

LIVE OAK (*QUERCUS VIRGINIANA* VAR. *FUSIFORMIS*) –
ASHE JUNIPER (*JUNIPERUS ASHEI*) INTERACTIONS
IN A CENTRAL TEXAS SAVANNA

THESIS

Presented to the Graduate Council of
Southwest Texas State University
in Partial Fulfillment of
the Requirements

For the Degree of

Master of SCIENCE

By

Patricia Ann Ramirez, B.S.

San Marcos, Texas
May 2002

ACKNOWLEDGMENTS

Many thanks go to my advisor, Dr. Paul Barnes, for his guidance and support throughout the duration of this research project. He shared his ideas and suggestions, yet also provided ample room for my own independence. I would also like to thank my committee members, Dr. David Lemke and Dr. David Gris  , for their advice regarding the content and structure of this thesis, and for the encouragement they shared before my defense.

The field work was facilitated by help from many individuals, especially Luz Morris, who spent countless hot, sunny afternoons and dark, early morning “predawns” assisting me with data collection during the first summer of sampling. Bryan Davis, former ranch manager at Freeman Ranch, provided invaluable assistance during the woody plant removal phase of the project and made sure I always felt welcome at the ranch. Thanks are also extended to other members of the lab, including Kristy Barker, Mike Eason, Kirk Jessup, Jennifer Mittelhauser, and Steve Reagan, for their help with data collection and general support, encouragement, and friendship. I would also like to thank my parents for their unconditional love and encouragement throughout my life.

Most importantly, I want to thank Marty Christman for his patience, love, and support prior to and throughout the duration of my graduate education. I cannot imagine this life journey without his friendship. He was especially handy at making my power breakfasts at 3 am before I departed for predawn measurements. Our dog Ashis was also a loyal companion for predawn field work, giving me confidence to run around the woods by myself in the middle of the night.

This research project was funded by a grant from the National Institutes of Health Bridges Program.

TABLE OF CONTENTS

LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
ABSTRACT	xi
INTRODUCTION	1
MATERIALS AND METHODS	10
Study Site.....	10
Understory Removal Experiment.....	15
Pre-removal Measurements.....	15
Physiological Measurements.....	19
Water Potential	19
Stomatal Conductance.....	23
Gas Exchange.....	25
Chlorophyll Content.....	26
Growth and Production Measurements	27
Shoot Elongation	27
Stem and Foliar Biomass	28
Leaf Litter Production	28
Facilitation Experiment	29

Statistical Analyses	30
RESULTS	33
Understory Removal Experiment.....	33
Pre-removal Characterization and Physiology.....	33
Physiological Responses to Understory Removal.....	38
Plant Water Potential.....	38
Stomatal Conductance.....	40
Leaf Gas Exchange.....	44
Chlorophyll Content.....	47
Growth and Production Responses to Understory Removal	47
Elongation and Biomass of Marked Shoots	47
Length and Biomass of Unmarked Shoots	50
Leaf Litter Production	52
Facilitation Experiment	55
DISCUSSION	58
Understory Effects on Live Oak.....	58
Overstory Effects on Ashe Juniper	63
Conclusions.....	65
APPENDIX A.....	68
LITERATURE CITED	69

LIST OF TABLES

Table 1.	Relative abundance of woody shrubs found in the understories of control and removal live oak – shrub clusters in pasture 4 of SWT Freeman Ranch, prior to understory removal. Data show means ($n_{\text{total}} = 20$, otherwise $n = 10$).....	17
----------	---	----

LIST OF FIGURES

Figure 1.	Location of the Edwards Plateau and the Southwest Texas State University Freeman Ranch in Texas.....	11
Figure 2.	Color infrared aerial photo of SWT Freeman Ranch showing pastures and the general location of the study site.....	12
Figure 3.	Representative live oak-shrub cluster showing the overstory live oak and the associated woody understory dominated by Ashe juniper.....	14
Figure 4.	Aerial photo of study site showing control (C) and removal (R) live oak-shrub clusters.	16
Figure 5.	Woody understory removal using “Tree Terminator.”	20
Figure 6.	Woody understory removal using hand tools.....	21
Figure 7.	Measuring plant water potential using a Scholander pressure chamber.	22
Figure 8.	Measuring stomatal conductance using a Licor 1600 Steady State Porometer.....	24
Figure 9.	Mean (+ SE; n = 10) leaf area index (LAI) for control (intact understory) and understory removal treatments prior to understory removal at Freeman Ranch, Hays County, Texas (May 2000). Data are from measurements made with a LiCOR LAI 2000 canopy analyzer, where the LAI of the understory was derived as the difference between total and overstory LAI.....	34
Figure 10.	Daily time-course of shoot water potential in control (—●—) and removal (—○—) live oaks, prior to understory removal (May 23, 2000), at Freeman Ranch, Hays County, Texas. Data are means \pm 1 SE, $n_{\text{control}} = 10$, $n_{\text{removal}} = 9$. Error bars within the size of the symbol are not shown.	35
Figure 11.	Net photosynthesis of control (—●—) and removal (—○—) live oaks, prior to understory removal (May 23, 2000) at Freeman Ranch,	

	Hays County, Texas. Data are from measurements made with a PP Systems CIRAS-1 portable photosynthesis system. Data are means ± 1 SE, n = 10 (at 9am $n_{\text{control}} = 9$, $n_{\text{removal}} = 7$).....	37
Figure 12.	Predawn (a) and midday (b) shoot water potentials of live oaks with (control; \bullet) and without (removal; \circ) intact overstory, over an annual growth cycle, and total weekly precipitation (c), at Freeman Ranch, Hays County, Texas. Water potential data are measurements made with a Scholander Pressure Chamber. Water potential data are means \pm SE, n = 10. ANOVA results are for post-removal data only. Error bars within the size of the symbol are not shown.....	39
Figure 13.	Mean morning (a) and afternoon (b) leaf stomatal conductance of live oaks with (control; \bullet) and without (removal; \circ) intact understory, over an annual growth cycle, at Freeman Ranch, Hays County, Texas. Data are means (\pm SE, n = 10) and are from measurements made with a Licor 1600 Steady State Porometer for lower (abaxial) leaf surface only.	41
Figure 14.	Shoot water potential (a) and leaf (lower surface only) stomatal conductance (b) of live oaks with (control; \bullet) and without (removal; \circ) intact understory, on May 15, 2001 at Freeman Ranch, Hays County, Texas. Water potential data are measurements made with a Scholander Pressure Chamber; stomatal conductance data are measurements made using a Licor 1600 Steady State Porometer. Data are means \pm SE, n = 10.	43
Figure 15.	Light-saturated net photosynthesis rates (midday) of live oaks with (control) and without (removal) intact understory at Freeman Ranch, Hays County, Texas. Data are from measurements made with a PP Systems CIRAS-1 portable photosynthesis system. Data are means \pm SE, n = 10.....	45
Figure 16.	Intrinsic water use efficiency (net photosynthesis/stomatal conductance) of live oaks with (control) and without (removal) intact understory at Freeman Ranch, Hays County, Texas. Data are from measurements made with a PP Systems CIRAS-1 portable photosynthesis system. Data are means \pm SE, n = 10.	46

Figure 17.	Relative chlorophyll content of control and removal live oaks at Freeman Ranch, Hays County, Texas. Measurements were made using a Minolta SPAD-502 Chlorophyll Meter. Data are means + SE, n = 10.....	48
Figure 18.	Mean (+ SE; n = 10; 5 shoots/replicate) shoot length (a) and growth increment (b) of live oaks with (control; ■, —●—) and without (removal; □, —○—) intact understory during the year 2000, at Freeman Ranch, Hays County, Texas. Growth increment is the shoot elongation between dates.....	49
Figure 19.	Mean (+ SE; n = 10, n _{control-2000} = 9; 4 shoots/replicate) foliar, stem, and total shoot biomass of live oaks with (control) and without (removal) intact understory at Freeman Ranch, Hays County, Texas. 2000 and 2001 shoots were harvested in February and September 2001, respectively.	51
Figure 20.	Mean (± SE; n = 10; 3 trays/replicate) litter mass collected during 2001 from live oaks with (control; —●—) and without (removal; —○—) intact understory at Freeman Ranch, Hays County, Texas.	53
Figure 21.	Mean (+ SE; n = 10; 3 trays/replicate) litter mass collected from live oaks with (control) and without (removal) intact understory during leaf abscission period (February - April 2001) at Freeman Ranch, Hays County, Texas.....	54
Figure 22.	Predawn (a) and midday (b) shoot water potentials of Ashe junipers associated with live oaks (—●—) and those not associated with any other trees (—○—), at Freeman Ranch, Hays County, Texas. Data are from measurements made with a Scholander Pressure Chamber. Data are means ± SE, n = 6. Error bars within the size of the symbol are not shown.....	56

ABSTRACT

LIVE OAK (*QUERCUS VIRGINIANA* VAR. *FUSIFORMIS*) –
ASHE JUNIPER (*JUNIPERUS ASHEI*) INTERACTIONS
IN A CENTRAL TEXAS SAVANNA

by

PATRICIA ANN RAMIREZ, B.S.

Southwest Texas State University

May 2002

SUPERVISING PROFESSOR: PAUL BARNES

Woody plants have increased in abundance and distribution in the grasslands and savannas of North America since the 1800's. This encroachment has been attributed to land use practices such heavy grazing by domestic livestock and fire suppression, climate change, enrichment of atmospheric CO₂, and the introduction of exotic species. On the Edwards Plateau of central Texas, Ashe juniper (*Juniperus ashei*) has increased in abundance since European

settlement in the mid-1800's and is a predominant member of the woody assemblages that often occur beneath live oak (*Quercus virginiana* var. *fusiformis*) trees, which possibly function as nurse plants.

To evaluate the effect of Ashe junipers and other shrubs on the overstory live oak, an understory removal experiment was conducted on live oak-shrub clusters in a central Texas savanna parkland. Predawn water potentials of oaks ranged from -0.04 to -1.01 MPa over a year, but did not differ ($p = 0.9$) between controls (intact understory) and understory removal treatments ($n = 10$). By comparison, midday water potentials, which ranged from -1.02 to -2.82 MPa, averaged 0.12 MPa lower ($p = 0.05$) for live oaks without an understory relative to controls. Mean stomatal conductances varied from 58 to 414 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and were significantly greater during both morning ($p = 0.02$) and afternoon ($p = 0.03$) periods in live oaks with understory removed, as compared to control live oaks; however, treatment differences were generally less than 22%. Over 6 sampling dates, net photosynthesis ranged from 9.9 to 23.9 $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($n = 10$) and was significantly greater ($p = 0.04$) in removal oaks as compared to control oaks. No significant treatment differences were found for intrinsic water use efficiency or relative chlorophyll content ($p = 0.68$; $p = 0.10$, respectively). In addition, there were no significant differences between treatment groups in stem length ($p = 0.27$), total shoot biomass ($p = 0.66$), or leaf litter production ($p = 0.93$). Thus,

while the removal of the Ashe juniper-dominated understory had a positive effect on live oak gas exchange, the effects were small, were not closely coupled to changes in plant water potential, and did not translate into increased growth or production. These findings imply that the intensity of understory competition on the overstory live oaks is rather weak, at least at this site, and may, therefore, be insufficient to competitively exclude the live oak nurse tree that initially facilitated these understory shrubs.

Studies were also conducted to test for continued overstory facilitation of mature Ashe juniper shrubs. Predawn and midday shoot water potentials of Ashe junipers exhibited a wide range throughout the year (between -6.69 and -0.38 MPa), especially when compared to the range measured in the live oaks. During both the predawn and midday sampling periods, there were no significant differences ($p = 0.66$; $p = 0.73$, respectively) between water potential measurements of Ashe junipers under live oak canopies and those not associated with any trees. These data suggest that, at this site, live oaks were not facilitating mature Ashe juniper shrubs.

INTRODUCTION

Since the 1800's woody plant abundance has increased in the grasslands and savannas of North America (Archer et al. 2000; McPherson 1997; van Auken 2000). Many of the invasive woody plants, such as *Prosopis glandulosa* (Archer et al. 1988; Grover and Musick 1990) and *Larrea tridentata* (Grover and Musick 1990), are actually native to the areas they have been encroaching. The causes of the encroachment of these and other woody species, which are typically unpalatable shrubs and trees, have been debated. In general, changes in land use practices, such as heavy grazing by domestic livestock and fire suppression, are thought to be the primary factors that have enhanced woody plant invasion. However, other factors, such as climate change, enrichment of atmospheric CO₂, and the introduction of exotic species may also contribute to this phenomenon (Archer et al. 2000; van Auken 2000).

The process of woody plant encroachment often involves certain woody species aiding or facilitating the ingress of other woody species. For example, following an increase in *Juniperus osteosperma* abundance in black sagebrush (*Artemisia nova*) communities in Nevada, *Pinus monophylla* also experienced an

increase in abundance, though somewhat delayed (Blackburn and Tueller 1970). Similarly, increase in woody plant cover in southern Texas grasslands and savannas appears to involve an initial colonization of herbaceous zones by *Prosopis glandulosa*, which then serves as a nucleus for subsequent establishment of other woody species in its understory. As a result, discrete tree-shrub clusters are produced that may then expand and coalesce to form closed-canopy woodlands (Archer et al. 1988). A similar phenomenon exists on the High Plains of western Texas where *P. glandulosa* facilitates the establishment of *Juniperus pinchotii* (McPherson et al. 1988).

A multitude of studies have documented spatial patterns and/or conducted manipulation experiments that suggest that facilitation is important in influencing plant community structure and diversity (Callaway 1995). There are several direct and indirect mechanisms by which a plant can facilitate the establishment and persistence of another plant. Direct mechanisms of facilitation are the result of resource modification and include improved light conditions, reduced soil and air temperatures, increased soil moisture, enhanced soil nutrient availability, and soil oxygenation. Indirect mechanisms of facilitation include substrate modification, protection from herbivores, increased pollination, enhanced concentration of propagules, and root grafts and mycorrhizal associations (reviewed in Callaway 1995). A plant that provides a seedling

protection from a harsh environment, thus facilitating its establishment and enhancing its chance of survival, is called a nurse plant (Barbour et al. 1999).

There is also a body of evidence to indicate that competition can be important in determining community structure (Fowler 1986). As with facilitation, there are different mechanisms of competition, both direct and indirect, including competition for resources such as water, minerals, and light, and herbivory and allelopathy, that may be involved (Fowler 1986; Scholes and Archer 1997). In many instances, the existence of competition within or between species in communities has been inferred from the analyses of spatial patterns and the size distributions of plants. These studies often assume that competition will eventually convert clumped distributions of plants into regular distributions (Fowler 1986; Scholes and Archer 1997). However, it has been argued that the spatial heterogeneity of the environment and restricted seed dispersal can override the tendency for competition to generate regular distributions of plants (Fowler 1986). Thus, pattern analysis alone may be insufficient evidence for the existence of competition. When possible, manipulative experiments involving the addition or removal of neighbors remain a preferred approach to documenting competition among plants.

For many nurse plant interactions, the overall effect of one individual plant upon another reflects a combined net effect of independent positive

(facilitative) and negative (competitive) interactions (Aguilar et al. 1992; Holzapfel and Mahall 1999). For example, although *Hilaria rigida* facilitates the establishment of *Agave deserti* in warm deserts by decreasing soil temperature and increasing soil nitrogen, it also competes with, and therefore limits seedling growth, of the agave by decreasing light levels and reducing water availability (Franco and Nobel 1988). This balance between net facilitative and net competitive effects can change with the life stages of the plants involved (Barnes and Archer 1996; Barnes and Archer 1999; Flores-Martinez et al. 1994; McAuliffe 1984; Valiente-Banuet et al. 1991; Yeaton 1978) and may also vary with the harshness of the physical environment (Callaway 1995). For example, a number of studies have used pattern analysis to suggest that facilitation by nurse plants is often of greatest importance during the seedling establishment phase but then competition becomes more prevalent as the “nursees” increase in age and size (Flores-Martinez et al. 1994; McAuliffe 1984; Valiente-Banuet et al. 1991; Yeaton 1978). In some cases it is thought that the nursees may, in time, competitively exclude the initial founding nurse plant (Barnes and Archer 1999; Flores-Martinez et al. 1994; McAuliffe 1984; Valiente-Banuet et al. 1991; Yeaton 1978). In the tree-shrub clusters in southern Texas savannas, results from removal experiments indicate a strong competitive effect of mature understory shrubs on the overstory *Prosopis glandulosa*, but minimal positive or negative effects of the

overstory on established shrubs (Barnes and Archer 1999). Thus, in this system facilitation may be most important early in cluster development and, over time, overstory-understory competitive interactions become strongly asymmetrical. To what extent this pattern holds for other tree-shrub clusters in other savanna systems has been little explored.

