WOODY PLANT EFFECTS ON SOIL SEED BANKS 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

Master of SCIENCE

By

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San Marcos, Texas
December 18th, 1998

This is dedicated to Bob and Nanny in their memory and to my parents

We are rooted to the air through our lungs and to the soil through our stomachs.

We are walking trees and floating plants.

John Burroughs 1908.

ACKNOWLEDGEMENTS

I would like to thank my major advisor, Dr. Paul Barnes, for his insight, support and encouragement throughout the entirety of this project. He is an excellent scientist and person whose enthusiasm for ecology is both remarkable and inspiring. I would also like to thank my committee members, Dr. David Lemke and Dr. Jim Ott, for their comments and expertise. These individuals stimulated my interests in plants, biology and the world around me. A special thanks to Dr. Paula Williamson for her encouragement and assistance in finding employment, to Dr. Francis Rose for his continued support and concern for graduate students, and to the Department of Biology for making a conducive learning environment.

To Jan Beck, Patty Phillips, and Kris Norman for generously offering their time to help me in the field and to Bryan Davis for his assistance on the Freeman Ranch. To my lab mates Jan Beck, Patty Phillips, Amanda Holdiman, Chad McMurtry, Jim Nelson, Kirk Jessup and Steve Reagan for their advice, patience, friendship and good senses of humor that made for an entertaining work environment and kept me smiling through the days and nights. Also, a very special thanks to Ryan Loftin, Roland Roberts, Evan Braswell, Jennifer Adams, Jennifer Mittelhauser, for their friendship and laughter.

Most importantly, I would like to thank my family for always believing in me and for their continued support throughout the years. I would like to thank my parents, Del Ruiseco and Paulette Price, for their reassurance, love and for teaching me the most important lessons in life, and John Ruiseco for being a wonderful brother.

TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

ABSTRACT

EFFECTS OF WOODY PLANTS ON THE SOIL SEED BANK IN A CENTRAL TEXAS SAVANNA

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December 1998

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Seed banks from three different habitats (grassland, recently-established junipers, and long-established live oak clusters) in a central Texas savanna ecosystem were compared to determine the effects of different woody plants on species composition and density of the soil seed bank. Specifically, this study tested the hypotheses that : 1) soil seed banks of grassland habitats are different from woody habitats; 2) seed banks beneath junipers are different than in adjacent grasslands; and, 3) within woody plant communities, seed banks of recently-established juniper are different than long-established oaks. To test these hypotheses, surface soil samples were collected seasonally (May, September, December, and March) from grass, juniper, and oak habitats from six replicate sites at the Southwest Texas State University Freeman Ranch. Processed soil and litter samples were placed in plastic flats in a glasshouse and germinable seed bank was observed for 8 to 14 months. Emerged seedlings were removed when they could be reliably identified. The results indicate that seed banks from open grasslands had a greater species richness and diversity than those from oak habitats. Seed banks from grassland and juniper habitats were comparable in species richness and seedling density, however, species compositions differed significantly between these two habitats. In particular, grassland habitats had a greater number of graminoid species and graminoid seedlings present whereas juniper habitats had a greater number of forb species and forb seedlings present. Oak habitats had the fewest graminoid and forb species and seedlings, but had the greatest number of woody plant seedlings. The composition of the seed bank did not resemble the composition of the above-ground plant community. Late-successional grass species were either absent or of limited abundance in the seed bank and it was therefore concluded that common restoration techniques that involve juniper removal can not rely on the soil seed bank for the re-establishment of climax grassland communities.

INTRODUCTION

Woody Plant Effects in Savannas

Savanna ecosystems are characterized by continuous grassland vegetation with a discontinuous woody plant layer. The stability and co-occurrence of these two distinct associations is thought to be influenced by a number of factors, including fire, grazing pressure, and moisture availability (Scholes and Archer 1997). In recent years, the relative abundance between grasses and trees has often been disrupted as an increase of woody plants has been documented worldwide in savannas and other arid and semi-arid ecosystems (Archer 1995). Factors implicated as contributing to woody plant encroachment have included modifications in climate, increased atmospheric carbon dioxide (CO_2) levels, increased grazing pressure, and altered fire regimes (for recent review see Archer 1994).

Individual woody plants alter the conditions in their immediate surroundings and these alterations are thought to be important in influencing tree/grass interactions and overall ecosystem function in savannas. When woody plants establish in open grasslands, they also modify the environment in their understories. Specifically, the microclimate beneath trees is changed as the overstory canopy intercepts solar radiation and shades the understory. For example, trees and shrubs have been found to reduce solar radiation in their understories by 45–67% resulting in a decrease of 3–11° C in soil surface temperature in some savannas (Parker and Muller 1982; Belsky et al. 1989; Ko and Reich 1993). These alterations in radiant energy flux may ultimately decrease water loss from evaporation and transpiration and thereby increase soil moisture available to understory plants.

Soil moisture availability in savannas is influenced by rainfall interception, soil infiltration, evaporation and relative humidity (Belsky 1994). Tree architecture (Haworth and McPherson 1994 as cited in Scholes and Archer 1997) can also affect the amount of rainfall reaching the understory by altering the intensity of a rainfall event (Belsky et al. 1989). Water accumulation at the base of trees can potentially exceed annual precipitation due to the concentrating effects of stem-flow (Thurow et al. 1987). More commonly however, a net loss occurs under trees due to interception of precipitation by the canopy (Thurow et al. 1987; Ko and Reich 1993). In addition, hydraulic lift, a phenomenon whereby soil water from deep roots is absorbed and transported to shallow roots, has been found to increase soil moisture in upper soil layers beneath some woody plants (Richards and Caldwell 1987).

Trees also affect the physical and chemical properties of the soil beneath their canopies. Trees have been shown to improve the nutrient status of the soil (Kellman 1979; Parker and Muller 1982; Belsky et al. 1989; Frost and Edinger 1991; Barnes and Archer 1995; Pugnaire et al. 1996), increase soil organic matter (Burkhardt and Tisdale 1969; Ko and Reich 1993), and increase soil microbial activity (Mordelet et al. 1993). As a result of these changes, increased availability of soil nutrients (i.e., nitrogen, potassium, phosphorus, and calcium) has been detected beneath trees (Belsky et al. 1989, Parker and Mueller 1982, Pugnaire et al. 1996). These effects usually decline with increased distance from the trunk (Belsky et al. 1989) and depth in the soil (Charley and West 1975).

Leaf litter from overstory plants can also contribute to lower soil surface temperatures and evaporation and can improve water infiltration rates (Kelly and Walker 1976; Tiedemann and Klemmedson 1977) which can further enhance nutrient cycling (Kellman 1979). The presence of a thick litter layer can also inhibit seedling emergence and survivorship of understory plants (Sydes and Grime 1981). Thus, if leaf litter is persistent, it can have long-lasting effects on herbaceous production in the understory (Thurow et al. 1997).

Changes in abiotic factors induced by trees (i.e., microclimate, soil properties, etc.) are known to influence the establishment, growth and survival of understory herbaceous plant species. The effects of trees on understory plants can be positive (facilitation), neutral, or negative (competition), depending on the species involved. For example, herbaceous biomass production in the understory has been reported to increase under some tree species (*Prosopis gladulosa*, *Acacia torilis*, and *Retama sphaerocarpa*) (Tiedemann and Klemmedson 1977; Weltzin and Coughenour 1990; Pugnaire et al. 1996) and to decrease under other tree species (*Juniperus pinchotii*, *Quercus macrocarpa* and a hybrid *Q. ellipsoidalis* x *velutina*) (Dye et al. 1995; Ko and Reich 1993).

In addition to effects on understory biomass production, trees can alter subcanopy species composition, diversity and density (Shmida and Whittaker 1981; Parker and Muller 1982; Hobbs and Mooney 1986; Weltzin and Coughenour 1990; Belsky et al. 1989). Zonation of herbaceous plant communities under trees has long been recognized and these community patterns appear to be correlated with tree-induced variation in abiotic factors (Arnold 1964; Armentrout and Pieper 1988). However, Hobbs and Mooney (1986) found a decrease of herbaceous seed production that was related to an increase in herbivory of plants growing under shrubs. These findings suggest that both biotic and abiotic factors can be altered under trees that can then have consequences for understory performance and species composition.

Given the effects of trees on the physical environment and the vegetation in the understory, trees can potentially alter the soil seed bank, however, relatively few studies have examined this (Donelan and Thompson 1980; Milberg 1995; Bakker et al. 1996). Understanding the effects of individual woody plants on seed banks is important for understanding tree/grass dynamics and overall ecosystem function in savannas.

Soil Seed Banks

Soil seed banks represent the reserve of viable seeds in the soil and on its surface (Roberts 1984). Seeds that do not immediately germinate or die, but instead become dormant form the soil seed bank. Seed banks function as regeneration mechanism and therefore aid in the structuring of plant communities (van der Valk and Pederson 1989).

Over evolutionary time plants have developed different life-histories for dealing with differences in environmental factors. Several categories of life history strategies are recognized in plants (e.g., Grime 1979). For example, short-lived plants are usually characterized by a small size, rapid development and a single reproductive event that produces many, small offspring. Long-lived plants are often characterized by a large size, slow development and a delayed, but repeated, reproduction that produces few, large progeny (Barbour et al. 1987). These divergent life histories are thought to be advantageous in habitats that differ in disturbance regimes and resource availability (Grime 1979).

Differences among plant species in patterns of seed production, seed dormancy and survival of seeds contribute to variation in the types of seed banks formed within and among plant communities. Seeds that germinate within one year of dispersal form transient seed banks, whereas seeds that survive for greater than one year form persistent seed banks (Simpson et al. 1989). Differences in longevity of seeds and parent plants often result in poor correlations between the species composition of above- and below-ground flora (Thompson and Grime 1979; Donelan and Thompson 1980; Coffin and Lauenroth 1989; Kunican and Smeins 1992).

Understanding and characterizing the ecology of soil seed banks is important for vegetation management and restoration since seed banks represent a pool of potential seedling recruits following disturbance. Understanding the composition and size of the soil seed bank can also be important for predicting vegetation change over time (i.e., succession) and to test whether natural seed dispersal can be relied upon for restoration efforts (van der Valk and Pederson 1989). Relying on the seed bank for re-vegetation of habitats is only successful if desired species are present in the seed bank. If desired species are not present in the seed bank, sowing seeds or transplanting maybe necessary for rapid and effective re-vegetation of landscapes.

