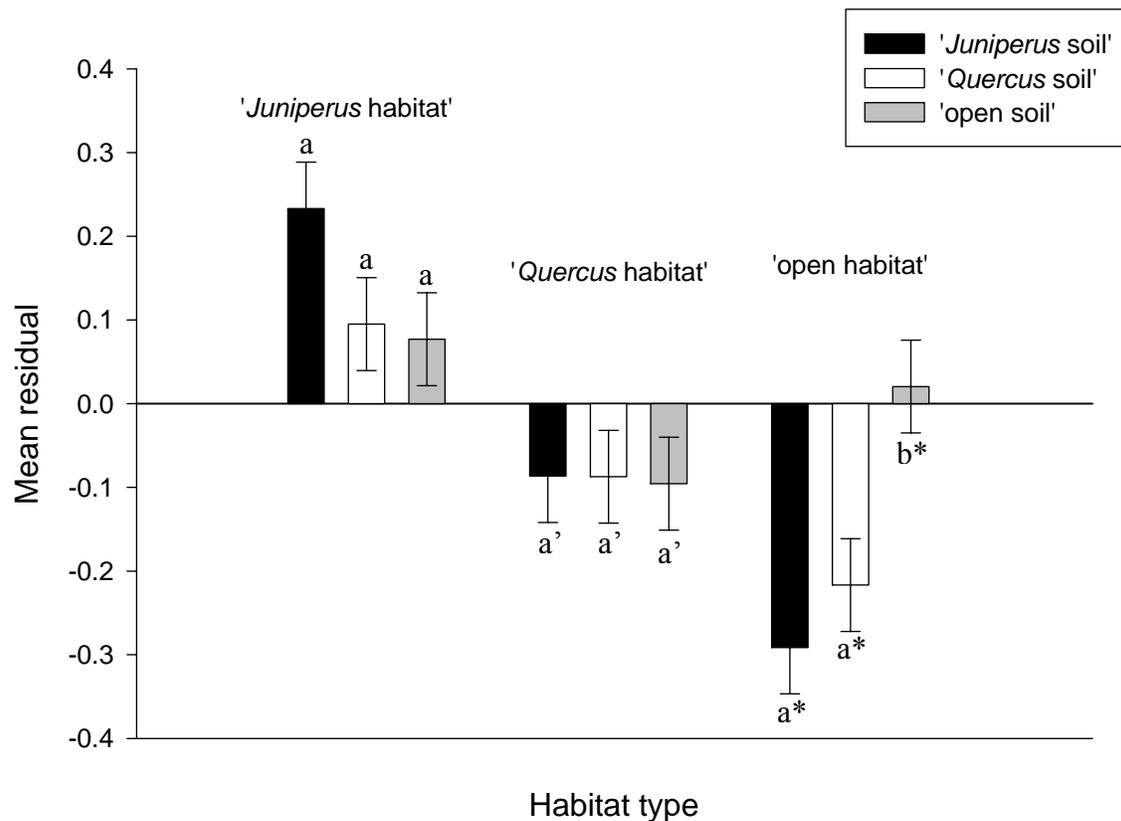


Figure 4.13. The effect of habitat type and soil type on the residual between the mean observed survival and the predicted survival from the mean germination date. Bars sharing letters within a habitat type are not significantly different, based upon Fisher's least significant differences (LSD) with an α -level corrected for multiple comparisons. Note that comparisons were made only among soil types within a single habitat type. Error bars are one standard error of the mean in each direction. The mean square error used in the denominator of the F-test was also used as the error term in computing each standard error. All calculations done with SAS, GLM procedure, LSMEANS option (SAS 1990).