Prior to European settlement in the mid-1800's, much of the landscape of the Edwards Plateau of central Texas probably consisted of relatively open savannas and grasslands (Buechner 1944; Foster 1917; Nadkarni et al. 1985). In the past 150 years, however, there has been a rapid increase in abundance of woody plants, especially Ashe juniper (*Juniperus ashei*) (Fonteyn et al. 1988), a fire-sensitive shrub with low forage value (Smeins and Fuhlendorf 1997). For example, between 1949 and 1983 on an unburned site on the western Edwards Plateau, total woody cover increased from 14 to 30% and from 8 to 35% on grazed and ungrazed land, respectively. During this time period, however, total canopy cover of plateau live oak (*Quercus virginiana* var. *fusiformis*) declined (from 26 - 49% to 18%), while that of Ashe juniper increased from 3 - 7% in 1949 to 32 - 40% in 1983 (Smeins and Merrill 1988).

As is the case for other examples of woody plant increase, the increase in abundance of Ashe juniper and other unpalatable woody species on the Edwards Plateau has been attributed to several factors, including fire suppression and

increased grazing by domestic livestock (Bray 1904; Buechner 1944; Foster 1917). Historically, it is thought that Ashe junipers were restricted to ravines, rocky ridges, and slopes where they were protected from frequent fire (Bray 1904; Buechner 1944; Foster 1917; van Auken 1988). Today, however, this shrub is ubiquitous and can occur on any type of terrain, from creek beds to upland areas. In a survey conducted during the late 1970's on the southern Edwards Plateau, van Auken et al. (1979) found Ashe juniper to be the most abundant woody species.

In many contemporary savanna settings on the Edwards Plateau, Ashe juniper appears to occur preferentially beneath plateau live oak trees, and thus, it has been hypothesized that live oaks serve as nurse plants for Ashe junipers and facilitate their establishment (Fowler 1988). At the Kerr Wildlife Management Area, Kerr County, Texas, located on the southern edge of the Edwards Plateau, pattern analysis (Fonteyn et al. 1988) confirmed that Ashe juniper was indeed more abundant beneath trees than in the open grasslands. Similarly, at a site on the eastern Edwards Plateau, Anderson et al. (2001) found significantly more Ashe juniper seedlings beneath live oak trees than in the open grassland. At present, the mechanisms of live oak facilitation of Ashe juniper are not well understood, but may include reduced soil and air temperature, reduced soil

desiccation, increased nutrient availability (leaf litter accumulation), or perch sites for birds that disperse seeds (Fowler 1988).

Following the establishment of Ashe junipers beneath live oak canopies, there are several possible scenarios regarding the interactions between the overstory live oak and the mature understory Ashe juniper. For example, it is conceivable that the live oak overstory could continue to facilitate the understory Ashe juniper, at least under certain situations (Anderson et al. 2001). Indeed, Phillips (1999) found that the cover and density of established Ashe junipers were significantly greater on the northern than southern sides of live oak clusters and she interpreted this as evidence for a continued facilitative effect of the live oaks on understory microclimate. As the understory Ashe junipers grow in size and resource demands, it is possible that they may begin to strongly compete with the overstory live oaks, in a similar fashion to the situation between understory shrubs and *Prosopis glandulosa* in southern Texas (Barnes and Archer 1999) and *Juniperus virginiana* and post oak (*Quercus stellata*) in eastern Texas (Rykiel and Cook 1986). It is also conceivable that the understory shrubs may have minimal or even positive effects on the overstory tree (e.g., Holzapfel and Mahall 1999). At present, few experimental tests of these scenarios have been conducted.

In more general terms, the ecological consequence of the increase in Ashe juniper abundance on Edwards Plateau ecosystems remains a subject of much debate. Many ranchers consider Ashe junipers to be the bane of their rangelands because they decrease herbaceous production, intercept rainfall, and may decrease deep percolation of water (Nelle 1997; Thurow et al. 1997). However, it has also been suggested that removal of Ashe juniper does not necessarily improve rangeland hydrology; if Ashe juniper removal is not combined with a sustainable grazing regime, runoff could increase and possibly enhance soil erosion (Nelle 1997). Adding to the debate, Ashe junipers are an important source of food for birds such as cedar waxwings and robins, they provide shelter and escape for animals, and their bark serves as nesting material for Golden-cheeked Warblers, an endangered songbird (Rollins and Armstrong 1997). Therefore, high rates of Ashe juniper removal could negatively affect many animal species.

In this study I explore the nature of Ashe juniper-live oak interactions in discrete tree-shrub clusters in a central Texas savanna. Specifically, I examine the effect of an Ashe juniper-dominated woody understory on its overstory plateau live oak by conducting a removal experiment to test the following hypothesis: In established live oak tree-shrub clusters, understory Ashe junipers have an overall negative, competitive effect on the arboreal live oaks. Additionally, I investigate

the possibility of continued facilitation of the overstory live oak on the established understory Ashe juniper by testing the hypothesis that the performance of mature Ashe junipers within these tree-shrub clusters is greater than that of isolated Ashe junipers not associated with live oak canopies.

MATERIALS AND METHODS

Study Site

Studies were conducted at the Southwest Texas State University (SWT) Freeman Ranch, which is contained within the Balcones Canyonlands subregion of the eastern Edwards Plateau and is located in southeastern Hays County, Texas (29° 56' N; 98° W) (Barnes et al. 2000) (Fig. 1). Freeman Ranch receives an average yearly rainfall of approximately 86 cm. Average minimum and maximum daily temperatures are 21.8 and 35 °C in July and 2.2 and 16 °C in January, respectively; mean annual temperature is 19.4 °C (Dixon 2000). Freeman Ranch, which is divided into 18 pastures, has likely been operated as a cattle and sheep ranch since the early to mid 1800's (Barnes et al. 2000) and is currently grazed by cattle, sheep, and goats. The study site was located in pasture 4 (Fig. 2).

The soils of Freeman Ranch overlie Edwards limestone, a sedimentary deposit of Cretaceous age. Five soil types have been identified on the ranch, including the Rumble-Comfort association, the Comfort-Rock outcrop complex,

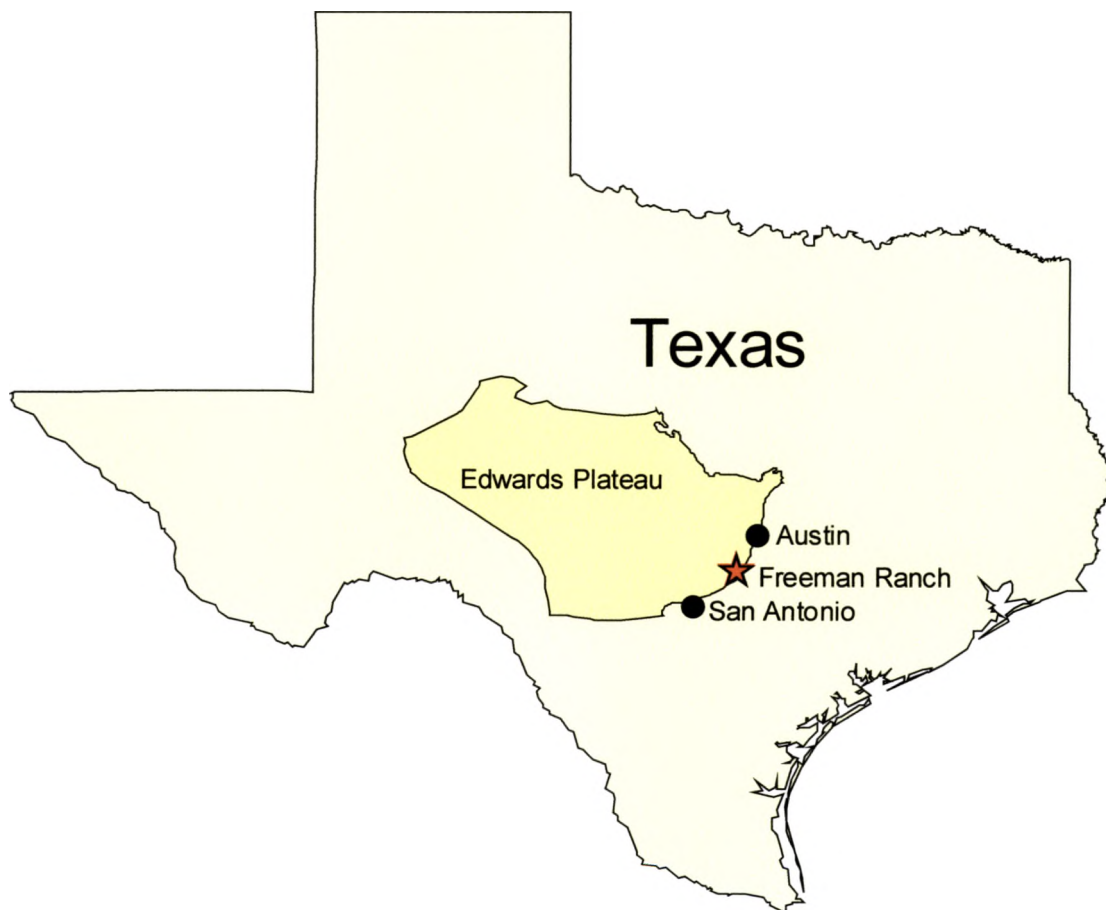


Figure 1. Location of the Edwards Plateau and the Southwest Texas State University Freeman Ranch in Texas.

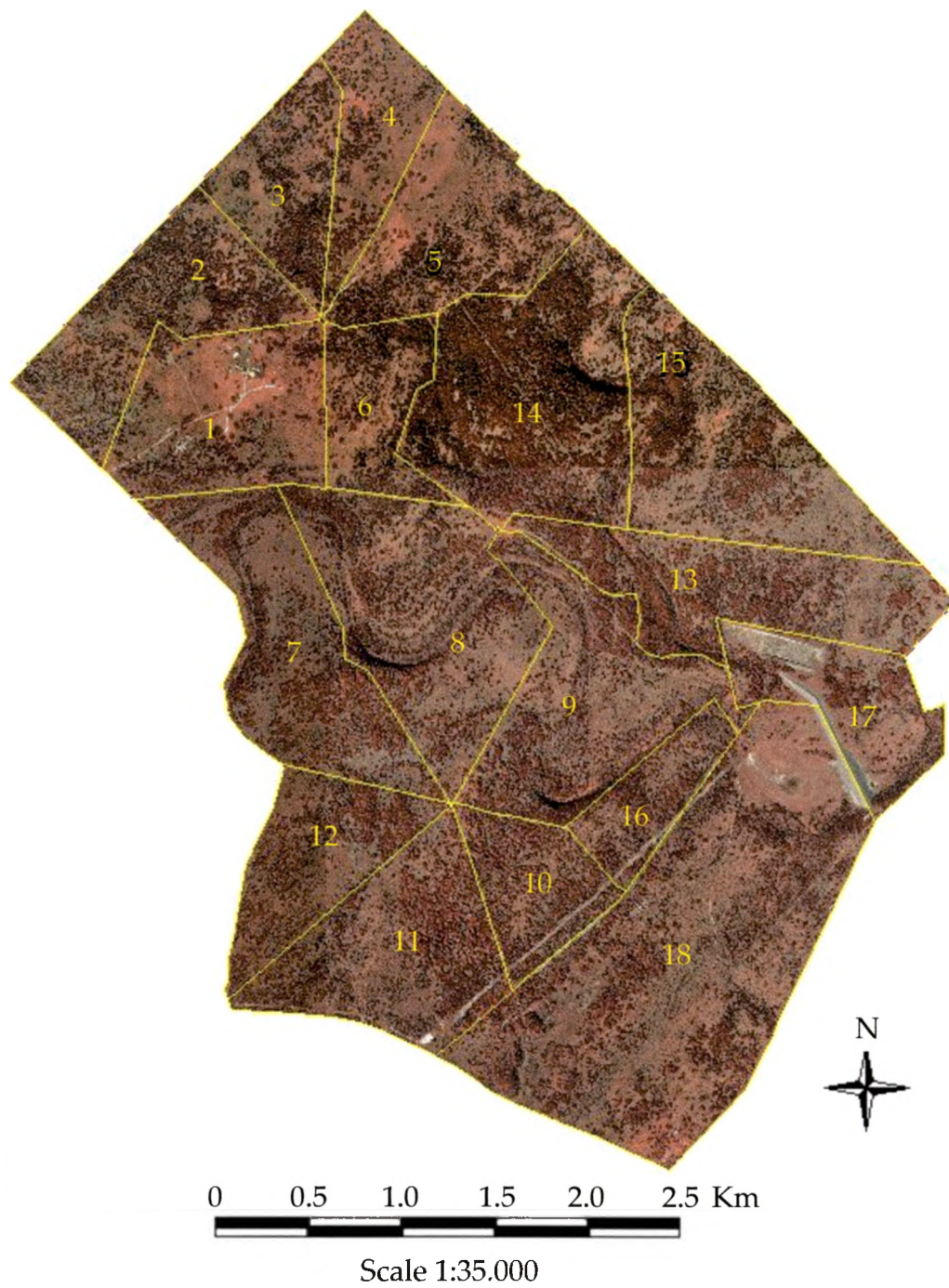


Figure 2. Color infrared aerial photo of SWT Freeman Ranch showing pastures and the general location of the study.

Tarpley clays, Orif soils, and the Medlin-Eckrant association. In general, these soil types are shallow and clay-rich (Barnes et al. 2000).

The landscape of Freeman Ranch is typical of the eastern Edwards Plateau, containing upland savanna parklands, lowland evergreen woodlands, and north-facing deciduous forests. In the upland savannas, woody plant clusters are interspersed among perennial grassland (Barnes et al. 2000) (Fig. 3). Each woody plant cluster, or *motte*, is typically composed of a central plateau live oak (*Quercus virginiana* P. Miller var. *fusiformis* (J.K. Small) C. Sargent; nomenclature follows Jones et al. 1997) surrounded by other woody shrubs; the dominant understory shrubs include Ashe juniper (*Juniperus ashei* J. Buccholz), hackberry (*Celtis laevigata* C. von Willdenow var. *reticulata* (J. Torrey) L. Benson), Texas persimmon (*Diospyros texana* G. Scheele), and elbowbush (*Forestiera pubescens* T. Nuttall var. *pubescens*) (Phillips 1999). The grassland component of the savanna is dominated by Texas wintergrass (*Nasella leucotricha* (K. von Trinius & F. Ruprecht) R. Pohl) and Texas grama (*Bouteloua rigidisetata* (E. von Stuedel) A. Hitchcock) (Barnes et al. 2000).

Plateau live oak (hereafter referred to as live oak) is a sub-evergreen tree or shrub that grows to 25 m (Flora of North America Editorial Committee 1993b) and loses its leaves during February and March. It is abundant on limestone



Figure 3. Representative live oak-shrub cluster showing the overstory live oak and the associated woody understory dominated by Ashe juniper.

hills of the Edwards Plateau, ranging west to the Pecos River and south to Mexico (Vines 1984). Ashe juniper is an evergreen shrub or tree that grows to 15 m. It occurs mostly on limestone hills from Missouri, Oklahoma, and Arkansas to northern Mexico (Flora of North America Editorial Committee 1993a).

Understory Removal Experiment

Pre-removal Measurements

Twenty discrete live oak–shrub clusters of similar size were selected for study during February and March 2000 in pasture 4 of Freeman Ranch (Fig. 4). During the study period cattle only intermittently grazed this pasture. The soils of this site are composed of the Rumble-Comfort soil type, and are reddish-brown, cherty clays loams (Barnes et al. 2000). Elevations of the study site range from 274 to 280 m above sea level.