Woody Plant Increase on the Edwards Plateau, Texas

Texas has a large land area (>370,000 km^2) with diverse geological substrates, soils, land forms, and climatic variability. This variation in edaphic and climatic features creates different natural regions characterized by unique types of vegetation (Fig. 1). In many of these natural regions, the vegetation has experienced a recent (100–200 years before present) increase in abundance of many woody species in areas that were once thought to be dominated by grasslands, savannas, and shrublands. Specifically, increases in *Prosopis glandulosa*, *Condalia hookeri*, *Zanthoxylum fagara*, *Larrea tridentata*, *Acacia* sp., *Juniperus pinchotii* and *J. ashei* have been documented in north, central and southern Texas (Ellis and Schuster 1968; Nelson and Beres 1987 cited in Archer 1990; McPherson et al. 1988; Smeins and Merrill 1988). Many species of juniper (*Juniperus* spp.) have increased in abundance throughout the western United States (Branscomb 1958; Johnsen 1962; Burkhardt and Tisdale 1969, 1976; Blackburn and Tueller 1970; Archer 1995). In central Texas, two species of juniper, Ashe juniper (*Juniperus ashei*) and redberry juniper (*J. pinchotti*), have been increasing in local abundance and are expanding their geographical distribution (Ellis and Schuster 1968; McPherson et al. 1988; Smeins and Merrill 1988).

Ashe juniper is an evergreen, dioecious, non-sprouting shrub that is usually less than 6 m in height and has a dense canopy (Smeins and Fuhlendorf 1997). Production of secondary compounds, (i.e., essential oils) by this species reduces its palatability to most domestic livestock (Launchbaugh et al. 1997). This species of juniper is found in canyons, ravines, arroyos, and on eroded flats on the Edwards Plateau of west-central Texas (Correll and Johnston 1970). Seedling studies have shown that Ashe junipers occur

Natural Regions of Texas

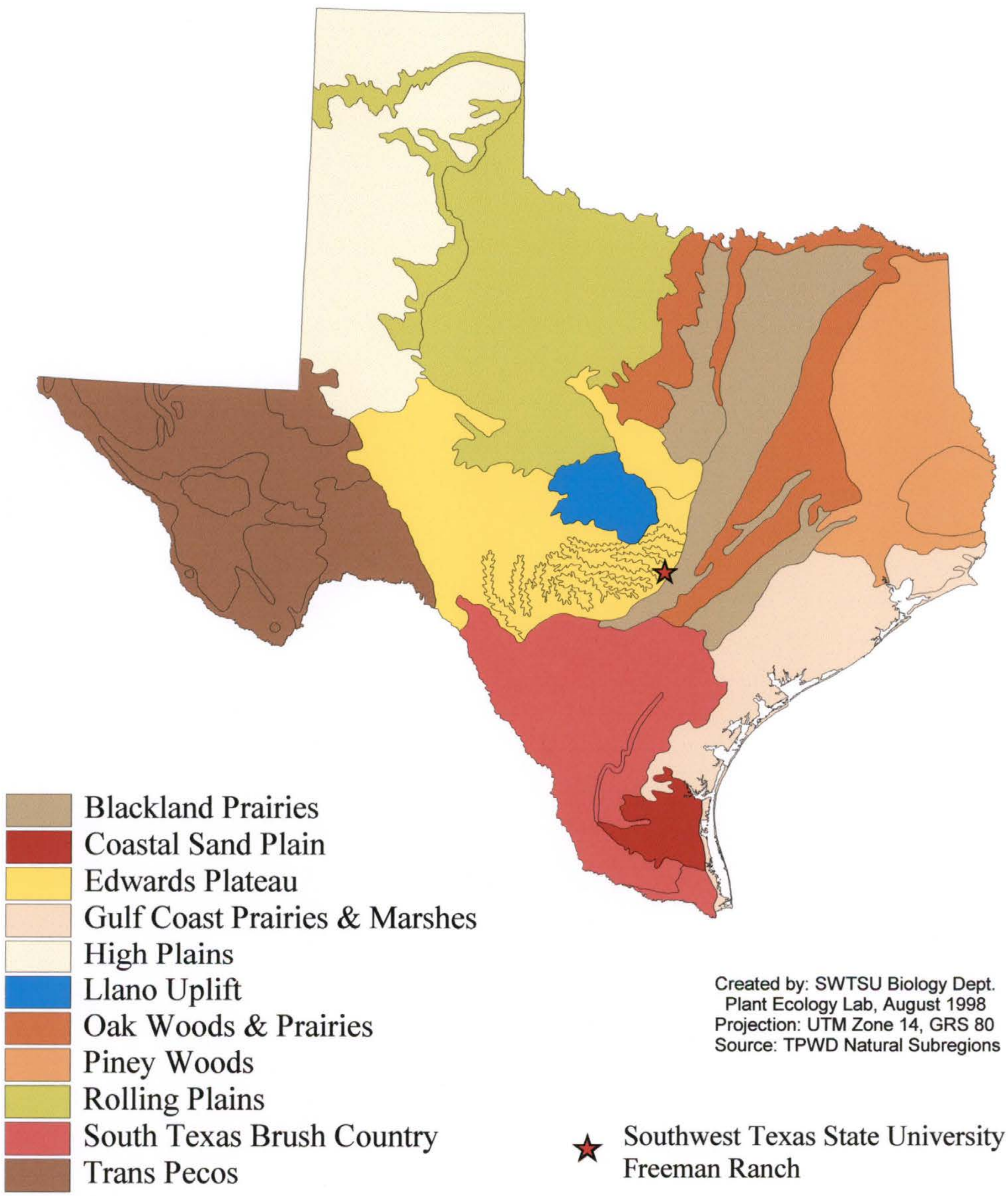


Figure 1. Natural Regions of Texas.

on the edges of woodlands, and readily invade the adjacent grasslands (Jackson and Van Auken 1997).

Increased densities of junipers have important consequences for land use and management in central Texas. For instance, as junipers increase there is typically an associated decrease in herbaceous production, density and diversity of grassland species (Armentrout and Pieper 1988; McPherson and Wright 1990; Dye et al. 1995). These changes in the herbaceous understory are associated with alterations in soil moisture, microclimate, and accumulation of a thick leaf litter layer (Schott and Pieper 1985; Fuhlendorf et al. 1997). The reduction in herbaceous plant production in juniper-infested areas can lower the carrying capacity for livestock and can, therefore, reduce the economic value of the land. In addition, junipers can affect the hydrology of a landscape by altering patterns and rates of interception, infiltration and evapotranspiration of precipitation (Thurow and Hester 1997). Finally, junipers are thought to use more water than other dominant woody species (i.e. live oaks) with which they are found in association (Owens 1996).

While the effects of junipers on understory vegetation have been well studied, less is known of the effects of junipers on the soil seed bank (Bakker et al. 1996). Specifically, it is unknown if recently-established junipers can alter the seed bank of sites previously inhabited by grassland plants and if the seed bank beneath junipers resembles that of other woody plants that have a long-term history of site occupation. Therefore, the primary objective of this study was to evaluate the influence of junipers and other woody plants on seed bank species composition and density on the Edwards Plateau of Texas. I hypothesized that 1) soil seed banks of grassland habitats would differ from woody habitats, 2) seed banks beneath junipers would be different than those in adjacent grasslands, and 3) differences in the seed banks would occur between two different woody habitats (juniper and oak). Specifically, in this study, recently-establish junipers (*J.ashei*) were selected to investigate the short-term effects of juniper on the soil seed bank. These data were compared to live-oak communities (*Quercus virginiana* var. *fusiformis*) which represented a woody plant that likely displayed a long-term site occupation, and the seed banks of both woody habitats were then compared to those of adjacent grassland sites.

MATERIALS AND METHODS

Site Description

The study was conducted at the Southwest Texas State University (SWT) Freeman Ranch located in Hays County, Texas (98° N , 29° W) on the Balcones Escarpment of the eastern Edwards Plateau. The Freeman Ranch occupies 1,411 ha (3,487 acres) and is located approximately 5 km west of the city of San Marcos and the SWT campus (Fig. 2). The property was acquired in 1984 by SWT and Frost Bank in a trust from Joe and Harry Freeman. Since the mid- to late-1800s, the ranch has been generally used as rangeland and has, therefore, experienced long-term grazing by domestic livestock (cattle, sheep, and goats). More precise, historical records of land use and grazing practices are, however, lacking. Prior to 1984, the ranch was apparently heavily stocked at a rate of 0.25 animal units (AU) /ha (0.62 AU/acre) in a 4 pasture system. The stocking rate was decreased beginning in 1984, and by 1988 an 18 pasture grazing system (i.e., a short-duration, high intensity grazing paddock system) was implemented with a lower stocking rate of 0.09 AU/ha (0.22 AU/acre) (B. Davis and D. Cox, personal communication). The present stocking rate is considered to be moderate in comparison with other ranches on the Edwards Plateau (McCalla et al. 1984; Smeins and Merrill 1988).

The Edwards Plateau is considered by some to be the southern-most extension of the Great Plains and is one of the dominant physiographic features in the state of Texas (Fig. 1). The Balcones Escarpment forms the southern and eastern borders of the Plateau and is a major physiographic break with the upland hill country to the west and the lower-elevation Blackland Prairies to the east. The elevation of the Plateau is highest in the northwest