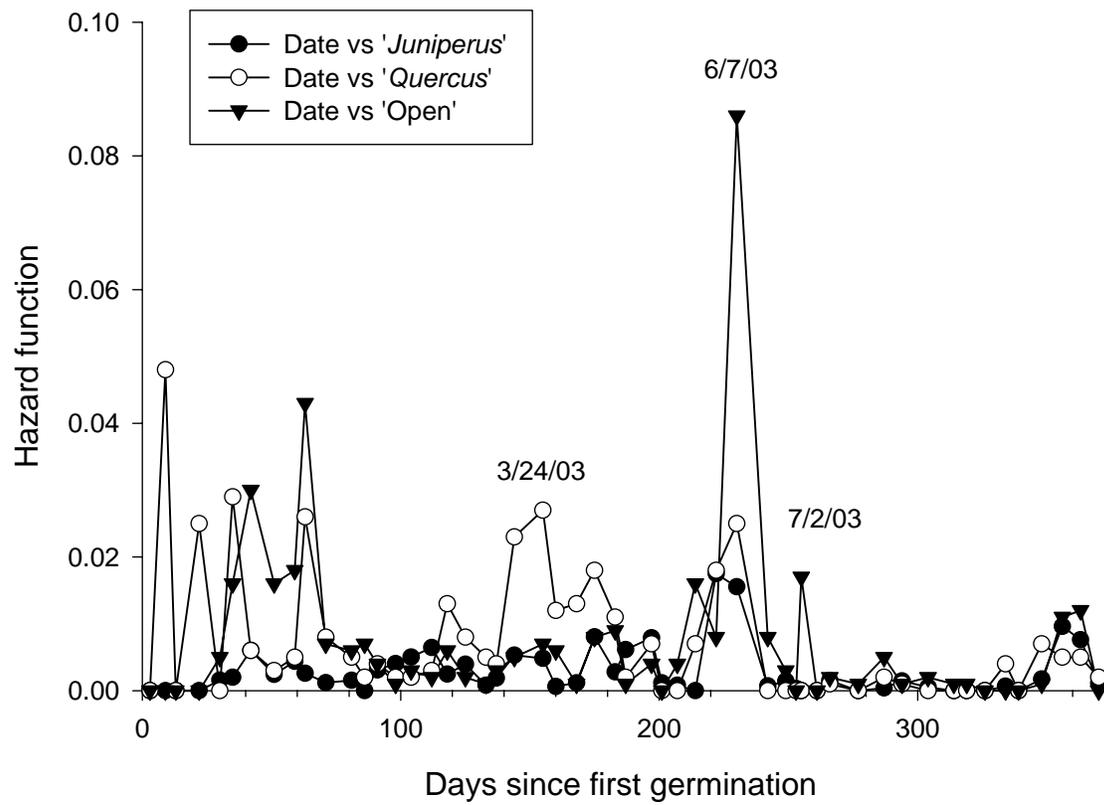


Figure 4.14. Hazard function of *J. ashei* individuals by habitat type

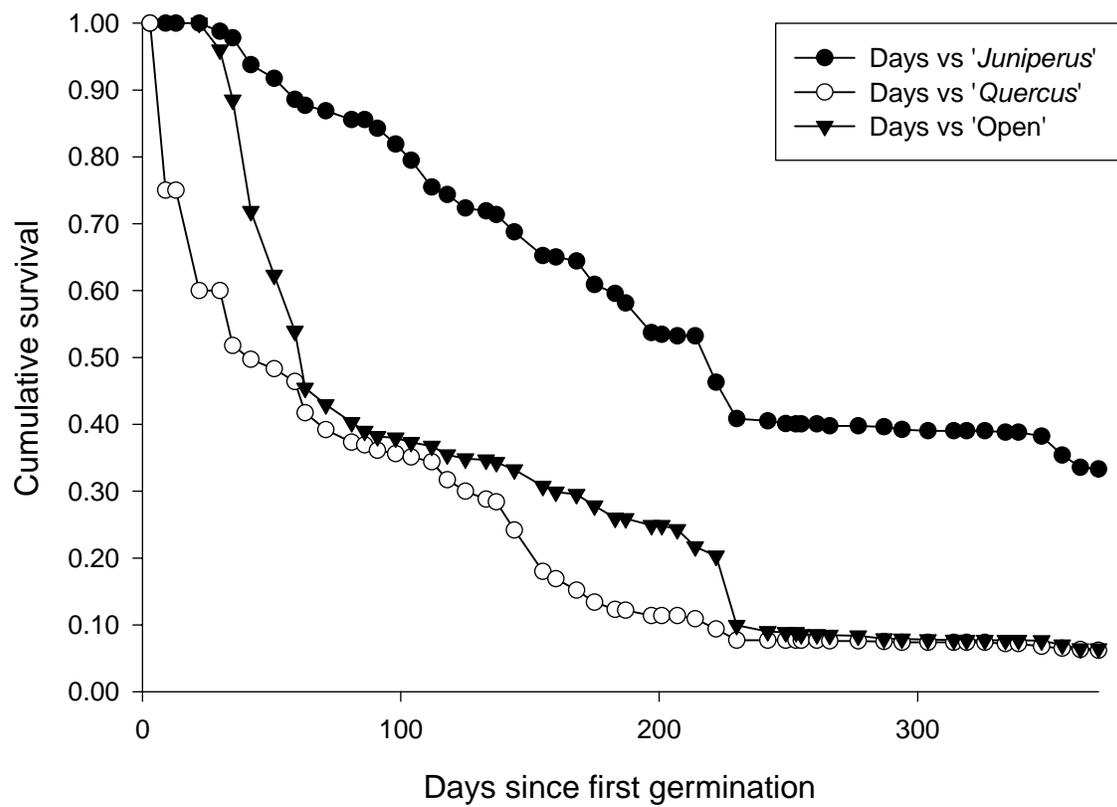


Figure 4.15. Cumulative survival of *J. ashei* individuals by habitat type

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Vita

Margaret Elizabeth Batchelor was born in Lafayette, Indiana on July 14, 1974, the daughter of Elizabeth Alice Solberg and James Joseph Solberg. After graduating in 1992 from William Henry Harrison High School in West Lafayette, Indiana, she attended Princeton University in Princeton, New Jersey. She received a Bachelor of Arts degree in Ecology and Evolutionary Biology from Princeton University in 1996. In September of 1996 she entered the graduate school of the University of Texas at Austin. She received a Masters of Science in Statistics from the University of Texas at Austin in December of 2002.

Permanent address: 2136 Sage Creek Loop, Austin, Texas, 78704

This dissertation was typed by the author.