Almost all (18 out of 20) live oak–shrub clusters selected for study had single-trunked live oaks. A total of 16 different woody species were found to occur beneath the live oak canopies (Table 1). However, the woody understory was heavily dominated by Ashe juniper, which constituted, on average, $59.9 \pm 3.7\%$ ($n = 20$) of the woody plants beneath the live oak canopies. There was no significant (Student's t -test, $p = 0.45$) difference in relative Ashe juniper

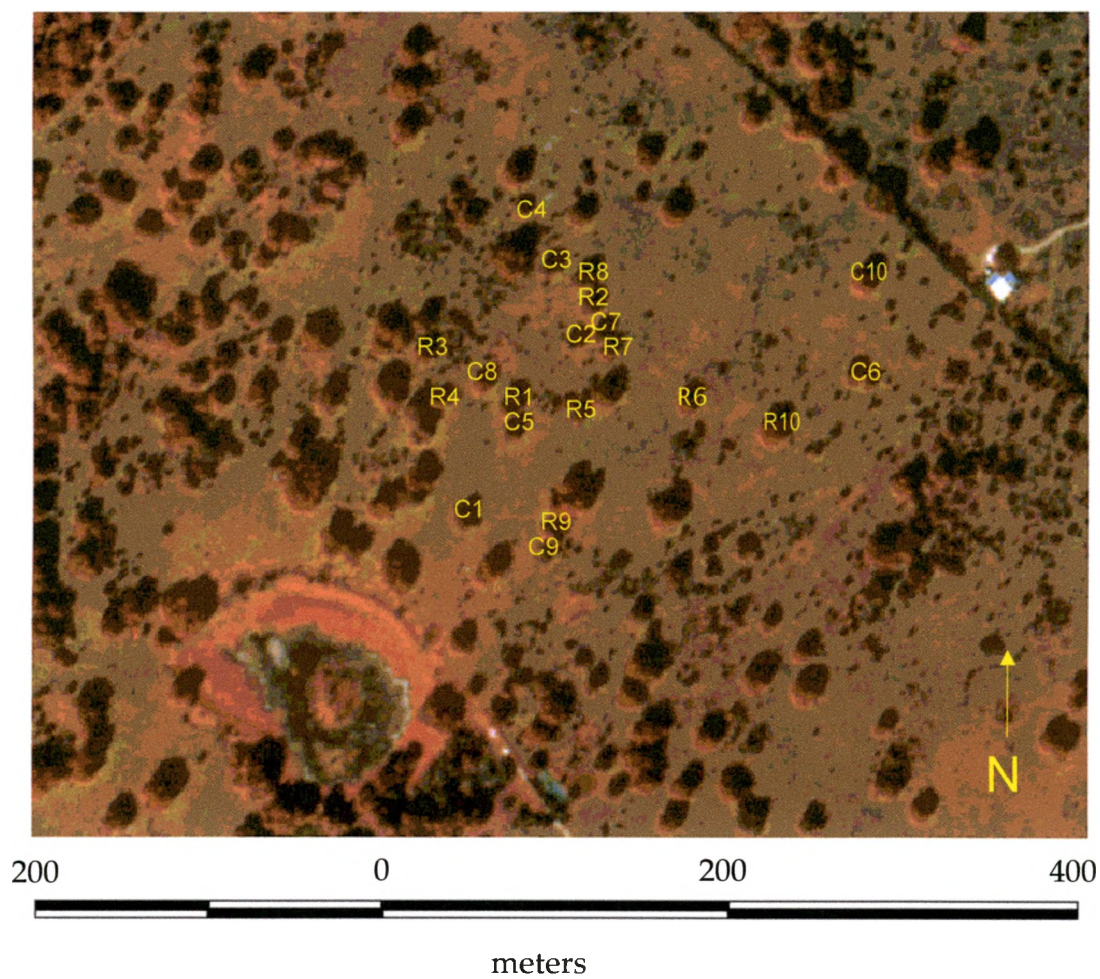


Figure 4. Aerial photo of study site showing control (C) and removal (R) live oak-shrub clusters.

Table 1. Relative abundance (percentage of total individuals) of woody shrubs found in the understories of control and removal live oak – shrub clusters in pasture 4 of SWT Freeman Ranch, prior to understory removal. Data show means ($n_{\text{total}} = 20$, otherwise $n = 10$).

Species	Relative abundance (%) of woody shrubs in clusters		
	Total	Control	Removal
<i>Acer negundo</i>	0.4	0.8	0.0
<i>Berberis trifoliolata</i>	2.5	2.7	2.3
<i>Celtis</i> spp.	5.4	4.0	6.9
<i>Croton fruticosus</i>	0.1	0.0	0.3
<i>Condalia hookeri</i>	0.5	0.0	0.9
<i>Diospyros texana</i>	8.1	6.6	9.5
<i>Forestiera pubescens</i>	10.6	10.5	10.7
<i>Ilex vomitoria</i>	1.9	1.6	2.2
<i>Juniperus ashei</i>	59.9	62.7	57.0
<i>Opuntia leptocaulis</i>	0.4	0.6	0.2
<i>Opuntia engelmannii</i>	0.8	0.9	0.7
<i>Prosopis glandulosa</i>	0.8	0.4	1.1
<i>Quercus virginiana</i> var. <i>fusiformis</i>	8.0	8.4	7.6
<i>Rhus aromatica</i>	0.3	0.5	0.0
<i>Ulmus crassifolia</i>	0.2	0.0	0.3
<i>Zanthoxylum hirsutum</i>	0.3	0.2	0.3

abundance between control ($62.7 \pm 5.7 \%$; $n = 10$) and treatment ($57.0 \pm 4.8 \%$; $n = 10$) clusters. Other dominant understory shrubs included *Forestiera pubescens*, *Quercus virginiana* var. *fusiformis*, and *Diospyros texana*, which is similar to the findings of Phillips (1999).

Non-destructive estimates of leaf area index (LAI) of each live oak overstory and its woody understory were made in May 2000 using a LI-COR LAI-2000 plant canopy analyzer. Measurements were taken during the early morning while the sunlight was still diffuse. Total LAI (overstory plus understory) was determined by placing the plant canopy analyzer at ground level at three arbitrary locations beneath the tree-shrub canopy. To determine the LAI of the live oak canopy, the plant canopy analyzer was inserted above the understory shrubs, yet beneath the oak canopy, in three separate locations for each cluster (not necessarily the same locations as the total LAI). Finally, the LAI of the woody understory was computed by subtracting the mean live oak overstory LAI from the mean cluster LAI for each tree-shrub cluster.

To compare the physiological status of the live oaks prior to understory removal, and to determine the time of day when the trees were most water stressed, the xylem water potential of each oak was measured at 5 times during the day (predawn, 9 am, 11:30 am, 2 pm, and 4 pm Central Standard Time (CST); see "Water Potential" below for detailed methods). Leaf gas exchange was

measured at 9 am, 1 pm, and 3 pm CST (see “Gas Exchange” below for detailed methods), and these values were used to calculate an average daily value for each tree.

In late May 2000, the woody understories of the 10 live oak-shrub clusters targeted as removal treatments were mechanically cleared using a Bobcat with a hydraulic blade attachment called the “Tree Terminator” (Fig. 5). This technique severed the woody plant stem at ground level and removed the plant from underneath the oaks. Any remaining woody plants were removed by hand using loppers and bow saws (Fig. 6). The 10 oak-shrub clusters targeted as controls were left intact and were not disturbed.

Physiological Measurements

Water Potential

Measurements of plant water potential were made on outer canopy shoots from the southern sides of trees. These shoots were fully exposed to the sun and were located 1 to 4 m above the ground. Stems were cut with pruning shears, usually about 8 to 18 cm from the stem tip, and were placed in Ziploc bags with moist paper towels to maintain humidity. The water potential was measured with a Scholander Pressure Chamber equipped with a 40 bar gauge (Fig. 7).



Figure 5. Woody understory removal using "Tree Terminator."



Figure 6. Woody understory removal using hand tools.



Figure 7. Measuring plant water potential using a Scholander pressure chamber.

During the first summer following imposition of the removal treatments, the water potential sampling schedule was generally twice per month and during the rest of the year it was once per month, weather permitting. Live oak water potential was measured at predawn and midday, which corresponds to time of daily maximum and minimum values. During the midday sampling period, which usually occurred between 1:30 and 4 pm CST, there were two rounds of data collection; each tree was sampled once during each round. These two afternoon measurements were used to calculate mean midday water potential for each tree, which was then used in the data analysis. Predawn and midday water potentials were analyzed separately.

Stomatal Conductance

Measurements of leaf stomatal conductance were made on sunlit, outer canopy leaves from the southern sides of trees (Fig. 8). Leaves were located 1 to 4 m above the ground. During the year 2000, both the upper and lower leaf surfaces of one leaf per tree were measured during each sampling period with a Licor 1600 Steady State Porometer. Total leaf conductance was then computed as the sum of the upper and lower conductances. Based on measurements during the 2000 growing season, it was determined that the ratio of upper leaf surface to



Figure 8. Measuring stomatal conductance using a Licor 1600 Steady State Porometer.

lower leaf surface stomatal conductance was approximately 0.03. Thus, the upper leaf surface contributed only a very small amount (3%) to the total leaf stomatal conductance. Therefore, during the 2001 sampling period, only the conductance of the lower leaf surface was measured.

The sampling schedule for live oak stomatal conductance was the same as water potential measurements – twice monthly during the first summer and monthly during the rest of the year. Live oak stomatal conductance was measured in the morning, usually between 8 and 10 am CST, and in the afternoon, usually between 1 and 4 pm CST, on sunny days. Morning and afternoon stomatal conductance measurements were analyzed separately.

In an attempt to better understand the relationship between water potential and stomatal conductance in this study, simultaneous measurements of these two physiological parameters were made throughout the day on May 15, 2001, at 9 am, 12 pm, and 3 pm CST.

Gas Exchange

Throughout the study period, the CO₂ and H₂O gas exchange of individual live oak leaves was measured periodically with an open-path gas exchange system (PP Systems CIRAS-1 portable photosynthesis system).

Measurements were taken on outer-canopy, sunlit leaves on clear days or on

partly cloudy days, in which case a light source was used (20 Watt quartz halogen lamp; photon flux density (400-700nm) =1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

Measurements were typically taken once daily and in the afternoon.

Intrinsic water use efficiency (WUE) was calculated from gas exchange data using the following formula:

$$\text{WUE} = A/g_s,$$

where A= net photosynthesis, and

g_s = leaf stomatal conductance.

Chlorophyll Content

A Minolta SPAD-502 Chlorophyll Meter was used several times (7 June 2000, 13 June 2000, 12 April 2001, and 27 September 2001) to measure chlorophyll content in the oak leaves. This instrument uses a non-destructive optical approach to estimate total chlorophyll. The chlorophyll meter was not calibrated against extracted chlorophyll, thus the readings here are intended only to compare the relative chlorophyll content of control versus removal treatments. For each live oak, three outer-canopy leaves were sampled and the mean was used to compare the relative chlorophyll content in control and removal live oak treatments.

Growth and Production Measurements

Shoot Elongation

Five terminal oak shoots exhibiting active growth were haphazardly chosen from the southern side of each experimental live oak in June 2000. Each shoot was tagged with a different colored zip tie for identification (red, yellow, green, white, or black). Stem length of each marked shoot was measured with a ruler, from the most recent bud-scale scar to the tip. Stems were measured three times during the year (June, July, and October 2000). In June 2001, one year after marking, the stems were harvested, separated into annual growth increments (2000 and 2001), oven-dried at 60° C for a minimum of 96 hours, and weighed. Shoot biomass used in the analysis included growth from 2000 and any side shoots originating from that part of the stem. The shoot growth from 2001 was excluded from analysis because many shoots did not elongate from the tip in 2001. Growth increments, or the amount of growth between sampling dates, were calculated as the difference between stem length at time(1) and time(2). The five stems from each tree were averaged before statistical analyses. If a stem was lost or broken, it was completely omitted from the data and the tree mean was calculated with fewer stems (10 stems out of 100 were either lost or broken).

Stem and Foliar Biomass

In early February 2001 (at the end of the 2000 growing season, but prior to annual leaf drop) and September 2001, 4 outer-canopy shoots from each tree (from a height of about 2 to 4 m above the ground) were randomly cut with a pole pruner for growth and biomass determination. In February 2001, one shoot was chosen from the north, south, east, and west sides of each tree; in September, all shoots were chosen from the south sides of the trees. Once in hand, the shoots were cut at the point of growth initiation the previous spring, as indicated by bud-scale scars. Stem lengths were measured with a ruler, from bud-scale scar to tip. Stems and foliage were oven-dried at 60° C for a minimum of 96 hours and weighed. For length and biomass, the mean of the four samples removed from each tree was used in statistical analyses.

Leaf Litter Production

Foliar biomass production of live oaks was estimated by collecting abscised leaves in litter traps positioned beneath each live oak tree. In early February 2001, prior to annual leaf abscission, 3 litter traps were placed beneath each live oak tree. Each litter trap consisted of a plastic tray (53 x 28 x 1 cm) with holes in the bottom to permit drainage of water. The trays were secured to the ground with metal stakes and were placed, when possible, mid-way between the

bole and the canopy edge, and in one of three approximate locations: northeast, south, and northwest of the bole. This arrangement was possible under the removal live oaks, however it was not always possible under the control live oaks. Due to the understory beneath the control live oaks, the main criterion in tray placement was that each tray was only beneath live oak canopy; therefore it was necessary to seek spots free from understory shrubs. Litter samples were collected in paper bags, oven-dried at 60° C for a minimum of 96 hours, and weighed. There were 5 sampling periods spanning 8 weeks, and sampling intervals ranged from 7 to 14 days. For statistical analysis, the total amount of litter captured per tree was calculated as the sum of its three litter traps over all days.

Facilitation Experiment

In addition to the understory removal experiment, which tested the effect of the woody understory on the live oak overstory, studies were also conducted to test for overstory facilitation of mature plants of Ashe juniper, the dominant woody understory species. Twelve Ashe juniper shrubs were chosen for these studies. For the control treatment, Ashe junipers chosen were out in the open grassland, approximately 10 to 30 m from live oak-Ashe juniper clusters, and were not associated with any other woody plant. Ashe junipers occurring

beneath live oak canopies served as the treatment plants and were chosen from within the control live oak-shrub clusters (i.e., intact understory) from the understory removal experiment.

To compare the physiological performance of Ashe juniper in the open (control) with those associated with live oaks (treatment), Ashe juniper water potential was measured using the same techniques for live oaks. Ashe juniper water potential was sampled on the same time schedule as live oaks, and when possible, water potential measurements of both species were taken on the same day. Each Ashe juniper shrub was measured once during the predawn period and twice during the midday sampling period. These two midday measurements were used to calculate mean midday water potential for each shrub, which was then used in the data analysis. Predawn and midday water potentials were analyzed separately.

Statistical Analyses

Prior to analyses, all data were checked for normality and appropriate transformations were applied. Variables that were log-transformed include shoot elongation, stem biomass (February and September 2001), and total shoot biomass (June 2001). Data that were square root-transformed include shoot lengths (February and September 2001), total shoot biomass (February and

September 2001), foliar biomass (February and September 2001), leaf litter production, LAI, and chlorophyll content. Growth increment data were inverse-transformed.

Data from the understory removal experiment were statistically analyzed as a completely randomized design with discrete tree-shrub clusters as the experimental unit ($n = 10$). Pre-removal data (water potential and gas exchange) were analyzed separately from data collected after experimental manipulation. Pre-removal water potential data were analyzed using a repeated measures analysis of variance (ANOVA), with time of day being the repeated measure. Pre-removal gas exchange (net photosynthesis) data were analyzed using a Student's *t*-test. For all physiological (i.e., water potential, stomatal conductance, net photosynthesis, intrinsic water use efficiency, and chlorophyll content) and shoot growth measurements, data were collected on the same plants over time. Thus, these data were analyzed as a repeated measures ANOVA with time (sampling date) being the repeated measure. For the simultaneous measurements of water potential and stomatal conductance collected on May 15, 2001, a double multivariate repeated measures ANOVA was performed on the data set. Leaf litter production was analyzed as a univariate analysis of covariance (ANCOVA), with LAI as the covariate.

Data from the facilitation experiment were analyzed differently due to the manner in which data were collected. Because control Ashe junipers (i.e., those not associated with a live oak) were not specifically numbered, individual trees could not be followed over the course of the year, thereby preventing the use of a repeated measures ANOVA to analyze the data. Therefore, the data from separate sampling dates were pooled over the entire year and were analyzed with a Student's *t*-test.