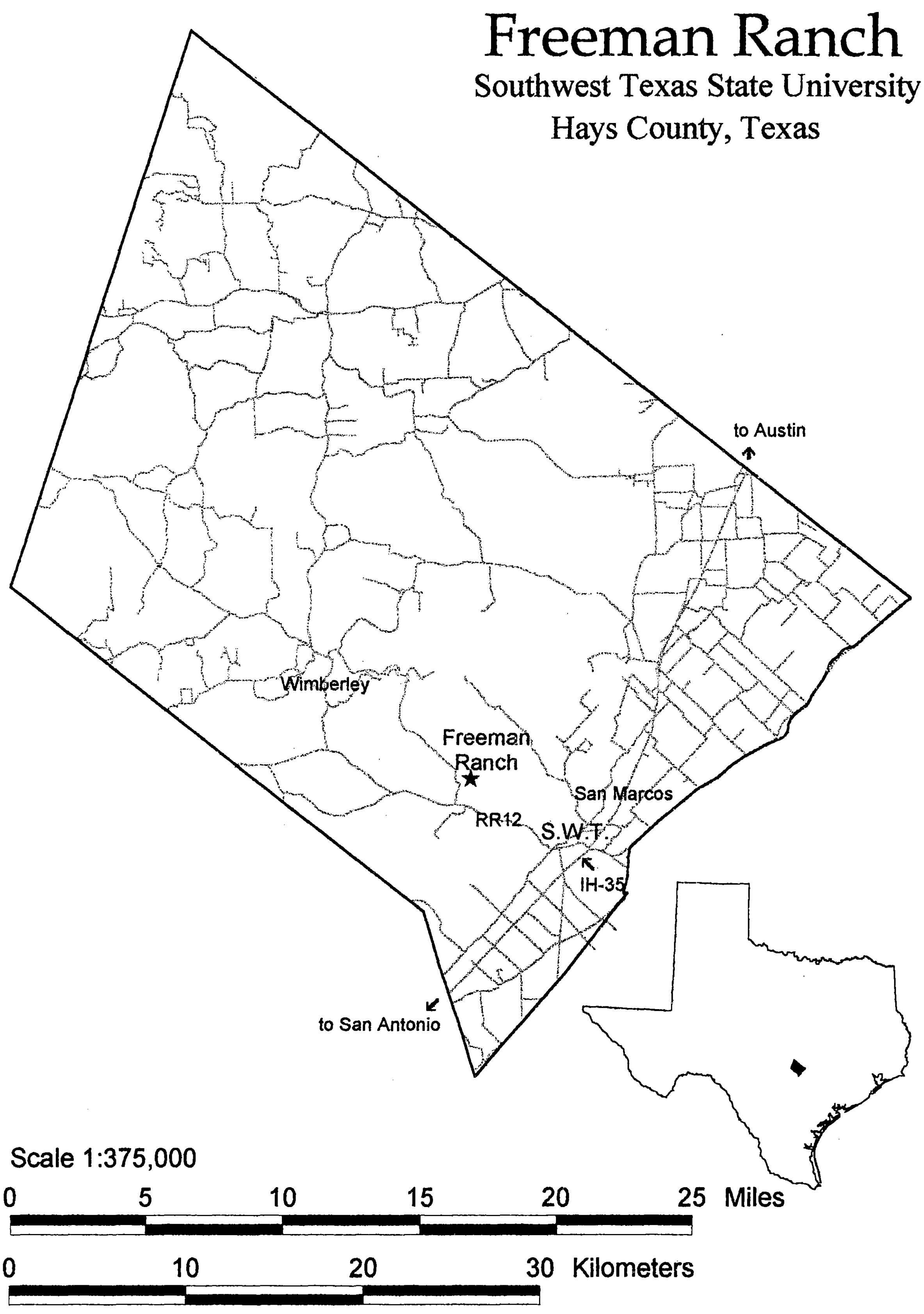


Figure 2. Geographic location of SWT Freeman Ranch in Hays County, Texas.

region (734 m above sea level at Big Lake) and decreases in a southeasterly direction (Riskind and Diamond 1988). The elevation at the Freeman Ranch varies from 91 to 274 m above sea level and the topography is undulating to hilly. The major drainage on the ranch is Sink Creek, an intermittent stream that feeds eastward into Spring Lake and then into the San Marcos River.

The Edwards Plateau is underlain by the Edwards formation and other Lower Cretaceous limestone formations (Sellards et al. 1932). The northern part of the Edwards Plateau exhibits little topographic relief and is dominated by Edwards limestone with frequent limestone outcrops (Riskind and Diamond 1986). The southern part of the Plateau, which includes the Freeman Ranch, has experienced greater erosion than the northern part of the plateau and thus, older formations, such as the Glen Rose formation, are frequently exposed.

The soils of eastern Hays County are classified as a combination of the Comfort, Rumple, and Eckrant soil series (USDA 1984). These soils are generally shallow, to moderately deep (2.4–4 cm), and have developed over hardened limestone. In particular, Comfort soils are dark-brown stony-clay soils found on summits and hill slopes, whereas Rumple soils are reddish-brown clay-loam soils found in stream divides and hill slopes. Eckrant soils are dark gray, extremely stony-clay soils found on sideslopes of high ridges.

Five soil types have been identified at the Freeman Ranch: Rumple-Comfort, Comfort-Rock, Tarpley Clay, Orif soils, and Medlin-Eckrant (Fig. 3). The majority of the ranch (>90%) is covered with Rumple-Comfort and Comfort-Rock soils and all study sites were located on these two soil types. Rumple-Comfort soils consist of 60% Rumple, 20% Comfort, and 20% Tarpley soils and are found on planes and gentle slopes. Comfort Rock soils are approximately 70% Comfort and 30% Rock outcrop soils and are found on side slopes and ridge tops in uplands. Tarpley Clay, Orif soils, and Medlin-Eckrant soil types are also found on the Ranch, though they are relatively rare. Tarpley Clay soils are

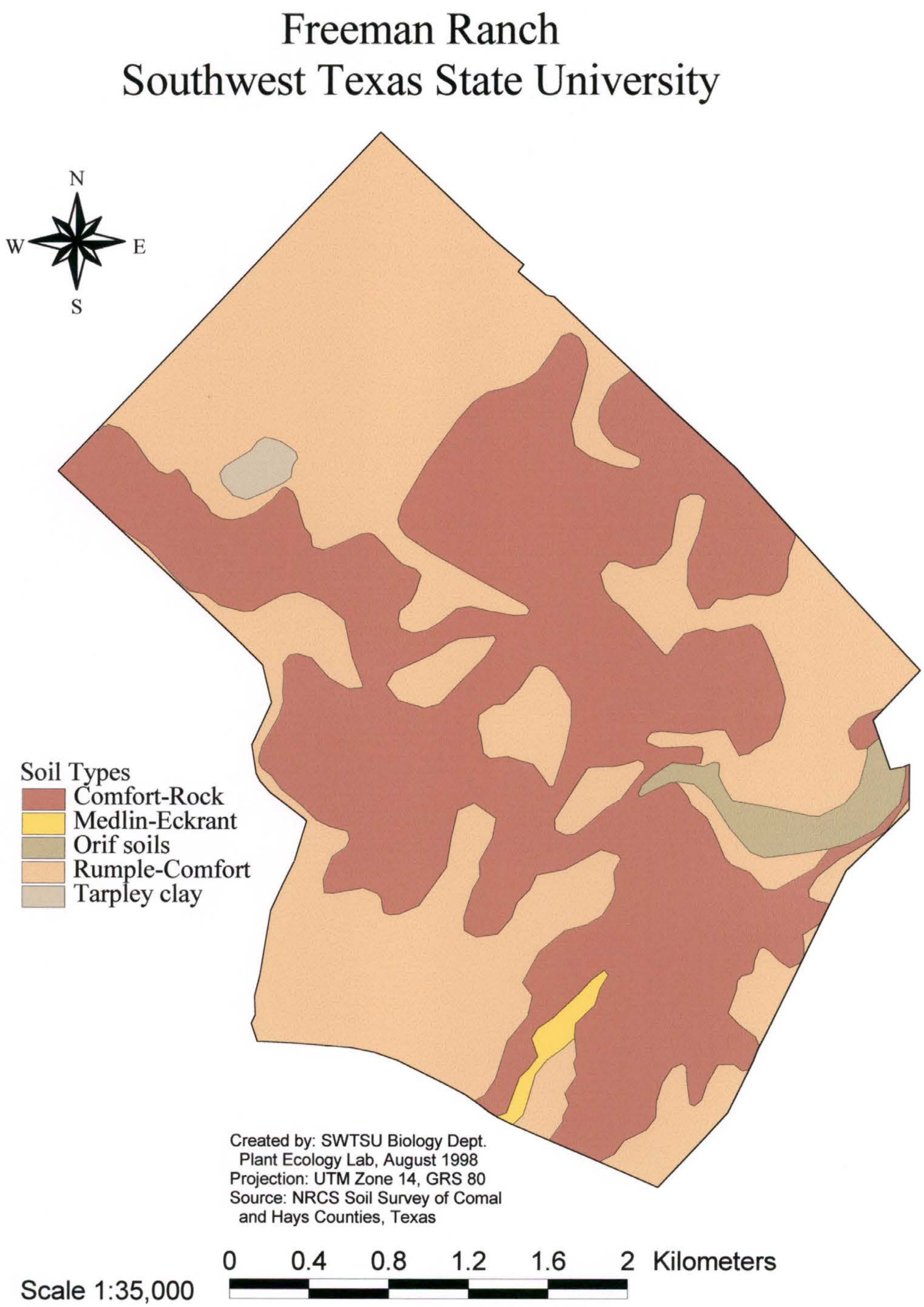


Figure 3. Soil Map of Freeman Ranch in Hays County, Texas.

dark-brown clay soils found on planes to slightly concave slopes on upland areas. Orif soils are grayish-brown, gravely loam sand soils found on nearly level soils on floodplains of creeks. Medlin soils, of the Medlin-Eckrant soil type, are grayish-brown stony clay soils found on lower side slopes and the Eckrant soils, of the Medlin-Eckrant soil type, are dark gray and extremely stony and are found on upper side slopes. Most of the soils on the ranch are well-drained with a slow permeability and a shallow rooting zone. Medium runoff occurs and erosion is of moderate concern (USDA 1984).

The climate of the Edwards Plateau ranges from subhumid in the east to semiarid in the west (Lydolph 1985). Mean annual precipitation for San Marcos is 87.1 cm with March the driest month (mean monthly precipitation of 4.1 cm) and May and September the wettest months (mean monthly precipitation of 11.2 cm) (Fig. 4a). The mean annual temperature for San Marcos is 19.4° C with July the warmest month (mean daily temperature of 28.3° C) and January the coolest month (mean daily temperature of 8.8° C) (Fig. 4b). On average, there are 108 days/year with maximum air temperatures at, or above, 32.2° C and 38 days with daily minimum temperatures at, or below, 1.1° C (Bureau of Business Research 1987). Precipitation is usually in the form of rainfall; snowfall is rare. The average frost-free growing season is 245 days (i.e., March through November).