RESULTS

Understory Removal Experiment

Pre-removal Characterization and Physiology

The estimated leaf area index (LAI) of the total canopy (overstory plus understory) of the live oak-shrub clusters ranged from 3.0 to 5.5 m²/m² early in the growing season (Fig. 9). The overstory (live oak) LAIs ranged from 1.1 to 3.1 m²/m², while that of the understory ranged from 0.8 to 3.8 m²/m². The total and understory LAIs prior to manipulation were not significantly different (Student's *t*-test, *p* = 0.82, 0.15) between treatments. Mean overstory LAI for the control group was 1.6 ± 0.2 m²/m² (*n* = 10), which was slightly less (*p* = 0.06) than the treatment (understory removal) group, 2.3 ± 0.2 m²/m² (*n* = 10). The overstory LAI:understory LAI ratio was 1.14 for all live oak-shrub clusters combined; the ratio was 0.9 and 1.3 for control and removal treatments.

Measurements made throughout a warm, sunny day (Fig. 10) in May (predawn, 9 am, 11:30 am, 2 pm, and 4 pm CST) indicated a significant (ANOVA, *p* < 0.001) effect of time of day on live oak water potential. In general, mean

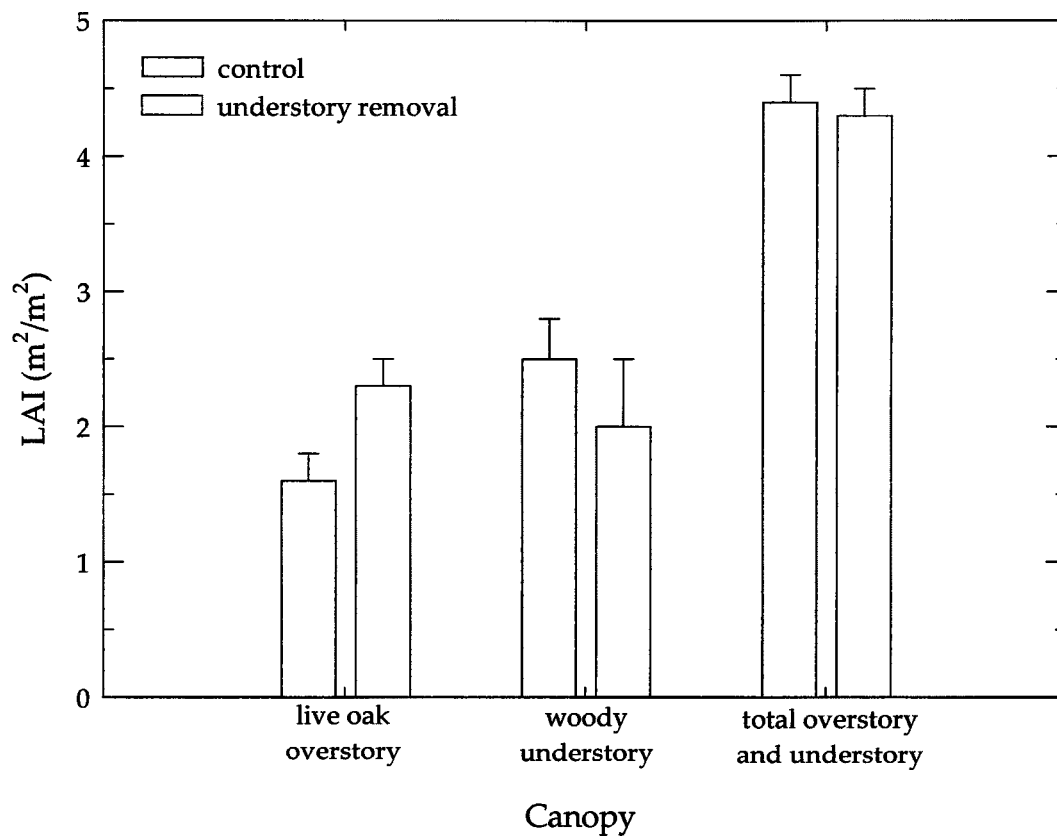


Figure 9. Mean (+ SE; $n = 10$) leaf area index (LAI) for control (intact understory) and understory removal treatments prior to understory removal at Freeman Ranch, Hays County, Texas (May 2000). Data are from measurements made with a LiCOR LAI 2000 canopy analyzer, where the LAI of the understory was derived as the difference between total and overstory LAI.

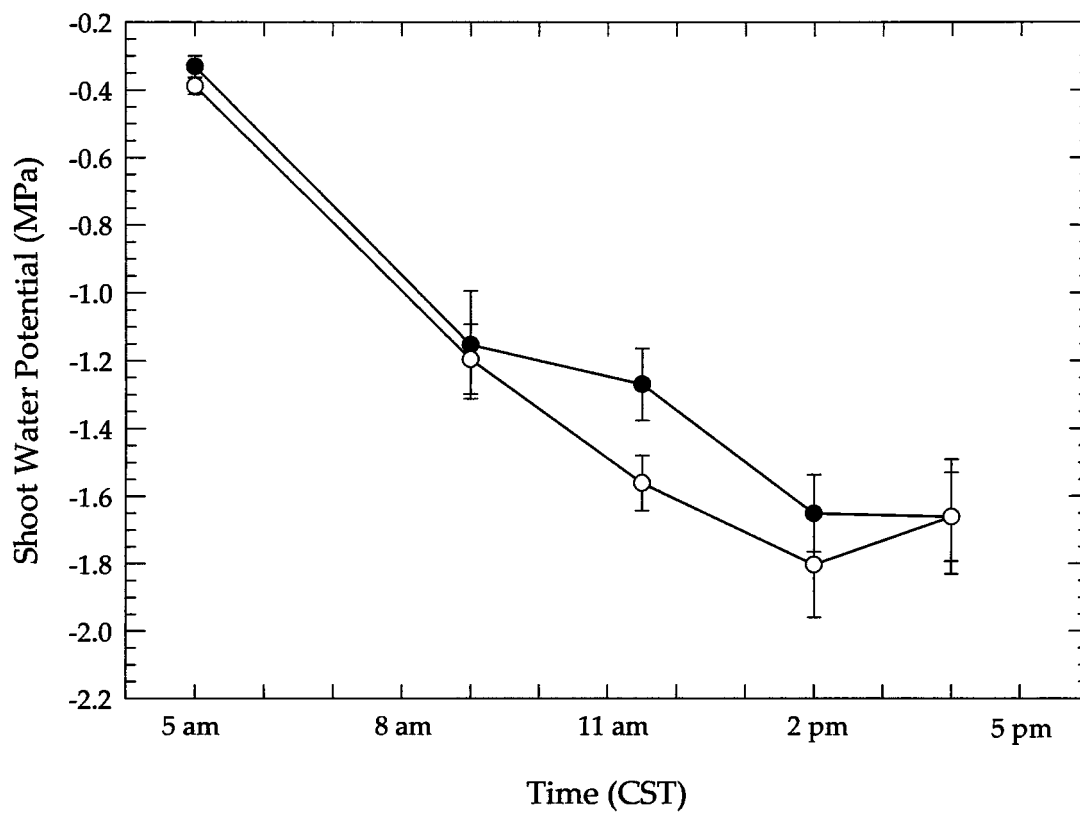


Figure 10. Daily time-course of shoot water potential in control (—●—) and removal (—○—) live oaks, prior to understory removal (May 23, 2000), at Freeman Ranch, Hays County, Texas. Data are means \pm 1 SE, $n_{\text{control}} = 10$, $n_{\text{removal}} = 9$. Error bars within the size of the symbol are not shown.

shoot water potential was highest at predawn, lowest at mid-afternoon (2 pm), and began to show signs of recovery by 4 pm (Fig. 10). However, a Student's *t*-test performed on these two afternoon sampling periods revealed no statistically significant ($p = 0.67$) differences between water potential data collected at 2 pm and 4 pm. The two afternoon (2 and 4 pm) water potential means were, however, significantly ($p = 0.02$) lower than the 11:30 am means. When averaged over the entire day, there was no significant difference (ANOVA, $p = 0.2$) in live oak water potential between the two treatments groups prior to manipulation, and there was also no significant ($p = 0.68$) time by treatment interaction.

Live oak net photosynthesis also varied throughout the day, and was highest midmorning (9 am), and lowest at 3 pm (Fig. 11). When averaged over the entire day, net photosynthesis rates were not significantly (Student's *t*-test, $p = 0.48$) different between treatment groups (16.5 ± 1.2 vs. 17.7 ± 1.0 $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for control and removal treatments, respectively; $n = 10$). From these diurnal measurements, it was concluded that the daily maximum water potential could be measured before dawn and the daily minimum water potential could be measured between 2 pm and 5 pm CST. Leaf gas exchange activity peaked midmorning and declined into the mid-afternoon.

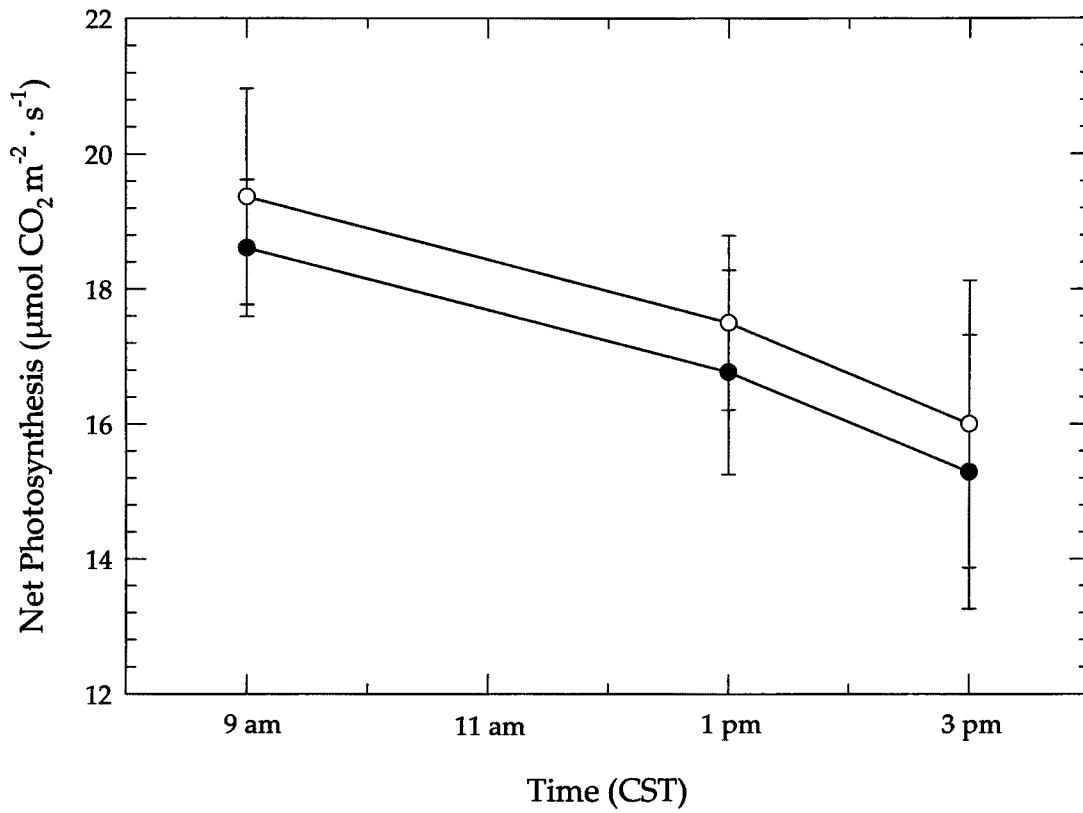


Figure 11. Net photosynthesis of control (—●—) and removal (—○—) live oaks, prior to understory removal (May 23, 2000) at Freeman Ranch, Hays County, Texas. Data are from measurements made with a PP Systems CIRAS-1 portable photosynthesis system. Data are means \pm 1 SE, $n = 10$ (at 9am $n_{\text{control}} = 9$, $n_{\text{removal}} = 7$).

Physiological Responses to Understory Removal

Plant Water Potential

Mean predawn shoot water potentials of live oaks varied significantly throughout the 13-month sampling period (ANOVA, $p < 0.001$), ranging from a low of -1.01 ± 0.09 MPa ($n = 10$) on September 21, 2000 to a high of -0.04 ± 0.01 MPa ($n = 10$) on June 27, 2000 (Fig.12a). Seasonal maxima and minima were associated with periods of high precipitation and drought, respectively, but maxima typically showed a lag of 1 – 2 weeks from major precipitation events (e.g., June 2000). When averaged over all post-removal sampling dates (10), mean predawn water potentials were not significantly (ANOVA, $p = 0.9$) different between control (-0.36 ± 0.03 MPa) and removal (-0.36 ± 0.03 MPa) live oaks. There was no time by treatment interaction ($p = 0.4$).

Midday shoot water potentials also varied significantly (ANOVA, $p < 0.001$) throughout the sampling period, but did not precisely track the predawn water potentials. Mean values ranged from a low of -2.82 ± 0.04 MPa ($n = 10$) on August 14, 2000 to a high of -1.02 ± 0.07 MPa ($n = 10$) on April 16, 2001 (Fig. 12b). In contrast to predawn water potentials, midday water potentials for removal live oaks were significantly more negative ($p = 0.05$) than control live oaks (-1.87 vs. -1.75 MPa, respectively).

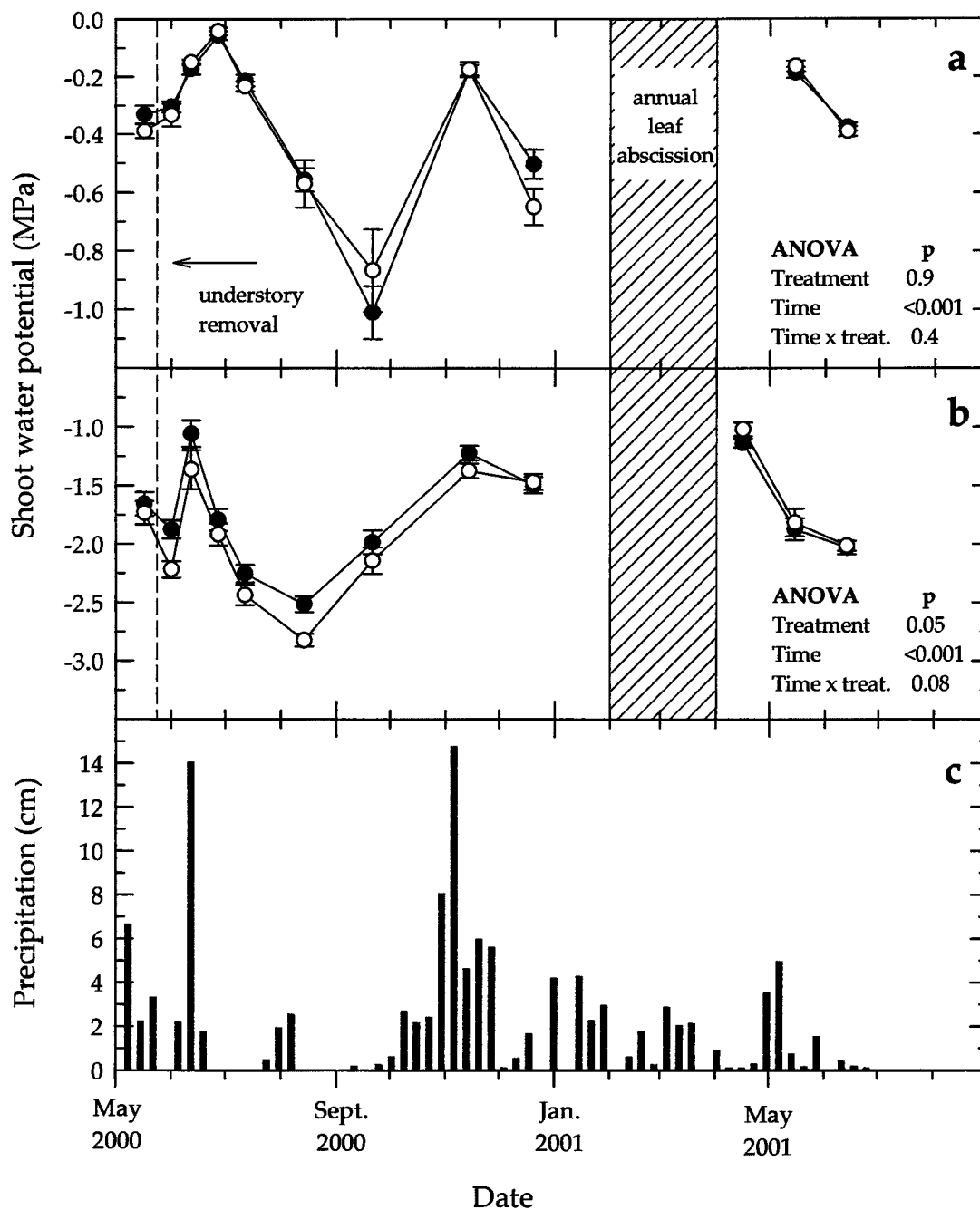


Figure 12. Predawn (a) and midday (b) shoot water potentials of live oaks with (control;—●—) and without (removal;—○—) intact overstory, over an annual growth cycle, and total weekly precipitation (c), at Freeman Ranch, Hays County, Texas. Water potential data are measurements made with a Scholander Pressure Chamber. Water potential data are means \pm SE, $n = 10$. ANOVA results are for post-removal data only. Error bars within the size of the symbol are not shown.

Statistical analyses indicated a marginal time by treatment interaction ($p = 0.08$) in midday water potential measurements. During the first year of study (2000) the midday water potentials of control live oaks were greater than that of removal live oaks on 7 out of 8 sampling dates (Fig. 12b). In contrast, during the year 2001, the midday water potentials of control live oaks were always less than removal live oaks.

In summary, predawn and midday shoot water potentials of live oaks both varied significantly throughout the sampling year. While there was no detectable difference in predawn water potential between treatments, midday water potentials were, on average, higher in control live oaks as compared to understory removal live oaks. While there was no indication that the magnitude of treatment differences increased over time in the first year of study, results suggest that the direction of treatment effects may have changed in the second year.

Stomatal Conductance

Maximum daily leaf (lower surface only) stomatal conductance of live oaks, measured in the morning, varied significantly (ANOVA, $p < 0.001$) throughout the year, ranging from $90.0 \pm 10.9 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($n = 10$) on September 18, 2000 to $414.4 \pm 20.5 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($n = 10$) on May 15, 2001 (Fig. 13a). When

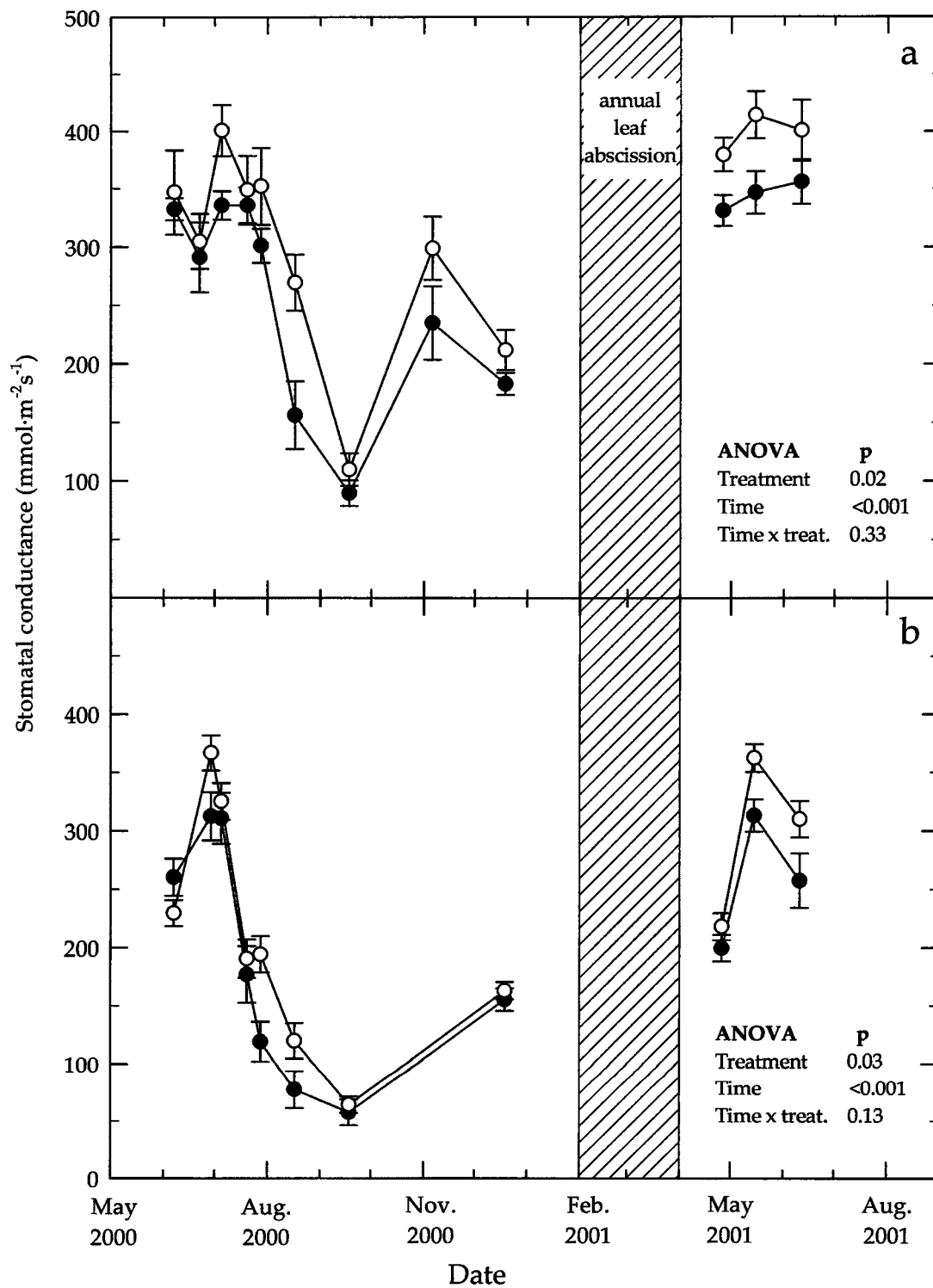


Figure 13. Mean morning (a) and afternoon (b) leaf stomatal conductance of live oaks with (control; ●) and without (removal; ○) intact understory, over an annual growth cycle, at Freeman Ranch, Hays County, Texas. Data are means (\pm SE, $n = 10$) and are from measurements made with a Licor 1600 Steady State Porometer for lower (abaxial) leaf surface only.

averaged over twelve sampling dates, maximum daily stomatal conductance was 16.5% greater ($p = 0.02$) in live oaks without an understory ($320.2 \pm 10.4 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $n = 10$) than control live oaks with an understory ($274.9 \pm 9.4 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $n = 10$). There was no time by treatment interaction ($p = 0.33$), indicating that treatment differences were consistent over time.

Afternoon stomatal conductance (lower leaf surface only) also varied significantly (ANOVA, $p < 0.001$) throughout the sampling period, with values ranging between $57.6 \pm 11.3 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($n = 10$) on September 18, 2000 and $366.9 \pm 19.5 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($n = 10$) on June 29, 2000 (Fig. 13b). Over the entire year, afternoon stomatal conductance was 13.5% greater ($p = 0.03$) in removal oaks ($231.4 \pm 10.6 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $n = 10$) than in control live oaks ($203.8 \pm 10.0 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $n = 10$). Again, there was no time by treatment interaction ($p = 0.13$).

In summary, values of morning and afternoon leaf stomatal conductance varied throughout the sampling year. Stomatal conductance was greater in understory removal live oaks than control live oaks, both in the morning and the afternoon. Furthermore, treatment differences were consistent over time.

On May 15, 2001, both shoot water potential and leaf (lower surface only) stomatal conductance varied significantly (ANOVA, $p < 0.001$) throughout the day (Fig 14). Mean stomatal conductance was greater ($p = 0.02$) in removal live

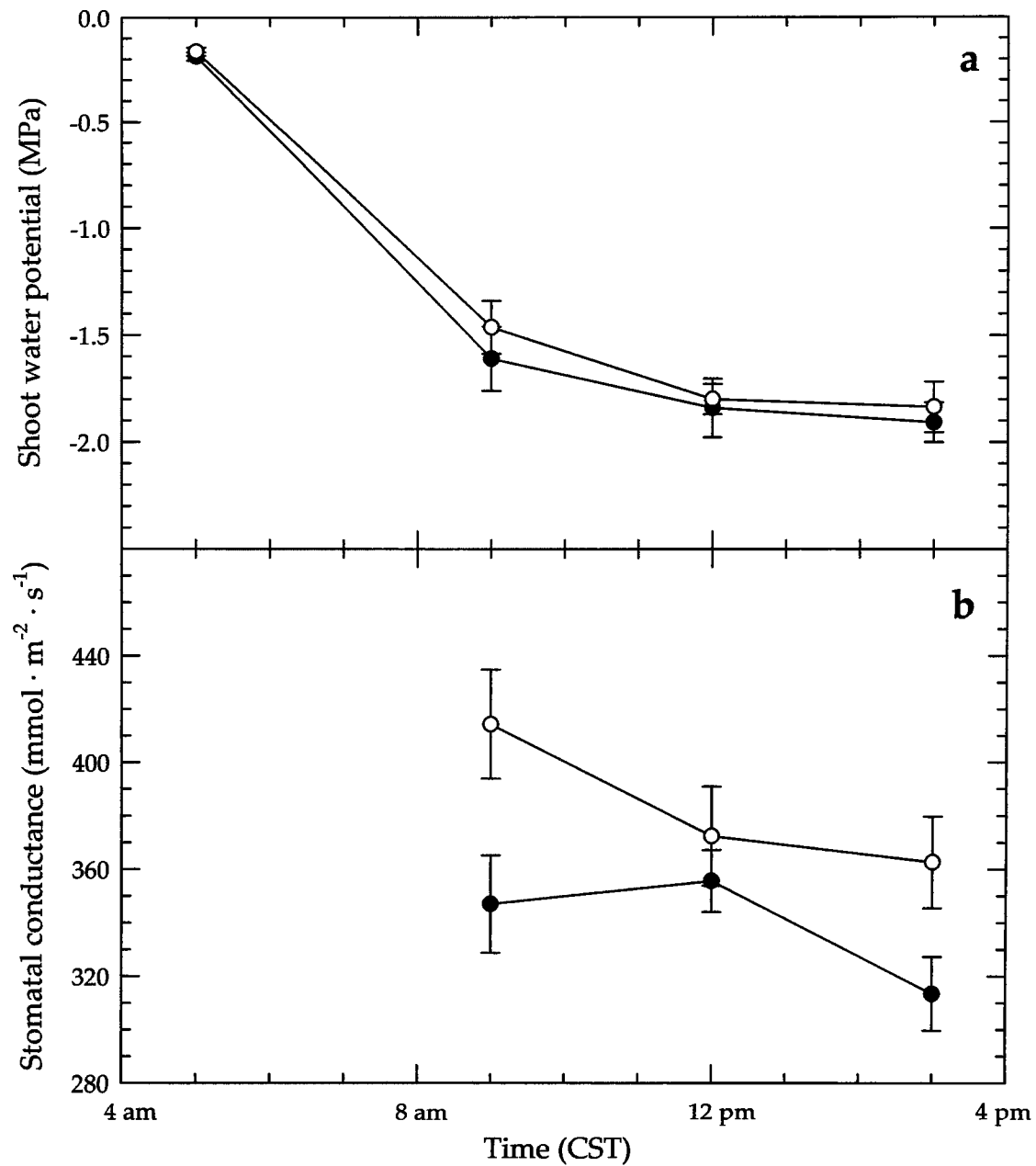


Figure 14. Shoot water potential (a) and leaf (lower surface only) stomatal conductance (b) of live oaks with (control; —●—) and without (removal; —○—) intact understory, on May 15, 2001 at Freeman Ranch, Hays County, Texas. Water potential data are measurements made with a Scholander Pressure Chamber; stomatal conductance data are measurements made using a Licor 1600 Steady State Porometer. Data are means \pm SE, $n = 10$.

oaks ($383.17 \pm 1.25 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $n = 10$) than control live oaks, ($338.70 \pm 8.93 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $n = 10$). However, mean water potential was similar ($p = 0.5$) between control ($-1.79 \pm 0.08 \text{ MPa}$; $n = 10$) and removal oaks ($-1.70 \pm 0.07 \text{ MPa}$; $n = 10$). There was no time by treatment interaction ($p = 0.51$), indicating that treatment differences were similar between sampling periods.

Leaf Gas Exchange

Net photosynthesis varied significantly over time (ANOVA, $p < 0.001$), with values ranging between $9.9 \pm 2.1 \text{ }\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($n = 10$) in August 2000 and $23.9 \pm 0.7 \text{ }\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($n = 10$) in May 2001 (Fig. 15). Over 6 sampling dates, net photosynthesis was significantly greater ($p = 0.04$) in removal live oaks ($18.3 \pm 0.7 \text{ }\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $n = 10$), as compared to control live oaks ($17.0 \pm 0.8 \text{ }\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; $n = 10$). There was no time by treatment interaction ($p = 0.93$), indicating that treatment differences were consistent over time.

Intrinsic water use efficiency (WUE; net photosynthesis/stomatal conductance) also varied significantly over time (ANOVA, $p < 0.001$). Values of intrinsic WUE ranged from 0.031 ± 0.004 to $0.078 \pm 0.004 \text{ }\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$ ($n = 10$; Fig. 16). There was no significant difference ($p = 0.68$) in intrinsic WUE between treatments. Averaged over six sampling periods, mean WUE was 0.058 ± 0.003 ($n = 10$) and 0.057 ± 0.003 ($n = 10$) for control and removal live oaks,

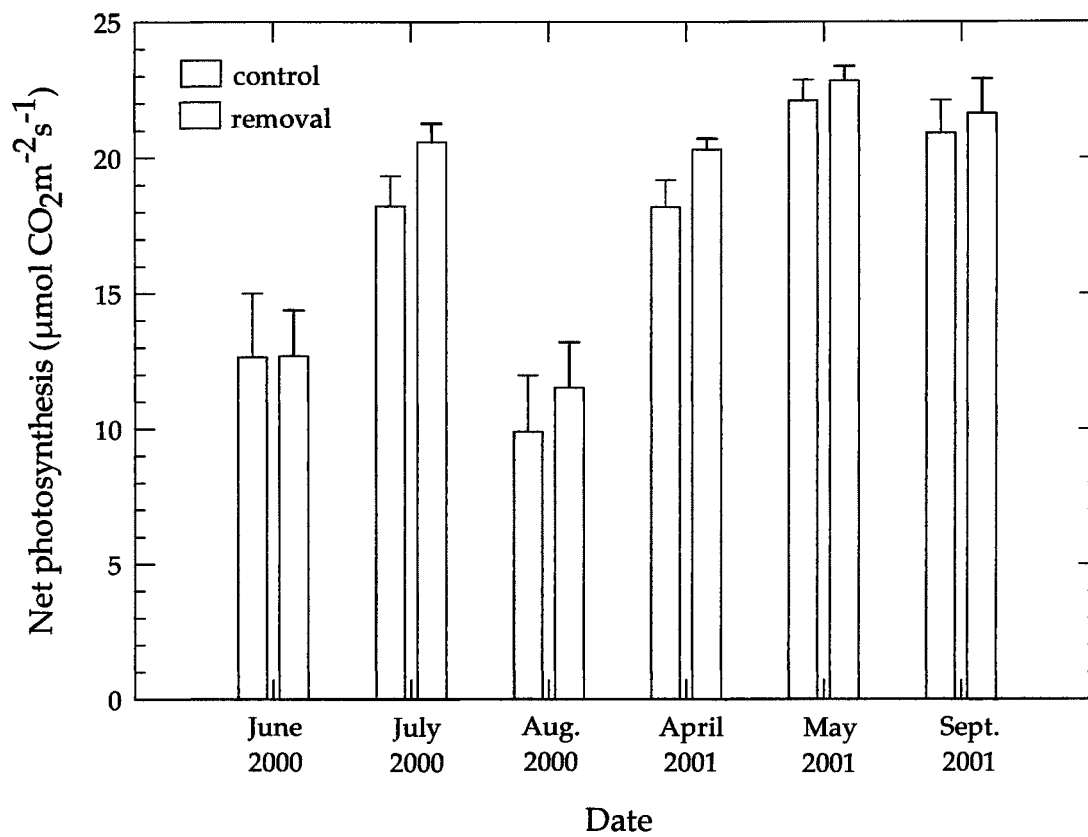


Figure 15. Light-saturated net photosynthesis rates (midday) of live oaks with (control) and without (removal) intact understory at Freeman Ranch, Hays County, Texas. Data are from measurements made with a PP Systems CIRAS-1 portable photosynthesis system. Data are means + SE, n = 10.