Vegetation of the Freeman Ranch

Prior to European settlement, the vegetation of the Edwards Plateau was thought to consist of a mixture of woodlands and savannas with woody vegetation predominating in the north and grasslands more abundant in the other regions (Weniger 1988). The woody vegetation was characterized by oaks, junipers and other species that likely occurred in discrete clusters (i.e., mottes) within the savannas or in closed-canopy woodlands on steep slopes and lowland drainages (Amos and Gelbach 1988). The grassland vegetation was

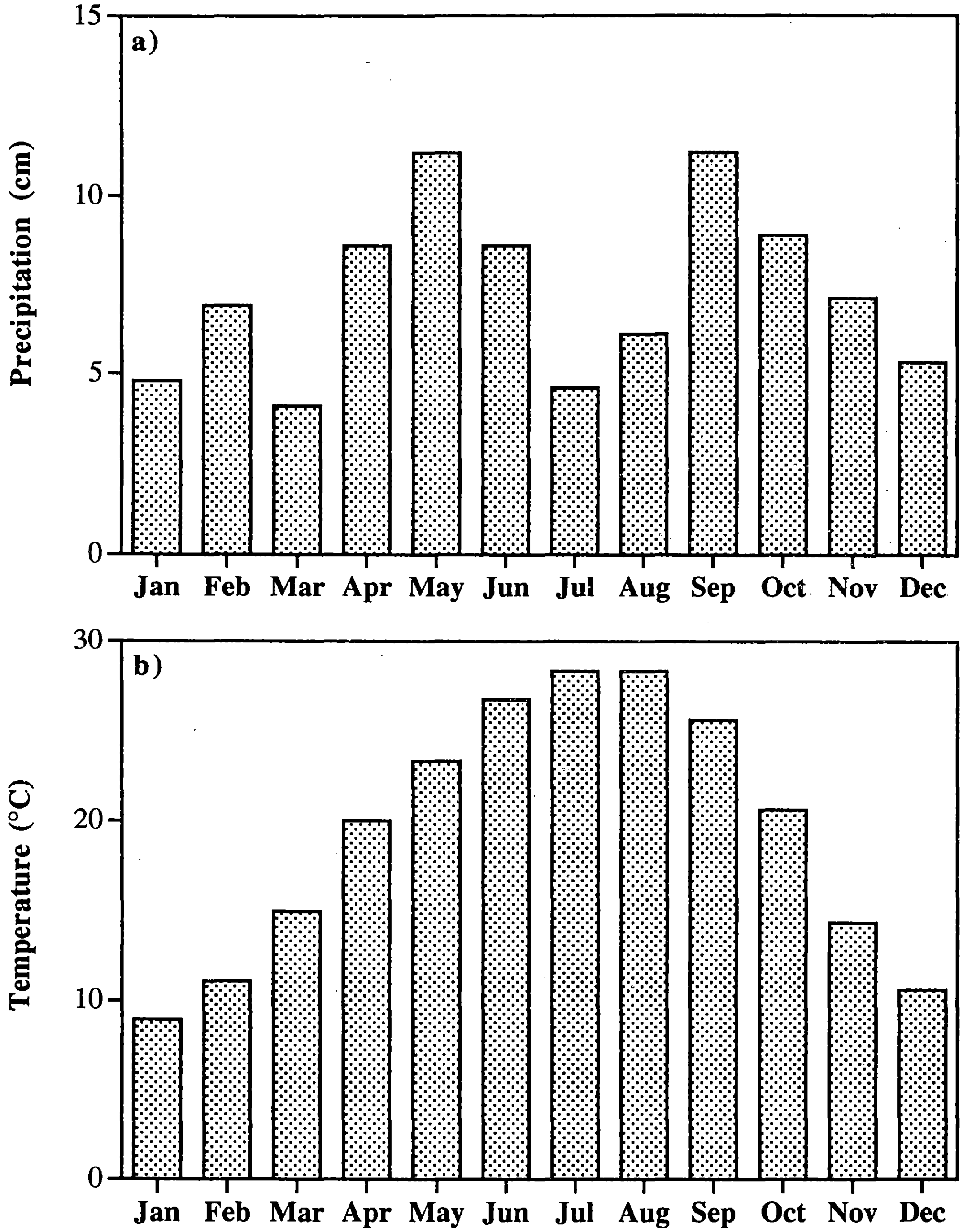


Figure 4. Mean monthly (a) precipitation and (b) temperature data for San Marcos, Texas, 1951-1980. Data are from the Bureau of Business Research, 1987.

thought to be dominated by taller grasses in the east, mixed grasses in the central region, and short grasses in the west (Riskind and Diamond 1988).

The present-day vegetation of the Edwards Plateau is thought to be heavily influenced by anthropogenic alterations of pre-settlement grazing and fire regimes (Riskind and Diamond 1988). For example, in the last 100 to 150 years, native species of juniper (*Juniperus ashei* and *J. pinchotti*) have increased both in abundance and extent (Ellis and Schuster 1968; Smeins and Merrill 1988). *Juniperus ashei* is common on eroded rocky slopes and often forms dense thickets or "cedar brakes" (Correll and Johnston 1979). The native tall- and midgrasses have largely been replaced by more grazing-tolerant species of short grasses and unpalatable forbs (Smeins and Merrill 1988).

The woody vegetation on the upland sites at the Freeman Ranch is currently dominated by trees of *Quercus virginiana* var. *fusiformis* (Plateau Live Oak), which tend to form discrete woody clusters or clumps with a multispecies woody understory consisting of *Juniperus ashei*, *Diospyros texana*, *Berberis trifoliolata*, *Celtis laevigata* var. *laevigata*, *Celtis laevigata* var. *reticulata*, *Forestiera pubescens*, *Ulmus crassifolia*, *Croton fruticulosus*, and *Sideroxylon lanuginosa* (Table 1). Two species of cacti, *Opuntia engelmannii* and *O. leptocaulis*, are the most common perennial succulents. Common vines in these woody clusters include *Smilax bona-nox*, Parthenocissus *quinquefolia*, and *Vitis* spp. Lowland intermittent drainages on the Ranch are vegetated by closed-canopy woodlands with many woody species in common with the uplands (P. Phillips and P. Barnes, unpubl. data).

The current grassland vegetation of Freeman Ranch is dominated by C_4 short- and midgrasses that include *Bouteloua rigidiseta*, *B. hirsuta*, *Eragrostis intermedia*, *Aristida purpurea*, *Aristida oligantha*, *Hiliaria belangeri*, *Panicum hallii*, *Cynodon dactylon*, and *Buchloe dactyloides* and the extensively-planted, exotic, *Bothriochloa ischaemum* (Table 2). Remnants of the once-dominant mid- to tallgrasses (i.e., *Schizachyrium scoparium*, *Bouteloua curtipendula*, *Bothriochloa laguroides*, and *Sorghastrum avenaceum* are

Table 1. Dominant woody plants found in upland oak clusters on the Freeman Ranch. Frequency data were collected during May 1996 from upland oak trees. Importance values for upland sites were calculated using relative frequency (0–100).

Species	**Absolute Frequency**	**Relative Frequency (%)**	**Importance Value**
Quercus virginiana var. *fusiformis*	45	17.0	17.0
Juniperus ashei	35	13.3	13.3
Diospyros texana	30	11.4	11.4
Smilax bona-nox	29	11.0	11.0
Berberis trifoliolata	27	10.2	10.2
Celtis laevigata	21	8.0	8.0
Forestiera pubescens	19	7.2	7.2
Parthenocissus quinquefolia	13	4.9	4.9
Ulmus crassifolia	10	3.8	3.8
Croton fruticulosus	7	2.7	2.7
Sideroxylon languinosa	7	2.7	2.7
Rubus riograndis	5	1.9	1.9
Opuntia engelmannii	4	1.5	1.5
Vitis sp.	4	1.5	1.5
Cissus incisa	4	1.5	1.5
Opuntia leptocaulis	2	0.8	0.8
Yucca rupicola	1	0.4	0.4
Prosopis glandulosa	1	0.4	0.4
Total	**264**	**100.0**	**100.0**

Table 2. Importance values (0–100) for herbaceous vegetation found in grassland sites on the Freeman Ranch. Importance values were calculated by summing the relative values for density, frequency, and cover and dividing by 3. Data were collected in October 1997 from 50, 0.25 m^2 quadrats along 5 transects in 5 different pastures. Unidentified plants were recorded as "Unk".

Species	Importance Value	Species	Importance Value
Croton monanthogynus	12.8	*Hilaria belangeri*	0.5
Bouteloua rigidiseta	11.5	Unk 23	0.5
Meximalva filipes	10.0	*Argythamnia humilis*	0.5
Gutierrezia texana	8.6	Unk 24	0.4
Nassella leucotricha	7.2	*Tragia* sp.	0.4
Bothriochloa ischaemum	5.1	Unk 16	0.4
Paspalum setaceum	4.2	*Aristida* sp.	0.3
Evolvulus sericeus	3.4	*Desmanthus* sp.	0.3
Panicum oligosanthes	2.2	Unk 45	0.3
Aristida 1 sp.	2.2	Unk 37	0.3
Eragrostis intermedia	2.2	*Cenchrus spinifex*	0.2
Unk 3	2.1	*Setaria* sp.	0.2
Oxalis drummondii	2.1	*Solanum elaeagnifolium*	0.2
Dichondra carolinensis	1.7	*Nothoscordum bivalve*	0.2
Wedelia texana	1.7	*Desmodium wrightii*	0.1
Bouteloua curtipendula	1.6	TOTAL	100.0
Aristida wrightii	1.5		
Aristida purpurea	1.4		
Yucca rupicola	1.3		
Ambrosia psilostachya	1.2		
Unk 25	1.2		
Calyptocarpus vialis	1.1		
Smilax bona-nox	1.0		
Unk 29	0.8		
Bouchetia erecta	0.8		
Unk 39	0.8		
Aristida 42	0.8		
Unk 44	0.7		
Unk 22	0.7		
Unk 11	0.6		
Iva angustifolia	0.6		
Agalinus edwardsiana	0.6		
Chloris virgata	0.6		
Ulmus crassifolia	0.6		

restricted to woody or rocky areas that are not readily accessible to cattle. Other common, native grasses include *Nassella leucotricha*, *Panicum oligosanthe* var. *oligosanthes*, *Panicum hallii*, *Paspalum setaceum*, and*Chloris virgata*. Several species of sedges (*Carex* spp. and *Cyperus* spp.) are common in the understory of wooded areas. Dominant forbs in grasslands include *Croton monanthogynus*, *Meximalva filipes*, and *Gutierrezia texana*.

Seed Bank Sampling Protocol

Surface soil samples were collected from three habitat types at the Freeman Ranch: under long-established live oak clusters, under recently-established Ashe juniper trees, and from open grasslands. Based on size-age relationships (Smeins and Fuhlendorf 1997), it was estimated that the junipers sampled under were between 20 and 40 years old (i.e., canopy diameter = 1.4 - 2.7 m and height = 1.48 - 2.7 m). Within each habitat type, six replicate sites were sampled seasonally over a complete year (May, September, and December 1996 and March 1997). The six individual replicates were located in different fenced pastures and thus may have experienced slightly different grazing and management regimes in the past (Fig. 5).

Soil samples from all three habitats at each site/pasture were collected from within a 10–20 ha area using an AMS core sampler (5 cm deep and 5 cm diameter cylinder; 98 cm^3 total volume) equipped with a sliding hammer attachment. At each site, nine individual samples (i.e., subsamples) were collected from each of the three habitats. Subsamples were then pooled such that a total of 884 cm^3 of soil was collected from each habitat type at each sampling site and date. A recommended minimum sample volume of soil for seed bank analysis is 500–600 cm^3 for grassland and 4000–6000 cm^3 for climax forest habitats (Roberts 1984). A total of 216 cores were collected from each of the three habitats. Oak and juniper soil cores were collected from approximately mid-canopy positions and adjacent grassy sites were sampled at least 1-2 meters away from any woody plants.

Figure 5. Approximate locations of sampling sites in different pastures of Freeman Ranch shown on color IR aerial photographs where vegetation is red-to-brown in color. Site 4 was sampled only during the summer of 1996 and Site 7 was sampled only during the fall, winter, and spring of 1996 and 1997.

The soil samples collected consisted of a mixture of soil and leaf litter. Soil+litter samples were allowed to air-dry for one to two weeks at room temperature in the lab. Each sample was then passed through a 3.35 mm mesh sieve to break up soil clumps and to remove rocks and living plant material from the soil and leaf litter mixture. This sieved soil-litter mixture was then placed in open plastic flats (53 cm x 26 cm x 6 cm; 2 samples per flat) over approximately 1 cm of sterile vermiculite to enhance drainage (Fig. 6). Flats were placed in a glasshouse where they received ambient and supplemental light (from 1000 W high pressure sodium vapor lamps). Soil samples were watered daily and fertilized monthly with a commercial fertilizer (Miracle Gro® 15-30-15 nitrogen: available phosphate: potash). Emerged seedlings were recorded over periods of 8 to 14 months, depending upon season. To control for possible contamination of flats by dispersing seeds within the glasshouse, sterile soil samples (2 per season) were placed in the glasshouse and monitored over the same time period as the soil samples. When seedlings could be reliably identified to species (usually after initiation of flowers), individual plants were removed from the flats and pressed. Voucher specimens of all plants identified in the seed bank samples were deposited in the SWT Biology Department Herbarium. Correll and Johnston (1970) was used for plant identification and Jones et al. (1997) was used for nomenclature.

The two most common methods for determining soil seed bank composition are 1) the physical separation of seeds from soil by sieving or flotation techniques followed by identification of seeds and 2) the seedling emergence method (Roberts 1984). The seedling emergence method, which is the method used in this study, determines the number of germinable seeds by taking a representative sample of soil and placing it in conditions suitable for seed germination. Non-germinating and non-viable seeds are not accounted for with this method and thus, this technique may underestimate the actual seed bank of some species (Roberts 1984). To maximize germination potential and thereby minimize any possible underestimate in total seed bank composition, individual samples were monitored

Figure 6. Photo of soil seed bank samples in glasshouse set-up.

over a long time period (8 - 14 months) that generally encompassed a range of light, temperature and photoperiod conditions.

Identification of 22 plants (4 dicot and 18 monocot species) was not possible due to death of the plants in a vegetative state; these are hereafter referred to as unknowns (Table 3). Five species were found in the controls and were therefore not included in the data analysis.

Statistics and Data Analysis

To allow for comparisons with other studies, the number of seedlings emerging from soil samples (i.e., seedling density) was calculated on a unit area basis (m^2). Species area curves were then constructed to examine sampling adequacy for species richness determination. When data were pooled across season, these curves revealed adequate sampling for all habitats since a diminishing return of species occurred with increasing area (Fig. 7). Evaluation of the composition of the seed bank in terms of plant growth form or functional group was achieved by classifying species as: annual vs. perennial; monocot vs. dicot; and graminoid, forb or woody species. Graminoids included all grasses (Poaceae) and sedges (i.e., *Carex* spp. and *Cyperus* spp.). Forbs included all herbaceous species exclusive of graminoids and dicot species with linear-shaped leaves. Woody species included all trees, shrubs, sub-shrubs, succulents and vines. Concentration of dominance or the degree to which the total abundance is concentrated in a few of the total species of the community was calculated using the reciprocal of Simpson's Index values (1/D) (Cox 1996). Species diversity was determined using the Shannon-Wiener Diversity index (H'; Barbour et al. 1987). Statistical comparisons of 1/D and H' for each habitat were made with a one-way ANOVA. Statistical analysis of species richness, growth form richness, and seedling density in the three different habitats was conducted using a one-way ANOVA. Homogeneity of variance was checked by using an FMAX test (Kirk 1995). Species richness data were square-root transformed

Table 3. Unknown monocot and dicot species and number of seedlings found in controls.

Species	control	grass	juniper	oak	Total
Unknown Dicots	0	2	2	0	**4**
Unknown Monocots	0	7	10	1	**18**
Cyperus sp.	1	0	0	0	**1**
*Fatoua villosa**	5	10	17	11	**43**
Iva angustifolia	1	0	0	0	**1**
Oxalis dillenii	4	0	0	0	**4**
Sphenopholis interrupta	1	0	0	0	**1**
Total	**12**	**10**	**17**	**11**	**50**

*Removed from study due to contamination of plots and greenhouse

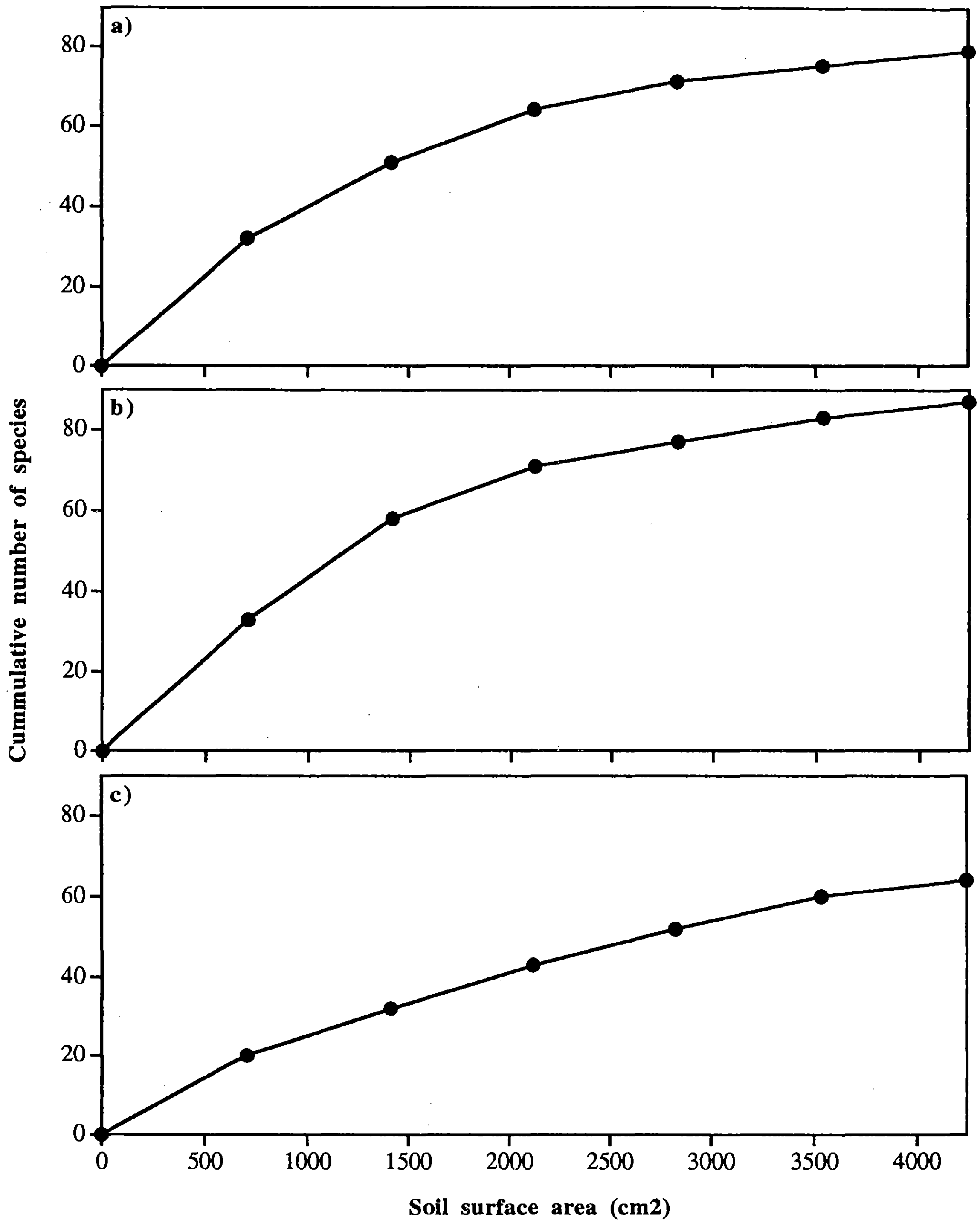


Figure 7. Species-area curves for all seasons for (a) grassland, (b) juniper, and (c) oak seed banks.

to obtain a more normal distributions. Mean comparisons were made using Tukey's test on SuperANOVA software (1991) and differences were considered to be significant at $P < 0.05$. Because samples collected at the different seasons (spring, summer, fall, winter) were not observed over identical time periods (i.e., 8–14 months), no statistical comparisons were made to determine the effect of time of year on seed bank composition and density. However, these data are portrayed herein to illustrate general seasonal patterns.

Information pertaining to plants species found in seed bank including authorities, synonyms, species longevity, growth habit and voucher number are located in Appendix A on page 64. Raw seasonal data can be found in Appendix B and raw habitat data can be found in Appendix C (pages 68 and 72, respectively).

RESULTS

General Patterns in Seed Bank Abundance and Composition

When averaged over season (summer, fall, winter and spring) and habitat (grassland, juniper and oak woodlands), 2648 ± 66 seedlings/m^2 were found to emerge from the soil seed banks at the Freeman Ranch (Table 4). A total of 116 plant species were present in these samples; however, 23 species accounted for over 80% of the total seedling abundance. Two annual dicots, *Oxalis dillenii* (Oxalidaceae) and *Parietaria obtusa* (Urticaceae), were the overwhelming dominant species, as measured by density, in the seed banks, and the annual *Limnodea arkansana* (Poaceae) was the most common grass species. *Opuntia engelmannii* (Cactaceae) was the most abundant woody species.

In general, annuals were more plentiful than perennials in the seed bank, both in terms of number of species (species richness) and seedling density (annuals: 68 species and 2141 seedlings/m^2; perennials: 48 species and 507 seedlings/m^2) (Fig. 8). Forbs were the dominant growth form to emerge from the soil (82 species and 2110 seedlings/m^2). Graminoids (grasses and sedges) were intermediate in importance (25 species and 512 seedlings/m^2) and woody species were relatively rare (9 species and 26 seedlings/m^2) (Fig. 8). Twenty-four grass species were present and included both C_3 and C_4 photosynthetic types (Table 5). However, while most of the C_3 grass species (70%) were annual, the majority of the C_4 grasses was perennial (93%) (Fig. 9).

Seasonal Trends

There were differences in the amount of time over which observations were made on the seed bank samples collected at the four sampling periods (summer, fall and winter =

Table 4. Number of seedlings/m^2 and relative density of each species found in seed banks sampled in the summer, fall, winter, and spring. Percent relative density was calculated by dividing the density for a species by the total density of all species and multiplying by 100.