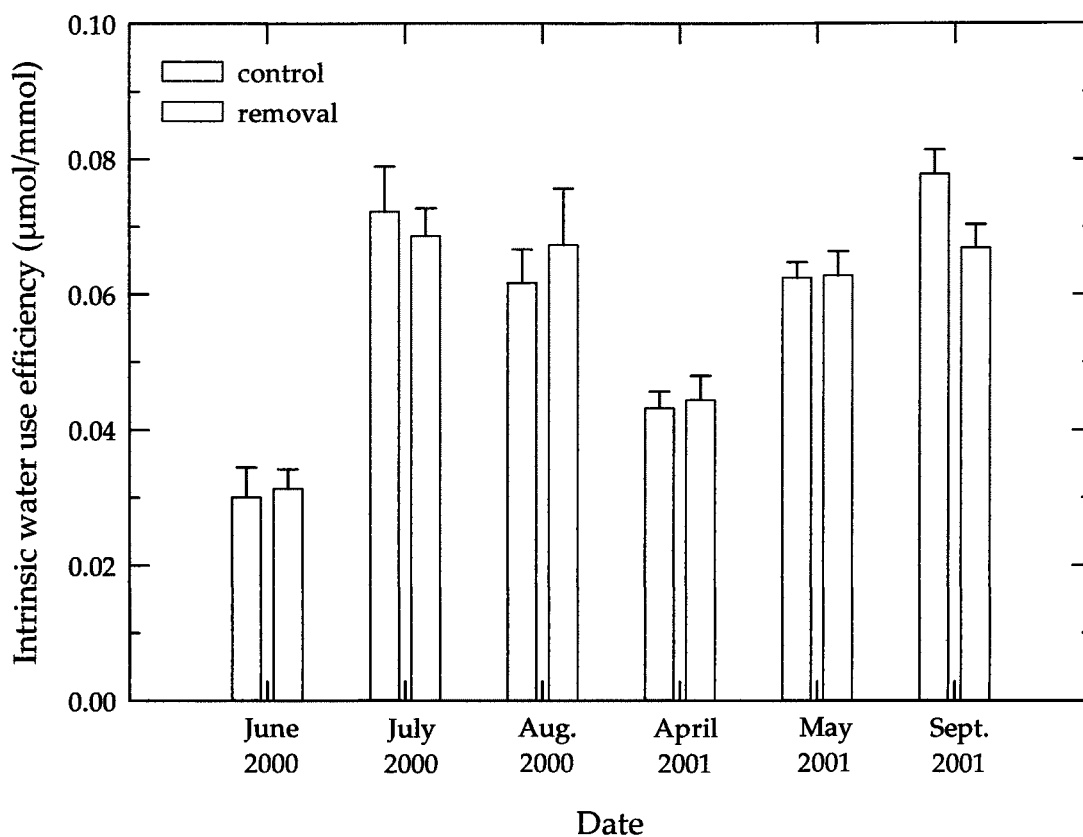


Figure 16. Intrinsic water use efficiency (net photosynthesis/stomatal conductance) of live oaks with (control) and without (removal) intact understory at Freeman Ranch, Hays County, Texas. Data are from measurements made with a PP Systems CIRAS-1 portable photosynthesis system. Data are means + SE, $n = 10$.

respectively. There was no time by treatment interaction ($p = 0.59$), suggesting that the intrinsic WUE was similar between treatments throughout the study period.

Chlorophyll Content

Mean relative chlorophyll content ranged between 29.6 ± 1.2 and 45.9 ± 0.7 SPAD units ($n = 10$; Fig. 17), and values varied significantly over time (ANOVA, $p < 0.001$). Over four sampling dates, relative chlorophyll content of removal live oaks (42.0 ± 1.3 SPAD units; $n = 10$) was marginally greater ($p = 0.10$) than control live oaks (40.3 ± 1.2 SPAD units; $n = 10$). There was no time by treatment interaction ($p = 0.27$).

Growth and Production Responses to Understory Removal

Elongation and Biomass of Marked Shoots

Mean stem lengths of marked shoots ranged from 8.9 ± 1.6 cm ($n = 10$) in June 2000 to 12.8 ± 1.8 cm ($n = 10$) in October 2000 (Fig. 18a), and increased significantly (ANOVA, $p < 0.01$) throughout the growing season. Overall, mean stem length was similar ($p = 0.27$) between control and removal live oaks. There was no significant ($p = 0.31$) time by treatment interaction.

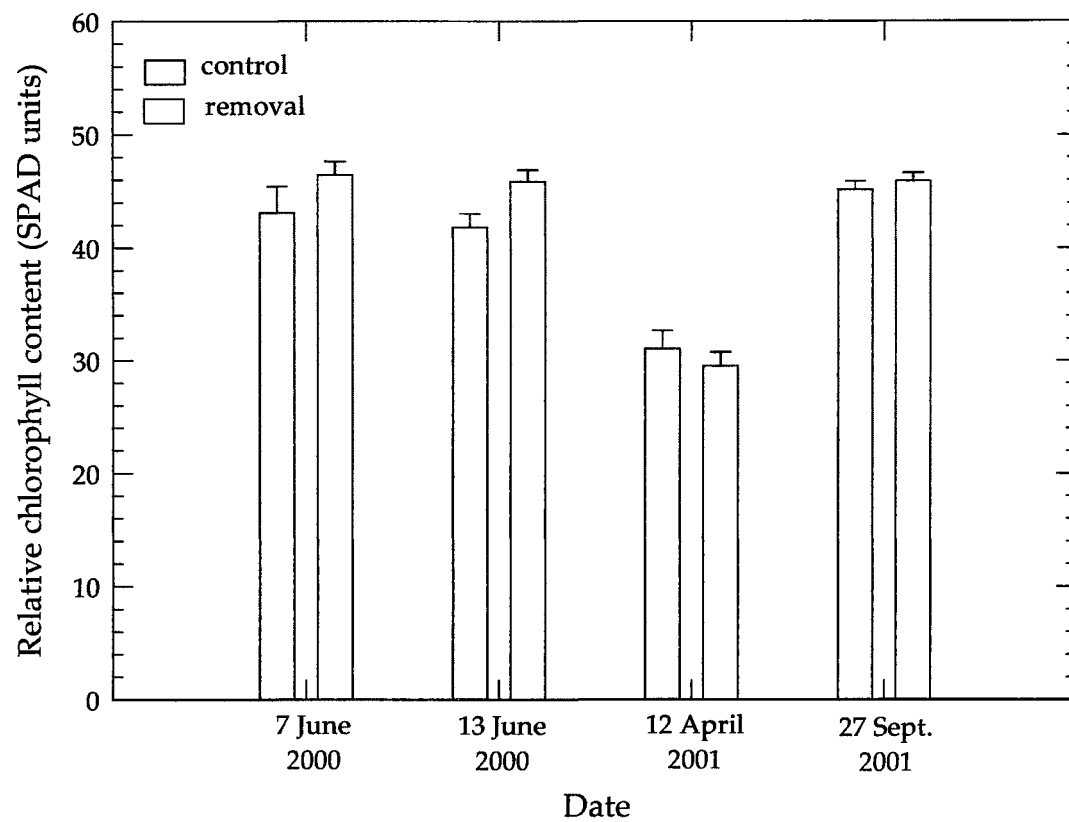


Figure 17. Relative chlorophyll content of control and removal live oaks at Freeman Ranch, Hays County, Texas. Measurements were made using a Minolta SPAD-502 Chlorophyll Meter. Data are means + SE, $n = 10$.

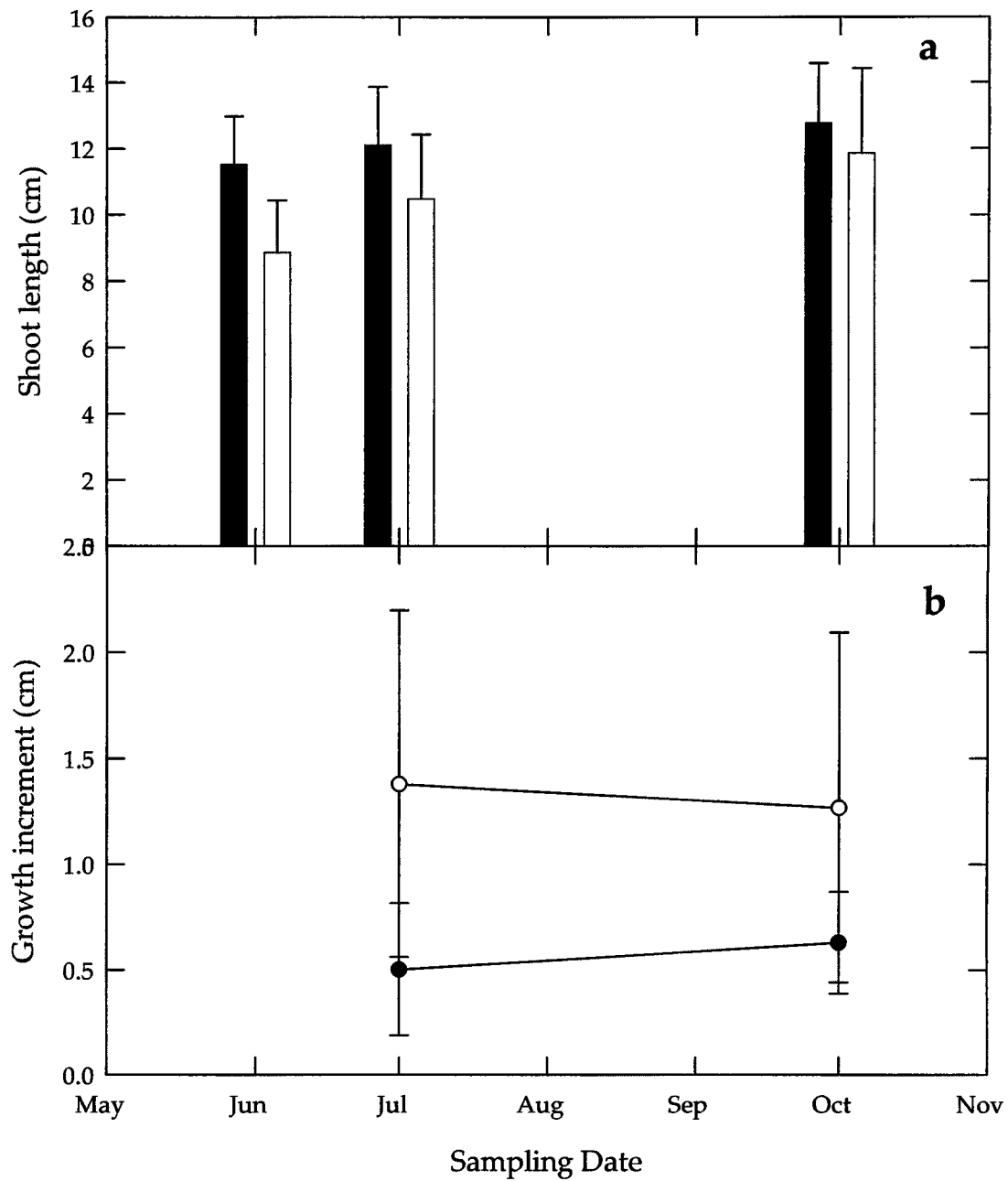


Figure 18. Mean (+ SE; $n = 10$; 5 shoots/replicate) shoot length (a) and growth increment (b) of live oaks with (control; ■, —●—) and without (removal; □ ; —○—) intact understory during the year 2000, at Freeman Ranch, Hays County, Texas. Growth increment is the shoot elongation between dates.

The combined growth increments for both treatment groups were similar (ANOVA, $p = 0.71$) between sampling dates (Fig. 18b). There was no significant ($p = 0.75$) difference in growth increment between control and removal live oaks, and there was no significant time by treatment interaction ($p = 0.10$).

These shoots were harvested in June 2001, dried, and weighed. The shoots from the control treatment had a mean biomass of 4.2 ± 0.9 g ($n = 10$), which was slightly greater than the removal treatment, 3.7 ± 0.9 g ($n = 10$). However, there was no significant (Student's t-test, $p = 0.62$) difference in mean shoot biomass between treatment groups. Thus there was no difference between live oaks in the control and removal treatment groups with respect to shoot elongation and biomass production during the first year of study.

Length and Biomass of Unmarked Shoots

On average, shoot length was similar ($p = 0.67$) between control and removal live oaks, and there was no time by treatment interaction ($p = 0.83$). Total (foliar plus stem) shoot biomass (Fig. 19) was similar between years ($p = 0.66$) and between treatments ($p = 0.50$), and there was no time by treatment interaction ($p = 0.39$). However, there were differences in foliar and stem biomass between years (Fig. 19). Foliar biomass was significantly greater ($p = 0.03$) in the year 2001 as compared to 2000, while stem biomass was slightly

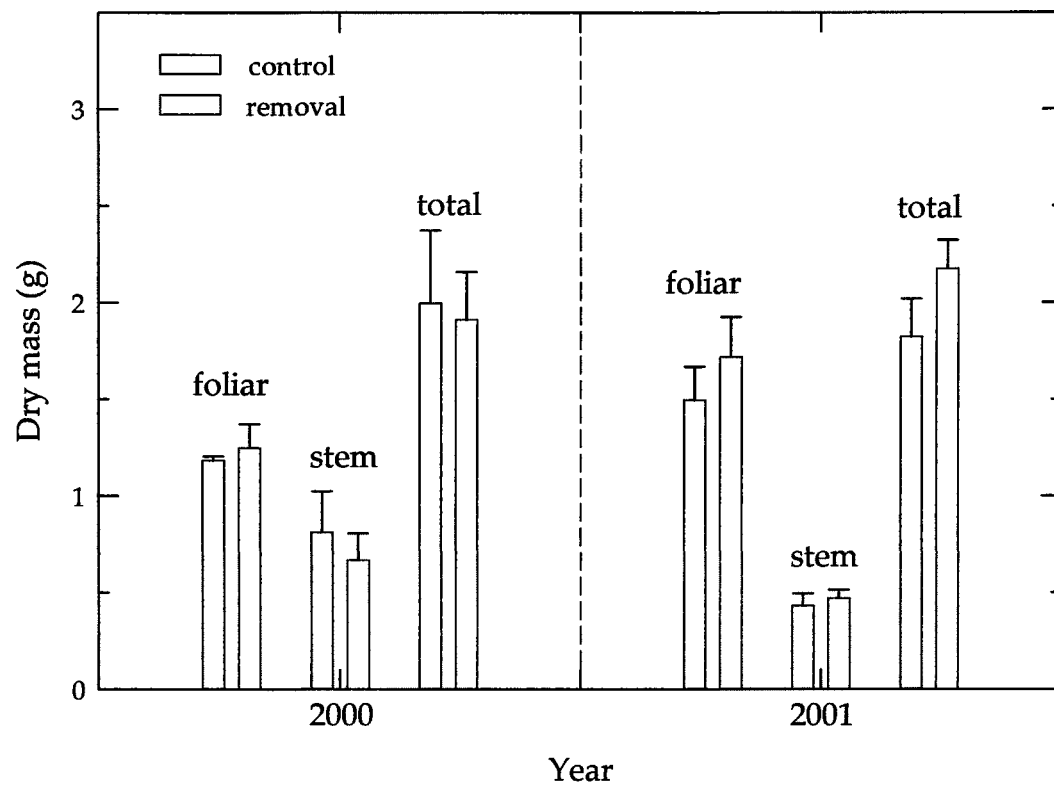


Figure 19. Mean (+ SE; $n = 10$, $n_{\text{control:2000}} = 9$; 4 shoots/replicate) foliar, stem, and total shoot biomass of live oaks with (control) and without (removal) intact understory at Freeman Ranch, Hays County, Texas. 2000 and 2001 shoots were harvested in February and September 2001, respectively.

greater ($p = 0.10$) in the year 2000. The ratio of foliar to stem biomass was 2.4 and 3.8 in the years 2000 and 2001, respectively. For both foliar and stem biomass, there was no time by treatment interaction ($p = 0.73$ and $p = 0.55$, respectively).

In summary, shoots removed in February and September 2001, which represent growth from the 2000 and 2001 growing season, respectively, did not show a significant difference between treatment groups in the growth variables measured, including stem length, foliar, stem, and total shoot biomass. Furthermore, measurements of shoot length and total shoot biomass were similar between years. However, there was a higher ratio of foliar to stem biomass in the year 2001, as compared to 2000.