Species	Summer	Fall	Winter	Spring	Mean	Rel. Density (%)
AGAVACEAE						
Nolina lindheimeriana	0.0	3.1	0.0	0.0	**0.8**	**0.03**
AMARANTHACEAE						
Amaranthus sp.	0.0	3.1	0.0	0.0	**0.8**	**0.03**
AMARYLLIDACEAE						
Habranthus texanus	3.1	0.0	0.0	0.0	**0.8**	**0.03**
ANACARDIACEAE						
Rhus lanceolata	0.0	0.0	3.1	0.0	**0.8**	**0.03**
APIACEAE						
Bifora americana	6.3	85.0	9.4	0.0	**25.2**	**0.95**
Chaerophyllum tainturieri	53.5	25.2	0.0	0.0	**19.7**	**0.74**
ASTERACEAE						
Ambrosia psilostachya	0.0	47.2	12.6	3.1	**15.7**	**0.59**
Baccharis neglecta	3.1	3.1	0.0	0.0	**1.6**	**0.06**
Calyptocarpus vialis	22.0	78.7	129.1	34.6	**66.1**	**2.50**
Centaurea melitensis	0.0	0.0	3.1	0.0	**0.8**	**0.03**
Cirsium texanum	3.1	31.5	3.1	3.1	**10.2**	**0.39**
Conzya sp.	3.1	6.3	3.1	0.0	**3.1**	**0.12**
Evax sp.	3.1	9.4	34.6	0.0	**11.8**	**0.45**
Gamochaeta purpurea	3.1	0.0	9.4	0.0	**3.1**	**0.12**
Gnaphalium sp.	0.0	0.0	3.1	0.0	**0.8**	**0.03**
Gutierrezia texana	0.0	22.0	12.6	0.0	**8.7**	**0.33**
Krigia cespitosa	3.1	88.2	3.1	0.0	**23.6**	**0.89**
Pyrrhopappus paucifloris	0.0	9.4	6.3	0.0	**3.9**	**0.15**
Rudbeckia hirta	22.0	126.0	28.3	3.1	**44.9**	**1.69**
Sonchus asper	9.4	0.0	0.0	0.0	**2.4**	**0.09**
Taraxacum officinale	3.1	6.3	0.0	0.0	**2.4**	**0.09**
Wedelia texana	9.4	0.0	9.4	3.1	**5.5**	**0.21**
BERBERIDACEAE						
Berberis trifoliolata	0.0	0.0	0.0	3.1	**0.8**	**0.03**
BRASSICACEAE						
Arabis petiolaris	0.0	3.1	0.0	0.0	**0.8**	**0.03**
Draba cuneifolia	9.4	0.0	3.1	0.0	**3.1**	**0.12**
Lepidium virginicum	6.3	34.6	6.3	3.1	**12.6**	**0.48**
Lesquerella sp.	0.0	3.1	0.0	0.0	**0.8**	**0.03**
CACTACEAE						
Opuntia engelmannii	6.3	9.4	37.8	9.4	**15.7**	**0.59**
CAMPANULACEAE						
Triodanis perfoliata	3.1	66.1	28.3	0.0	**24.4**	**0.92**

Table 4. Continued

Species	Summer	Fall	Winter	Spring	Mean	Rel. Density (%)
CARYOPHYLLACEAE						
Arenaria benthamii	28.3	63.0	9.4	3.1	**26.0**	**0.98**
Arenaria sp.	0.0	0.0	6.3	0.0	**1.6**	**0.06**
Cerastium sp.	0.0	0.0	6.3	0.0	**1.6**	**0.06**
Silene antirrhina	0.0	25.2	0.0	0.0	**6.3**	**0.24**
COMMELINACEAE						
Commelina erecta	3.1	0.0	18.9	0.0	**5.5**	**0.21**
CONVOLVULACEAE						
Dichondra carolinensis	3.1	9.4	15.7	15.7	**11.0**	**0.42**
Evolvulus sericeus	3.1	9.4	0.0	0.0	**3.1**	**0.12**
CYPERACEAE						
Cyperus spp.	63.0	103.9	56.7	78.7	**75.6**	**2.85**
EBENACEAE						
Diospyros texana	3.1	0.0	0.0	0.0	**0.8**	**0.03**
EUPHORBIACEAE						
Acalypha lindheimeri	9.4	0.0	0.0	3.1	**3.1**	**0.12**
Argythamnia humilis	18.9	22.0	3.1	22.0	**16.5**	**0.62**
Croton fruticulosus	6.3	0.0	3.1	0.0	**2.4**	**0.09**
Croton monanthogynus	81.9	110.2	198.4	9.4	**100.0**	**3.78**
Euphorbia cyathophora	3.1	0.0	3.1	0.0	**1.6**	**0.06**
Euphorbia dentata	6.3	0.0	3.1	3.1	**3.1**	**0.12**
Euphorbia sp.	22.0	9.4	6.3	6.3	**11.0**	**0.42**
Phyllanthus polygonoides	15.7	28.3	15.7	31.5	**22.8**	**0.86**
Tragia sp.	0.0	3.1	0.0	0.0	**0.8**	**0.03**
FABACEAE						
Astragalus sp.	12.6	18.9	6.3	3.1	**10.2**	**0.39**
Desmanthus virgatus	3.1	0.0	0.0	0.0	**0.8**	**0.03**
Indigofera miniata	0.0	0.0	0.0	3.1	**0.8**	**0.03**
Medicago minima	53.5	75.6	44.1	31.5	**51.2**	**1.93**
Medicago polymorpha	0.0	3.1	0.0	3.1	**1.6**	**0.06**
Pediomelum rhombifolium	0.0	0.0	0.0	3.1	**0.8**	**0.03**
Senna lindheimeriana	3.1	0.0	3.1	0.0	**1.6**	**0.06**
Vicia sp.	22.0	34.6	12.6	28.3	**24.4**	**0.92**
GERANIACEAE						
Geranium carolinianum	0.0	3.1	3.1	0.0	**1.6**	**0.06**
HYDROPHYLLACEAE						
Nama jamaicense	91.3	176.4	229.9	97.6	**148.8**	**5.62**
Phacelia congesta	0.0	0.0	0.0	3.1	**0.8**	**0.03**
IRIDACEAE						
Sisyrinchium sp.	3.1	28.3	3.1	0.0	**8.7**	**0.33**
LAMIACEAE						
Brazoria scutellarioides	6.3	18.9	0.0	0.0	**6.3**	**0.24**

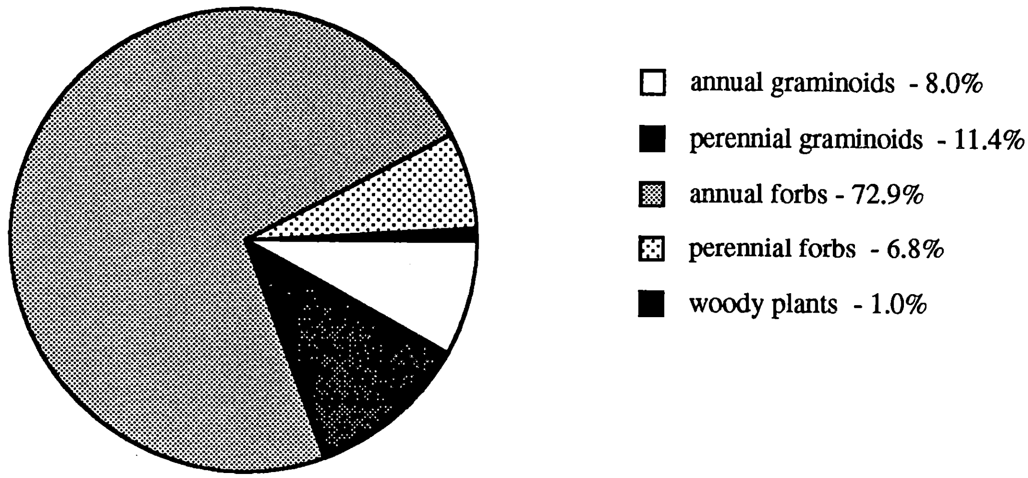
Table 4. Continued

Species	Summer	Fall	Winter	Spring	Mean	Rel. Density (%)
Hedeoma acinoides	3.1	12.6	0.0	0.0	**3.9**	**0.15**
Stachys crenata	15.7	50.4	31.5	9.4	**26.8**	**1.01**
LILIACEAE						
Nothoscordum bivalve	9.4	3.1	0.0	0.0	**3.1**	**0.12**
LINACEAE						
Linum hudsonioides	3.1	15.7	0.0	3.1	**5.5**	**0.21**
MALVACEAE						
Abutilon fruticosum	9.4	3.1	0.0	3.1	**3.9**	**0.15**
Sida abutilifolia	53.5	28.3	28.3	63.0	**43.3**	**1.64**
MOLLUGINACEAE						
Mollugo verticillata	6.3	0.0	0.0	3.1	**2.4**	**0.09**
ONAGRACEAE						
Gaura sp.	3.1	6.3	0.0	0.0	**2.4**	**0.09**
Oenothera triloba	0.0	0.0	9.4	0.0	**2.4**	**0.09**
OXALIDACEAE						
Oxalis dillenii	340.1	1102.3	541.7	296.0	**570.0**	**21.53**
Oxalis drummondii	9.4	56.7	28.3	9.4	**26.0**	**0.98**
PLANTAGINACEAE						
Plantago patagonica	0.0	3.1	0.0	0.0	**0.8**	**0.03**
Plantago virginica	6.3	47.2	47.2	0.0	**25.2**	**0.95**
POACEAE						
Aristida oligantha	0.0	0.0	3.1	0.0	**0.8**	**0.03**
Bothriochloa ischaemum	31.5	3.1	69.3	69.3	**43.3**	**1.64**
Bouteloua rigidiseta	40.9	0.0	6.3	0.0	**11.8**	**0.45**
Bromus catharticus	3.1	9.4	0.0	0.0	**3.1**	**0.12**
Bromus japonicus	3.1	34.6	0.0	0.0	**9.4**	**0.36**
Buchloe dactyloides	12.6	0.0	3.1	0.0	**3.9**	**0.15**
Cenchrus spinifex	3.1	0.0	0.0	3.1	**1.6**	**0.06**
Cynodon dactylon	3.1	6.3	6.3	9.4	**6.3**	**0.24**
Desmazeria rigida	3.1	6.3	0.0	0.0	**2.4**	**0.09**
Digitaria cognata	9.4	0.0	28.3	3.1	**10.2**	**0.39**
Elymus virginicus	3.1	0.0	0.0	0.0	**0.8**	**0.03**
Eragrostis intermedia	34.6	15.7	40.9	12.6	**26.0**	**0.98**
Hilaria belangeri	0.0	0.0	0.0	3.1	**0.8**	**0.03**
Hordeum pusillum	25.2	63.0	3.1	3.1	**23.6**	**0.89**
Limnodea arkansana	107.1	252.0	47.2	0.0	**101.6**	**3.84**
Nassella leucotricha	78.7	103.9	40.9	18.9	**60.6**	**2.29**
Panicum hallii	25.2	9.4	9.4	18.9	**15.7**	**0.59**
Panicum oligosanthes	3.1	15.7	9.4	15.7	**11.0**	**0.42**
Paspalum dilatatum	0.0	0.0	0.0	6.3	**1.6**	**0.06**
Paspalum setaceum	12.6	12.6	25.2	3.1	**13.4**	**0.51**
Setaria scheelei	0.0	0.0	3.1	0.0	**0.8**	**0.03**