Leaf Litter Production

Temporal patterns of leaf abscission were generally similar between treatments (Fig. 20) with the exception of the period from February 26 to March 7, 2001, during which time removal live oaks produced more leaf litter than control live oaks. Total leaf litter production was slightly greater (ANOVA, $p = 0.22$) in removal live oaks ($95.6 \pm 7.8 \text{ g/m}^2$; $n = 10$) as compared to control live oaks ($80.2 \pm 9.5 \text{ g/m}^2$; $n = 10$) (Fig. 21). However, when data were analyzed using pre-removal oak LAI as a covariate, there was no significant difference (ANCOVA, $p = 0.93$) in the amount of leaf litter produced between treatments,

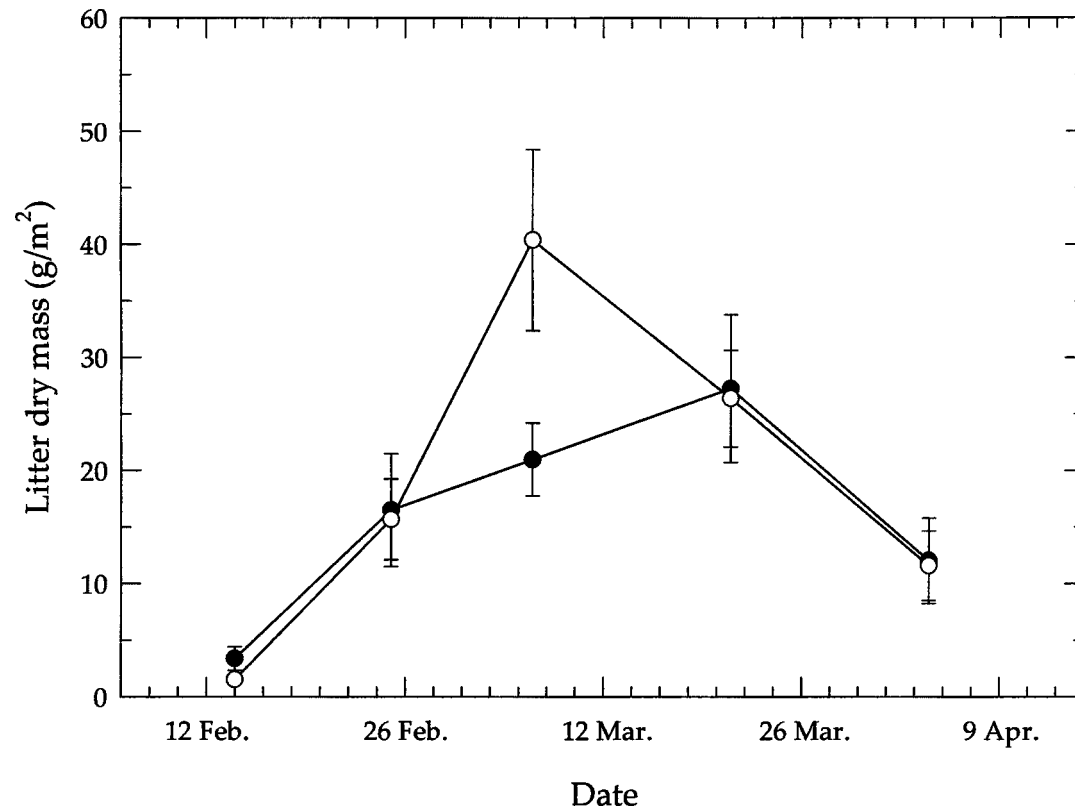


Figure 20. Mean (\pm SE; $n = 10$; 3 trays/replicate) litter mass collected during 2001 from live oaks with (control; \bullet) and without (removal; \circ) intact understory at Freeman Ranch, Hays County, Texas.

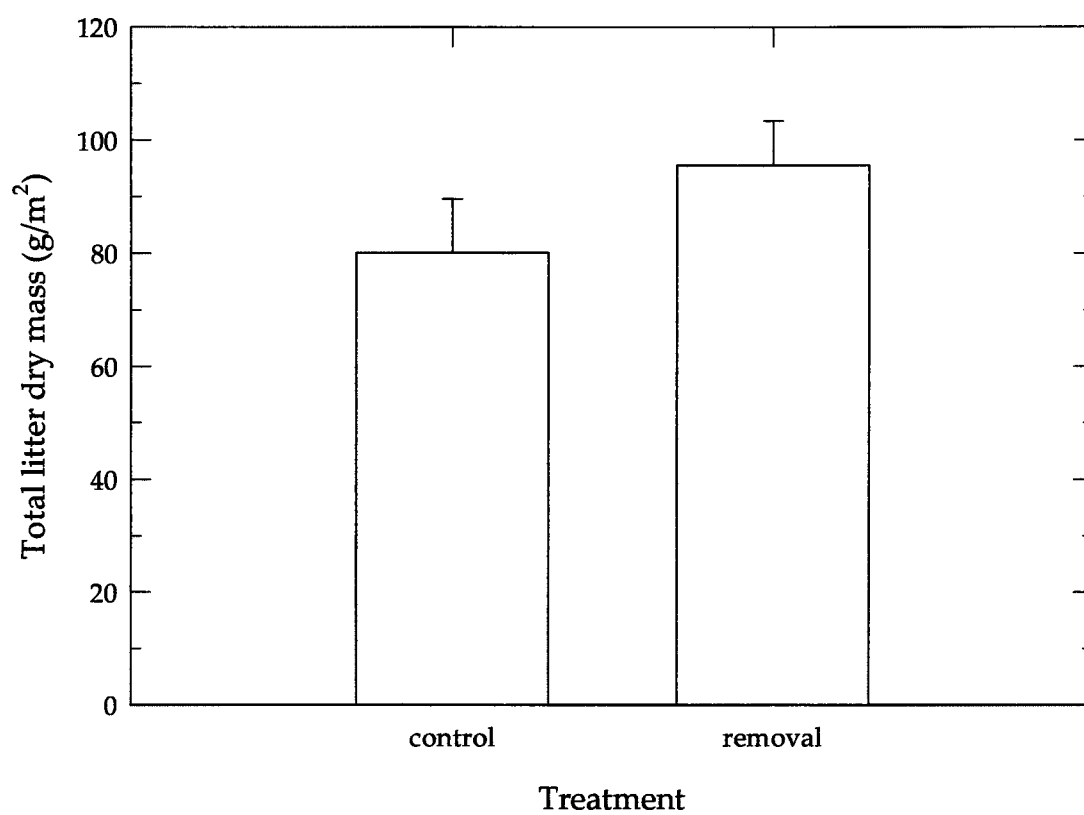


Figure 21. Mean (+ SE; $n = 10$; 3 trays/replicate) litter mass collected from live oaks with (control) and without (removal) intact understory during leaf abscission period (February - April 2001) at Freeman Ranch, Hays County, Texas.

suggesting that treatment differences in litter production were due to pre-removal differences in LAI, and not understory effects.

Facilitation Experiment

Ashe juniper predawn shoot water potential varied substantially throughout the sampling year, ranging between -5.87 ± 0.37 MPa ($n = 4$) on September 21, 2000 and -0.38 ± 0.03 MPa ($n = 6$) on June 12, 2000 (Fig. 22a). Over 8 sampling periods, mean predawn water potential was -1.67 ± 0.27 MPa ($n = 44$) and -1.51 ± 0.25 MPa ($n = 43$) for Ashe junipers under live oaks and in the open, respectively. There was no significant difference (Student's *t*-test, $p = 0.66$) in predawn water potential between treatments.

Similarly, the midday shoot water potential of Ashe junipers had a large range throughout the year, varying between -6.69 ± 0.54 MPa ($n = 6$) on September 21, 2000 and -1.30 ± 0.09 MPa ($n = 6$) on June 12, 2000 (Fig. 22b). Averaged over 9 sampling dates, midday water potential was similar (Student's *t*-test, $p = 0.73$) between Ashe junipers under live oaks (-2.58 ± 0.22 MPa; $n = 52$), as compared to Ashe junipers out in the open (-2.69 ± 0.24 MPa; $n = 54$).

In summary, predawn and midday shoot water potentials of Ashe junipers exhibited a large range throughout the year, especially when compared

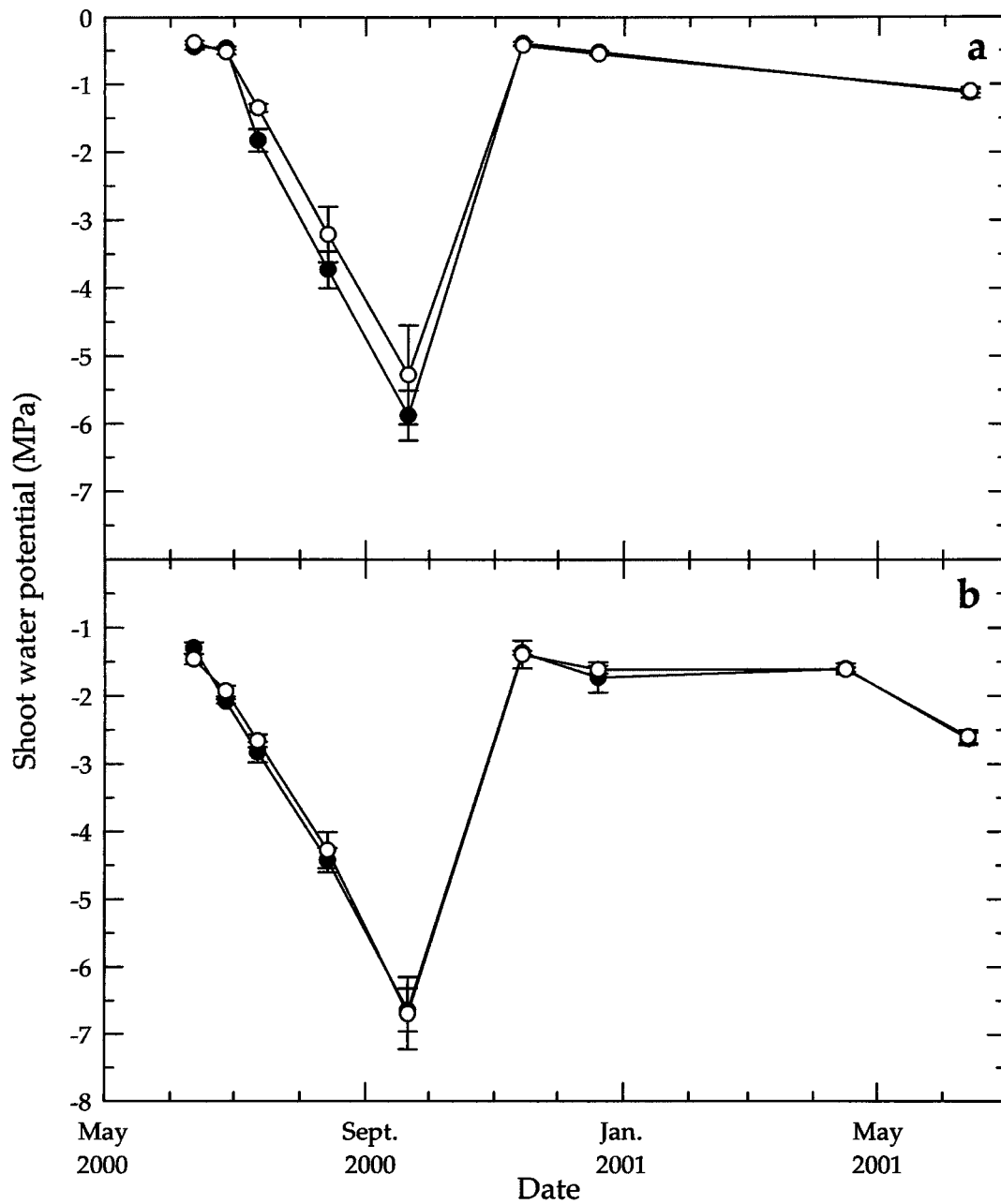


Figure 22. Predawn (a) and midday (b) shoot water potentials of Ashe junipers associated with live oaks (—●—) and those not associated with any other trees (—○—), at Freeman Ranch, Hays County, Texas. Data are from measurements made with a Scholander Pressure Chamber. Data are means \pm SE, $n = 6$. Error bars within the size of the symbol are not shown.

to the range measured in the live oaks. During the predawn and midday sampling periods, there were no significant differences between water potential measurements of Ashe junipers under live oak canopies and those not associated with any trees.

DISCUSSION

Understory Effects on Live Oak

It was originally hypothesized that in established live oak-shrub clusters on the Edwards Plateau of central Texas, understory Ashe junipers would have a negative, competitive effect on the arboreal live oaks. To test this hypothesis, the Ashe juniper-dominated woody understory was removed from 10 live oak-shrub clusters (i.e., removal treatments), while another 10 clusters were left intact (i.e., controls). Results from physiological measurements conducted over a 1-year period following manipulation indicated that understory removal did result in significant increases in rates of live oak leaf gas exchange (H_2O and CO_2). However, although differences between treatments were statistically significant, they were rather small in magnitude (i.e., less than 16% increase relative to controls). Also, these higher rates of photosynthesis did not translate into greater biomass production (stem and leaf) and stem elongation. These findings imply that the intensity of understory competition on the overstory live oaks is rather weak, at least at this site, and may, therefore, be insufficient to competitively exclude the live oak nurse tree that initially facilitated these understory species.

In contrast, removal of the woody understory in mesquite-shrub clusters in southern Texas savannas elicited large (2x) increases in mesquite photosynthesis rates and stem growth such that it was hypothesized that understory competition may be an important factor in contributing to the demise of the mesquite nurse tree (Barnes and Archer 1999).

Throughout the duration of the study period, the seasonal trends in live oak shoot water potential, leaf stomatal conductance, and net photosynthesis responded similarly to periods of drought and high precipitation. For example, following substantial rainfall events, there usually was a positive response in water potential and leaf gas exchange, whereas throughout long dry spells, there was a decrease in shoot water potential and leaf gas exchange. The understory Ashe juniper showed similar relative responses in shoot water potential, though this species consistently exhibited much more negative water potentials (both predawn and midday) than the live oaks. Similar findings were reported by Fonteyn et al. (1985), who also found that Ashe juniper water potential was more affected by decreases in soil moisture than live oaks. They therefore concluded that while both species are drought resistant, live oaks should be classified as drought avoiders while Ashe junipers are drought tolerators. Drought tolerant plants are those that presumably lack regulatory adaptations, such as stomatal closure and efficient root systems, while drought avoiding plants possess such

adaptations. It is therefore likely that, in this current study, the combination of a shallow root system and limited stomatal control over transpiration contributed to the more negative water potentials of Ashe junipers. In contrast, having deeper roots and drought avoidance mechanisms (stomatal closure) probably helped live oaks maintain higher water potential values. Interestingly, live oaks in the removal treatments often exhibited slightly lower daytime water potentials than controls. This response may be a consequence of the higher transpiration rates in these plants and may not be indicative of a greater degree of water stress. Similarly, in a study of two oak species, *Quercus velutina* and *Q. marilandica*, in Oklahoma, Hall and McPherson (1980) reported that *Q. velutina* had lower water potentials and higher transpiration rates than *Q. marilandica*, and they also concluded that higher transpiration rates contributed to these lower water potentials. These findings further indicate that plant water potential, especially in larger trees, may not, in and of itself, always be a reliable physiological indicator of plant responses to neighbor removal (e.g., Barnes and Archer 1999).

The plant water potential data reported in this study do, however, suggest that Ashe junipers and live oaks likely are accessing water from different soil depths, with Ashe juniper being more shallowly rooted than live oaks. Indeed, in a recent study in central Texas, Jackson et al. (1999) found live oak roots at a depth of 22 m, while Ashe juniper roots were found no deeper than 8 m. Because

of the differences in rooting depths, it is possible that live oak performance is not strongly influenced by the removal of the Ashe juniper-dominated woody understory. In a removal experiment in California, Manning and Barbour (1988) found that the water potentials of subshrubs with deep roots were not influenced when their more shallowly rooted neighbors were removed, while the removal of deeply-rooted subshrubs significantly increased the water potential of shallowly-rooted subshrubs. Thus, in these live oak-shrub clusters there may be sufficient partitioning of belowground resources to allow for stable coexistence between overstory and understory elements.

It is possible that the effects of understory removal on these live oaks would become more apparent over a longer time period than was possible in this study. The live oaks in this study were all relatively large (mean basal trunk diameter 55.4 cm; Appendix A) and they may respond slowly to relatively short-term (i.e., months) changes in resource availability. Indeed, Barker (unpublished data) examined stem elongation of live oak trees at another site at Freeman Ranch and found that live oaks that had their understory removed 5 years prior to examination displayed significantly greater stem elongation per year than did live oaks with an intact understory. However, differences in growth need not always require long periods of response time as Smith and Goodman (1986)

found enhancement in growth in as little as 8 months in a tree removal experiment in an *Acacia* savanna in southern Africa.