Table 4. Continued

Species	Summer	Fall	Winter	Spring	Mean	Rel. Density (%)
Sphenopholis interrupta	44.1	166.9	34.6	0.0	**61.4**	**2.32**
Sporobolus compositus	22.0	6.3	3.1	3.1	**8.7**	**0.33**
Vulpia octoflora	0.0	9.4	3.1	0.0	**3.1**	**0.12**
POLEMONIACEAE						
Gilia incisa	0.0	9.4	12.6	3.1	**6.3**	**0.24**
PORTULACACEAE						
Portulaca pilosa	6.3	0.0	0.0	3.1	**2.4**	**0.09**
RUBIACEAE						
Galium aparine	0.0	3.1	0.0	0.0	**0.8**	**0.03**
Galium spp.	12.6	18.9	34.6	15.7	**20.5**	**0.77**
Richardia tricocca	3.1	0.0	0.0	9.4	**3.1**	**0.12**
SCROPHULARIACEAE						
Mecardonia procumbens	0.0	12.6	12.6	0.0	**6.3**	**0.24**
Nuttallanthus texanus	0.0	56.7	31.5	0.0	**22.0**	**0.83**
Verbascum thapsus	3.1	0.0	0.0	0.0	**0.8**	**0.03**
SMILACACEAE						
Smilax bona-nox	0.0	6.3	0.0	3.1	**2.4**	**0.09**
SOLANACEAE						
Bouchetia erecta	78.7	157.5	50.4	163.8	**112.6**	**4.25**
Physalis cinerascens	0.0	12.6	0.0	0.0	**3.1**	**0.12**
Solanum ptycanthum	0.0	0.0	3.1	15.7	**4.7**	**0.18**
ULMACEAE						
Celtis laevigata	0.0	3.1	0.0	0.0	**0.8**	**0.03**
URTICACEAE						
Parietaria obtusa	472.4	308.6	500.8	163.8	**361.4**	**13.65**
VERBENACEAE						
Glandularia bipinnatifida	3.1	0.0	0.0	0.0	**0.8**	**0.03**
Glandularia pumila	3.1	15.7	0.0	0.0	**4.7**	**0.18**
Verbena canescens	28.3	34.6	12.6	0.0	**18.9**	**0.71**
Verbena halei	25.2	151.2	69.3	59.8	**76.4**	**2.88**
VITACEAE						
Vitis sp.	0.0	0.0	3.1	0.0	**0.8**	**0.03**
Total	**2198.3**	**4239.1**	**2749.4**	**1404.6**	**2647.9**	**100.00**
Mean/sample	**122.1**	**235.5**	**152.7**	**78.0**	**147.1**	
Total species (116 species)	**80.0**	**77.0**	**72.0**	**53.0**	**116.0**	

a) Seedling Density



b) Species Richness

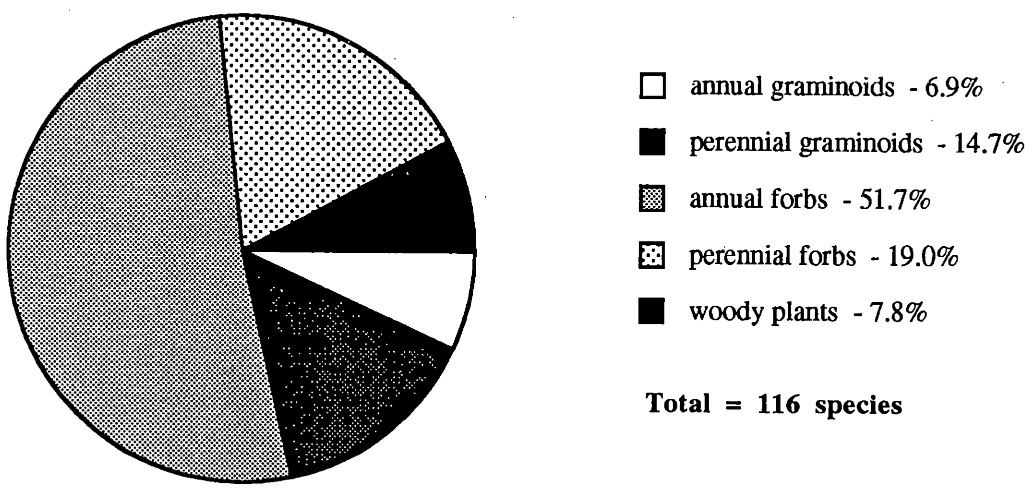
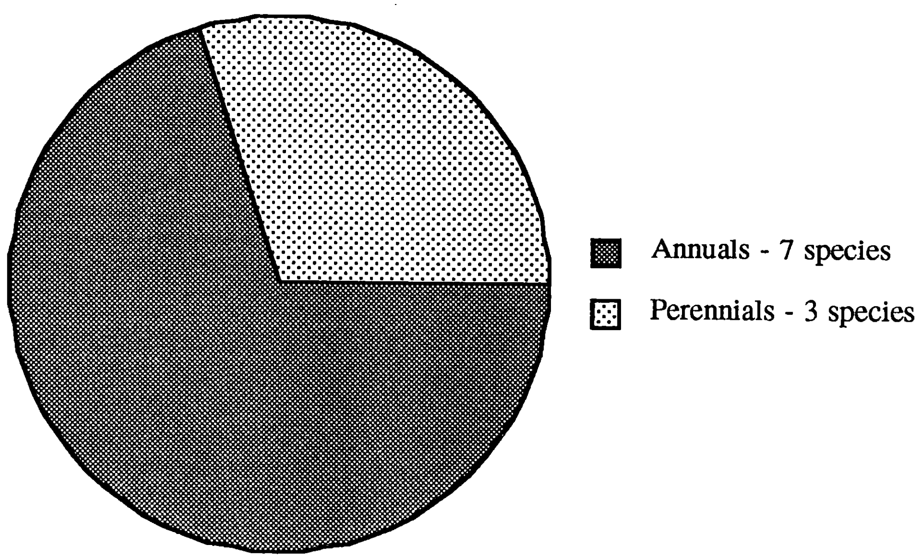


Figure 8. Seed bank composition for (a) seedling density and (b) species richness of annual and perennial graminoids, forbs, and woody plants. Data pooled across habitat and season.

Table 5. Absolute and relative seedling densities/m^2 of grass species found in soil seed banks of grass, juniper, and oak habitats.

Grass species	Annual/ Perennial	C3/C4	Grass	Density Juniper	Oak	Average Density	Relative Density
Limnodea arkansana	A	C3	162.2	88.0	2.0	**84.0**	**24.1**
Sphenopholis interrupta	A	C3	132.9	17.6	2.0	**50.8**	**14.6**
Nassella leuchotricha	P	C3	33.2	89.9	27.4	**50.2**	**14.4**
Bothriochloa ischeamum	P	C4	60.6	35.2	11.7	**35.8**	**10.3**
Eragrostis intermedia	P	C4	21.5	35.2	7.8	**21.5**	**6.2**
Hordeum pusillum	A	C3	58.6	0.0	0.0	**19.5**	**5.6**
Panicum hallii	P	C4	31.3	5.9	2.0	**13.0**	**3.7**
Paspalum setaceum	P	C4	25.4	7.8	0.0	**11.1**	**3.2**
Bouteloua rigidiseta	P	C4	27.4	2.0	0.0	**9.8**	**2.8**
Panicum oligosanthes	P	C3	2.0	25.4	0.0	**9.1**	**2.6**
Digitaria cognata	P	C4	5.9	17.6	2.0	**8.5**	**2.4**
Bromus japonicus	A	C3	19.5	3.9	0.0	**7.8**	**2.2**
Sporobulus compositus	P	C4	3.9	15.6	2.0	**7.2**	**2.1**
Cynodon dactylon	P	C4	5.9	0.0	9.8	**5.2**	**1.5**
Buchloe dactyloides	P	C4	7.8	2.0	0.0	**3.3**	**0.9**
Bromus catharticus	A	C3	0.0	0.0	7.8	**2.6**	**0.7**
Vulpia octoflora	A	C3	7.8	0.0	0.0	**2.6**	**0.7**
Desmazeria rigidum	A	C3	3.9	2.0	0.0	**2.0**	**0.6**
Cenchrus spinifex	P	C4	3.9	0.0	0.0	**1.3**	**0.4**
Paspalum dilatatum	P	C4	2.0	0.0	2.0	**1.3**	**0.4**
Aristida oligantha	A	C4	2.0	0.0	0.0	**0.7**	**0.2**
Hilaria belangeri	P	C4	2.0	0.0	0.0	**0.7**	**0.2**
Setaria scheelei	P	C4	0.0	2.0	0.0	**0.7**	**0.2**
Elymus canadensis	P	C3	0.0	0.0	1.9	**0.6**	**0.2**
Total seedlings m^2	-	-	**619.5**	**349.8**	**78.1**	**349.2**	**100.0**
Total species (24)	-	-	**21**	**15**	**12**	**24**	**24**

a) C_3 grasses



b) C_4 grasses

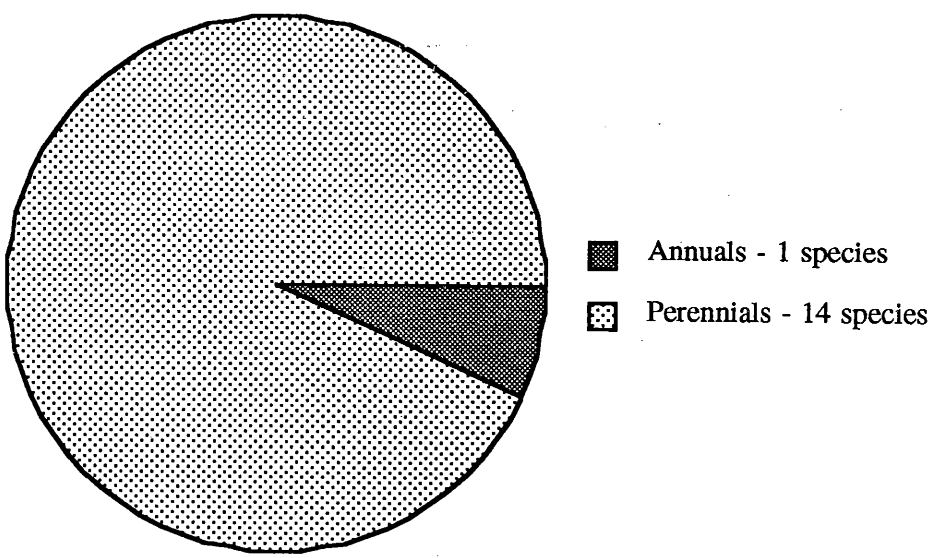


Figure 9. Percentage of species with annual and perennial longevity for (a) C_3 and (b) C_4 grasses.