It is also likely that the effects of the Ashe juniper-dominated understory on live oaks will depend on soils and site differences. At this site on the eastern Edwards Plateau, there were considerable size discrepancies between the overstory live oaks and the understory woody plants. On other sites on the Edwards Plateau however, the live oaks and understory Ashe junipers are more similar in size to each other. In many of these cases, the Ashe juniper canopy grows up through the live oak canopy, and the Ashe junipers may be as tall or even taller than the live oak. Owens (1996) found that when live oaks and Ashe junipers are similar in canopy size, Ashe junipers have an LAI roughly 3 times greater than live oaks. As a result of their high LAI, Ashe junipers were found to have significantly greater rates of canopy-level carbon gain and water loss than similar-sized live oaks (Owens 1996). It is on these sites where historical increases in Ashe juniper abundance coincide with declines in live oak abundance (Smeins and Merrill 1988), which implies competitive replacement of live oaks by juniper. This situation may occur on shallow soils where there is insufficient opportunity for resource partitioning belowground. On these sites the Ashe junipers and other understory shrubs may indeed exert a stronger competitive effect upon the live oaks, possibly to the point of exclusion, as has

been found in other nurse plant systems (Barnes and Archer 1999; Flores-Martinez et al. 1994; McAuliffe 1984; Valiente-Banuet et al. 1991; Yeaton 1978). Clearly, additional experimental studies of live oak-Ashe juniper interactions are required before it is possible to make broad generalizations in this region characterized by great variation in topo-edaphic factors, climate and land management.

Overstory Effects on Ashe Juniper

Previous studies (i.e., Fowler 1986; Anderson et al. 2001) have shown that Ashe juniper seedlings and mature shrubs tend to occur more frequently under live oak canopies than in the open grasslands. This spatial pattern suggests that live oaks facilitate Ashe junipers at least at the seedling establishment phase. Other studies suggest that this facilitation may involve overstory effects on understory microclimate. For example, Phillips (1999) found that the cover and density of established Ashe junipers and other understory species was significantly greater on the cooler, more shaded northern sides of oak clusters than on the more exposed, warmer southern sides of clusters. Whether nurse tree facilitation of understory shrubs occurs beyond the seedling establishment phase is unknown. Thus, in addition to the studies examining understory effects on the overstory live oaks, this study also tested the hypothesis that the overstory

live oaks have a continued facilitative effect on understory Ashe junipers. In contrast to the removal experiment, this aspect of the study was comparative and not manipulative (i.e., Ashe junipers of similar size that occurred in habitats with (live oak clusters) and without (open grasslands) a live oak canopy were compared). Although measurements taken on these Ashe junipers were not as extensive or intensive as those taken on live oaks, the results indicate that mature live oak trees have no positive or negative effect on Ashe juniper shrubs. However, only a single physiological parameter was measured (shoot water potential) and, as indicated above, it may not be prudent to base conclusions on this one parameter. Studies by Anderson et al. (2001) indicated that established, mature plants of certain species (i.e., *Diospyros texana*) may actually be negatively affected by the presence of a live oak canopy. By comparison, in the mesquite savannas of southern Texas, the presence or absence of a mesquite appears to have few persistent effects on mature understory shrubs (Barnes and Archer 1996; Barnes and Archer 1999). Thus, effects of overstory trees on understory shrubs may vary from neutral to positive or negative depending on species and system. As is the case for other nurse plant associations, the balance between net facilitative and net competitive effects may well change with the life stages of the plants involved (Barnes and Archer 1996; Barnes and Archer 1999; Flores-Martinez et al. 1994; McAuliffe 1984; Valiente-Banuet et al. 1991; Yeaton 1978).

Conclusions

Ashe junipers are generally not valued by land managers and conservationists for a multitude of reasons, including their tendency to increase in abundance under current management practices, their pollen causes allergies (“cedar fever”) for many people, they are not palatable to livestock, and in young, dense stands they do not create an aesthetically pleasing habitat for humans (Diamond et al. 1997). In fact, Taylor (1997) argues that Ashe juniper increase “is a serious problem on approximately 10 million acres,” a negative sentiment commonly shared by many landowners. Many ranchers prefer to remove Ashe junipers from their rangelands because they decrease herbaceous production, intercept rainfall, and may decrease deep percolation of water (Thurow 1997; Nelle 1997). However, if Ashe juniper removal is not combined with a sustainable grazing regime, runoff could increase and possibly enhance soil erosion (Nelle 1997). Complete removal of Ashe juniper could also have a negative impact on animals that utilize the shrubs as a food source or as habitat. Results from the present study suggest caution in assuming that Ashe junipers have a pervasive, negative impact on overstory live oaks and argue against the indiscriminate clearing of Ashe junipers because of these perceived negative effects.

Although the results of this study do not necessarily indicate that understory Ashe junipers have a competitive effect on overstory live oaks, there is still concern about future decline of live oak populations. Live oaks infected by oak wilt, a fungal vascular disease that causes a response in the host tree that leads to leaf wilt, almost always succumb to the infection (Anderson 2001). It is possible that future live oak decline may also be a result of heavy browsing by native and exotic herbivores such as white-tailed deer. Russell and Fowler (1999) reported the existence of many live oak saplings (and small root sprouts) on nearby sites, but a lack of recruitment into the adult age classes, and suggested intense browsing by the native deer as a factor inhibiting successful adult recruitment.

In conclusion, there are many considerations and factors that drive land management decisions and these decisions vary depending whether the goal is conservation, rangeland enhancement, or restoration. It is important to remember that Ashe junipers are native to the Edwards Plateau and have only recently increased in abundance and distribution, most likely as the result of land use changes (Bray 1904; Foster 1917; Buechner 1944; Nadkarni et al. 1985). However, other factors that are suspected to enhance woody plant encroachment, such as climate change and enrichment of atmospheric CO₂ (Archer 2000; van Auken 2000), are likely to perpetuate, and could have a

stronger influence on the physiognomy of future landscapes than anything that can be done by small-scale land managers.

APPENDIX A

Diameters of live oaks, measured
61 cm (24 in) above ground surface.
For trees with more than one bole at
61 cm, both diameters are shown.

Tree	Diameter (cm)
R1	67.0
R2	54.0
R3	52.0
R4	38.5
R5	49.0
R6	58.4
R7	37.7
R8	50.2; 50.0
R9	50.0
R10	73.8
C2	44.0
C3	57.4
C4	50.0
C5	52.1
C6	34.2; 40.3
C7	35.8; 36.0
C8	39.4; 40.8
C9	34.2; 36.4
C10	50.6; 71.2

LITERATURE CITED

- Aguiar, M.R., A. Soriano, and O.E. Sala. 1992. Competition and facilitation in the recruitment of seedlings in Patagonian steppe. *Functional Ecology* 6:66-70.
- Anderson, L.J., M.S. Brumbaugh, and R.B. Jackson. 2001. Water and tree-understory interactions: a natural experiment in a savanna with oak wilt. *Ecology* 82:33-49.
- Archer, S., C.S., C.R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* 58:111-127.
- Archer, S., T.W. Boutton, and K.A. Hibbard. 2000. Trees in grasslands: biogeochemical consequences of woody plant expansion. *in* E.-D. Schulze, S.P. Harrison, M. Heimann, E.A. Holland, J. Lloyd, I.C. Prentice, and D. Schimel, editors. *Global Biogeochemical Cycles in the Climate System*. Academic Press, San Diego.
- Barbour, M. G., J.H. Burk, W.D. Pitts, F.S. Gillman, and M.W. Schwartz. 1999. *Terrestrial Plant Ecology*, 3rd edition. Benjamin/Cummings, Menlo Park, CA.
- Barnes, P.W. and S. Archer. 1996. Influence of an overstorey tree (*Prosopis glandulosa*) on associated shrubs in a savanna parkland: implications for patch dynamics. *Oecologia* 105:493-500.
- Barnes, P.W., and S. Archer. 1999. Tree-shrub interactions in a subtropical savanna parkland: competition or facilitation? *Journal of Vegetation Science* 10:525-536.
- Barnes, P.W., S.-Y. Liang, K.E. Jessup, L.E. Ruiseco, P.L. Phillips, and S.J. Reagan. 2000. *Soils, Topography and Vegetation of the Freeman Ranch*. Southwest Texas State University Press, San Marcos, Texas.

- Blackburn, W. and P.T. Tueller. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. *Ecology* **51**:841-848.
- Bray, W. L. 1904. The timber of the Edwards Plateau of Texas: its relation to climate, water supply, and soil. U.S.D.A. Bureau of Forestry **49**:1-30.
- Buechner, H. K. 1944. The range vegetation of Kerr County, Texas, in relation to livestock and white-tailed deer. *American Midland Naturalist* **31**:697-743.
- Callaway, R. M. 1995. Positive interactions among plants. *The Botanical Review* **61**:306-349.
- Diamond, D.D., C.D. True, and K. He. 1997. Regional priorities for conservation of rare species in Texas. *The Southwestern Naturalist* **42**:400-408.
- Dixon, R. 2000. Climatology of the Freeman Ranch, Hays County, Texas. Freeman Ranch Publication Series 3-2000:1-9.
- Flora of North America Editorial Committee. 1993. *Flora of North America North of Mexico: Pteridophytes and Gymnosperms*. Oxford University Press, New York.
- Flora of North America Editorial Committee. 1993. *Flora of North America North of Mexico: Magnoliophyta: Magnoliidae and Hamamelidae*. Oxford University Press, New York.
- Flores-Martinez, A., E. Ezcurra, and S. Sanchez-Colon. 1994. Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*. *Journal of Ecology* **82**:325-330.
- Fonteyn, P.J., T.M. McClean, and R.E. Akridge. 1985. Xylem pressure potential of three dominant trees of the Edwards Plateau of Texas. *The Southwestern Naturalist* **30**:141-146.
- Fonteyn, P.J., M.W. Stone, M.A. Yancy, J.T. Baccus, and N.M. Nadkarni. 1988. Determination of community structure by fire. Pages 79-90 in B.B. Amos and F.R. Gehlbach, editor. *Edwards Plateau vegetation: plant ecological studies in central Texas*. Baylor University Press, Waco, Texas.

- Foster, J. H. 1917. The spread of timbered areas in central Texas. *Journal of Forestry* **15**:442-445.
- Fowler, N. 1986. The role of competition in plant communities in arid and semi-arid regions. *Annual Review of Ecology and Systematics* **17**:89-110.
- Fowler, N.L. 1988. Grasslands, nurse trees, and coexistence. Pages 91-100 in B.B. Amos and F.R. Gehlbach, editor. *Edwards Plateau vegetation: plant ecological studies in central Texas*. Baylor University Press, Waco, Texas.
- Franco, A.C. and P.S. Nobel. 1988. Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. *Ecology* **69**:1731-1740.
- Grover, H. D. and H.B. Musick. 1990. Shrubland encroachment in southern New Mexico, U.S.A.: an analysis of desertification processes in the American southwest. *Climatic Change* **17**:305-330.
- Hall, S.L. and J.K. McPherson. 1980. Geographic distribution of two species of oaks in Oklahoma in relation to seasonal water potential and transpiration rates. *The Southwestern Naturalist* **25**:283-295.
- Holzapfel, C. and B.E. Mahall. 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. *Ecology* **80**:1747-1761.
- Jackson, R.B., L.A. Moore, W.A. Hoffman, W.T. Pockman, and C.R. Linder. 1999. Ecosystem rooting depth determined with caves and DNA. *Proceedings of the National Academy of Sciences* **96**:11387-11392.
- Jones, S.D., J.K. Wipff, and P.M. Montgomery. 1997. *Vascular plants of Texas: A comprehensive checklist including synonymy, bibliography, and index*. University of Texas Press, Austin.
- Manning, S.J., and M.G. Barbour. 1988. Root systems, spatial patterns, and competition for soil moisture between two desert subshrubs. *American Journal of Botany* **75**:885-893.
- McAuliffe, J.R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia* **64**:319-321.

- McPherson, G.R. 1997. Ecology and Management of North American Savannas. The University of Arizona Press, Tuscon.
- McPherson, G.R., H.A. Wright, and D.B. Webster. 1988. Patterns of shrub invasion in semiarid Texas grasslands. *American Midland Naturalist* **120**:391-397.
- Nadkarni, N.M., P.J. Fonteyn, and J.T. Baccus. 1985. Putting the brakes on cedar. *Texas Parks and Wildlife* **43**:36-38.
- Nelle, S. 1997. A holistic perspective on juniper. Juniper Symposium. Texas A&M Research and Extension Center, Technical Report 97-1: 4/3-4/8.
- Owens, M.K. 1996. The role of leaf and canopy-level gas exchange in the replacement of *Quercus virginiana* (Fagaceae) by *Juniperus ashei* (Cupressaceae) in semiarid savannas. *American Journal of Botany* **83**:617-623.
- Phillips, P.L. 1999. Composition of the woody plant understory of Plateau live oak (*Quercus virginiana* var. *fusiformis*) clusters in a central Texas savanna. M.S. Southwest Texas State University, San Marcos, Texas.
- Rollins, D. and B. Armstrong. 1997. Cedar through the eyes of wildlife. Juniper Symposium. Texas A&M Research and Extension Center, Technical Report 97-1: 4/23-4/31.
- Russell, F.L. and N.L. Fowler. 1999. Rarity of oak saplings in savannas and woodlands of the eastern Edwards Plateau, Texas. *The Southwestern Naturalist* **44**:31-44.
- Rykiel, E.J. Jr. and T.L. Cook. 1986. Hardwood-redcedar clusters in the post oak savanna of Texas. *31* **1**:73-78.
- Scholes, R.J. and S.R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**:517-544.
- Smeins, F.E. and S.D. Fuhlendorf. 1997. Biology and ecology of Ashe (Blueberry) juniper. Juniper Symposium. Texas A&M Research and Extension Center, Technical Report 97-1: 3/33-3/47.

- Smeins, F.E. and L. B. Merrill. 1988. Long-term change in a semiarid grassland. Pages 101-114 in B.B Amos and F.R. Gehlbach, editor. Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor University Press, Waco, TX.
- Smith, T.M. and P.S. Goodman. 1986. The effects of competition on the structure and dynamics of *Acacia* savannas in southern Africa. *Journal of Ecology* 74:1031-1044.
- Taylor, C.A. 1997. Foreword. Juniper Symposium. Texas A&M Research and Extension Center, Technical Report 97-1.
- Thurrow, T., A.P. Thurrow, C. Taylor, Jr., R. Conner, and M. Garriga. 1997. Environmental and economic tradeoffs associated with vegetation management on the Edwards Plateau. Juniper Symposium. Texas A&M Research and Extension Center, Technical Report 97-1: 2/3-2/10.
- Valiente-Banuet, A., F. Vite, and J.A. Zavala-Hurtado. 1991. Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. *Journal of Vegetation Science* 2:11-14.
- van Auken, O.W., A.L. Ford, A. Stein, and A.G. Stein. 1979. Woody vegetation of upland plant communities in the southern Edwards Plateau. *Texas Journal of Science* 32:23-35.
- van Auken, O. W. 1988. Woody vegetation of the southeastern escarpment and plateau. Pages 43-56 in B.B. Amos, and F.R. Gehlbach, editor. Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor University Press, Waco, Texas.
- Vines, R. A. 1984. Trees of central Texas. University of Texas Press, Austin.
- Yeaton, R. I. 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan desert. *Journal of Ecology* 66:651-656.

VITA

Patty Ramirez was born on Earth Day 1975 in Johnson City, Tennessee. She attended various schools in Hawaii and Texas and graduated from Mac Arthur High School in San Antonio, Texas, in 1993. Patty attended The University of Texas at Austin, where she earned a Bachelor of Science Ecology, Evolution, and Conservation Biology, with a minor in Spanish. In the fall of 1997, she served as a Student Conservation Association Resource Assistant for the United States Forest Service Pacific Northwest Research Station in Olympia, Washington. She then followed her heart to Madison, Wisconsin, where she worked as a lab technician in the Entomology department at the University of Wisconsin-Madison. Throughout most of her graduate education, Patty lived on a small piece of beautiful land in rural Blanco County, Texas, enjoying the pastoral life with her boyfriend Marty, two dogs (Ashis and Azle), two cats (Enzo and Patches), and a flock of free-ranging chickens.