11–14 months; spring = 8 months) and, thus, statistical comparisons of these seasonal data were not possible. Nevertheless, it is worth noting general trends in seasonality to assess, in a qualitative sense, when during the year germination and seedling establishment may be most pronounced under field conditions for the different habitats and plant life forms.

In general, when data were pooled across habitat type, species richness of the seed banks was similar for summer (80 species), fall (77 species) and winter (72 species), but was somewhat lower in spring (53 species) (Table 4). By comparison, seedling density peaked in the fall (4239/m^2), was similar in summer (2198/m^2) and winter (2749/m^2), and lowest in the spring (1404/m^2). Again, the lower species richness and seedling density in the spring samples may simply reflect a shorter observation period than the other sampling periods.

For all three habitat types, both species richness and seedling density tended to peak in the fall (Figs. 10a, 11a). This was also the case for annuals (Figs. 10b, 11b) and forbs (Figs. 10c, 11c), but less so for perennials (Figs. 10b, 11b) and graminoids (Figs. 10c, 11c). Few woody species were present in the seed banks and, therefore, little seasonal variation in this group was apparent (Figs. 10c, 11c). Within the grasses, there appeared to be distinct seasonal differences among habitat types, annuals vs. perennials and C_3 vs. C_4 species (Figs. 12, 13). For example, the seedling density of annual grasses peaked in fall (Fig. 13b) and this coincided with the peak in C_3 abundance (Fig. 13c). By comparison, the C_4 grasses, which were mostly perennial, were least abundant in the fall samples (Figs. 12b, c; 13b, c).

For individual species, several different seasonal patterns in abundance were evident (Fig. 14; Table 6). Some species showed single peaks in abundance at certain times of the year, but the timing of this peak varied from species to species. For example, *Sphenopholis interrupta* and *Bifora americana* had their greatest seedling density in the fall, whereas *Nama jamaicense* was most prevalent in the winter soil samples. Some species, such as *Bothriochloa ischaemum*, were present in all samples except one (fall for this

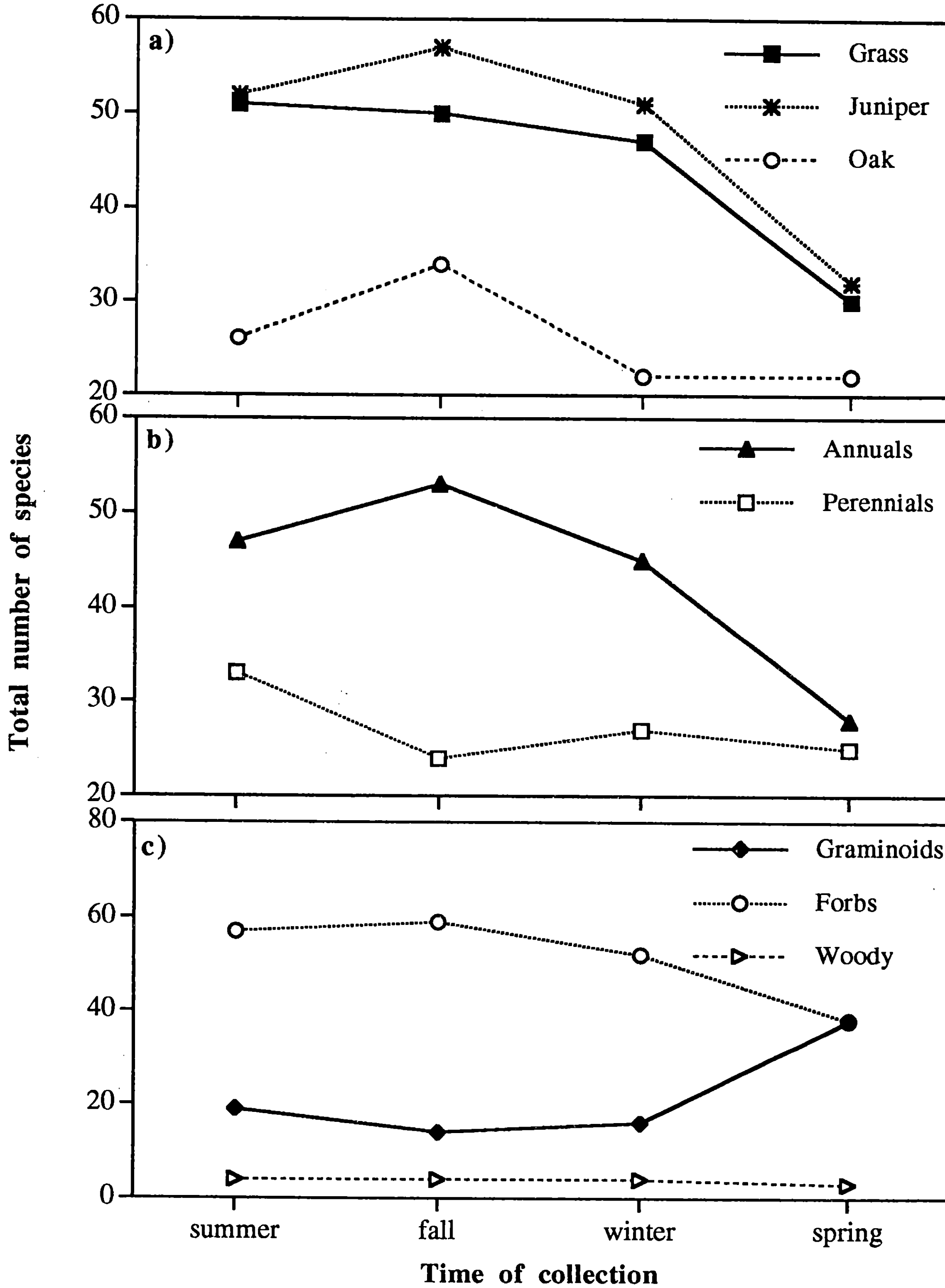


Figure 10. Total number of species for (a) grass, juniper, and oak habitats (n = 6), (b) annuals and perennials (n = 18), and (c) graminoid, forb, and woody plant forms (n = 18) in different seasonal sampling dates.

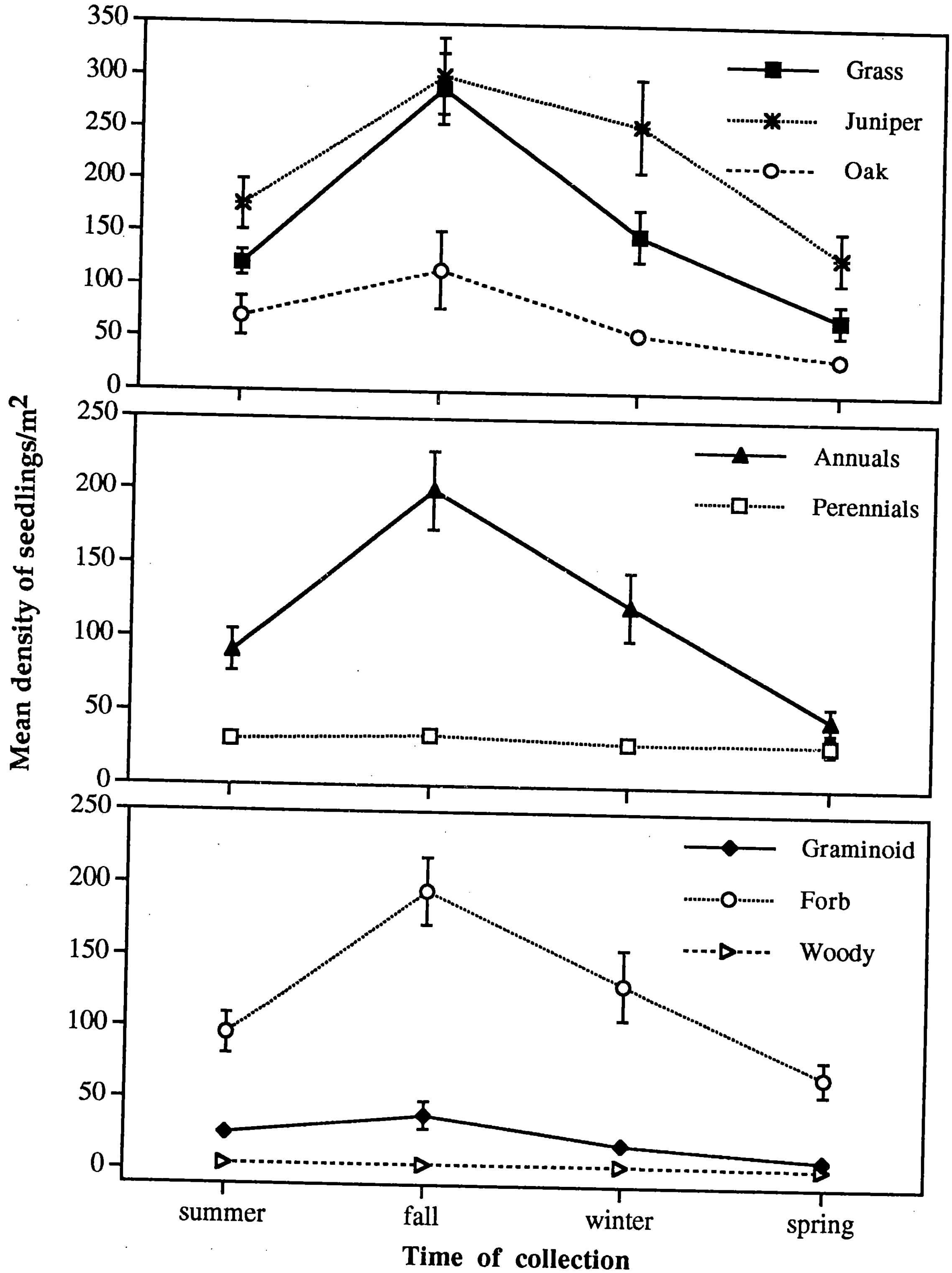


Figure 11. Mean (±SE) seedling density/m ^{2} for (a) grass, juniper, and oak habitats (n = 6), (b) annuals and perennials (n = 18), and (c) graminoid, forb, and woody plant forms (n = 18) for different seasonal sampling dates.

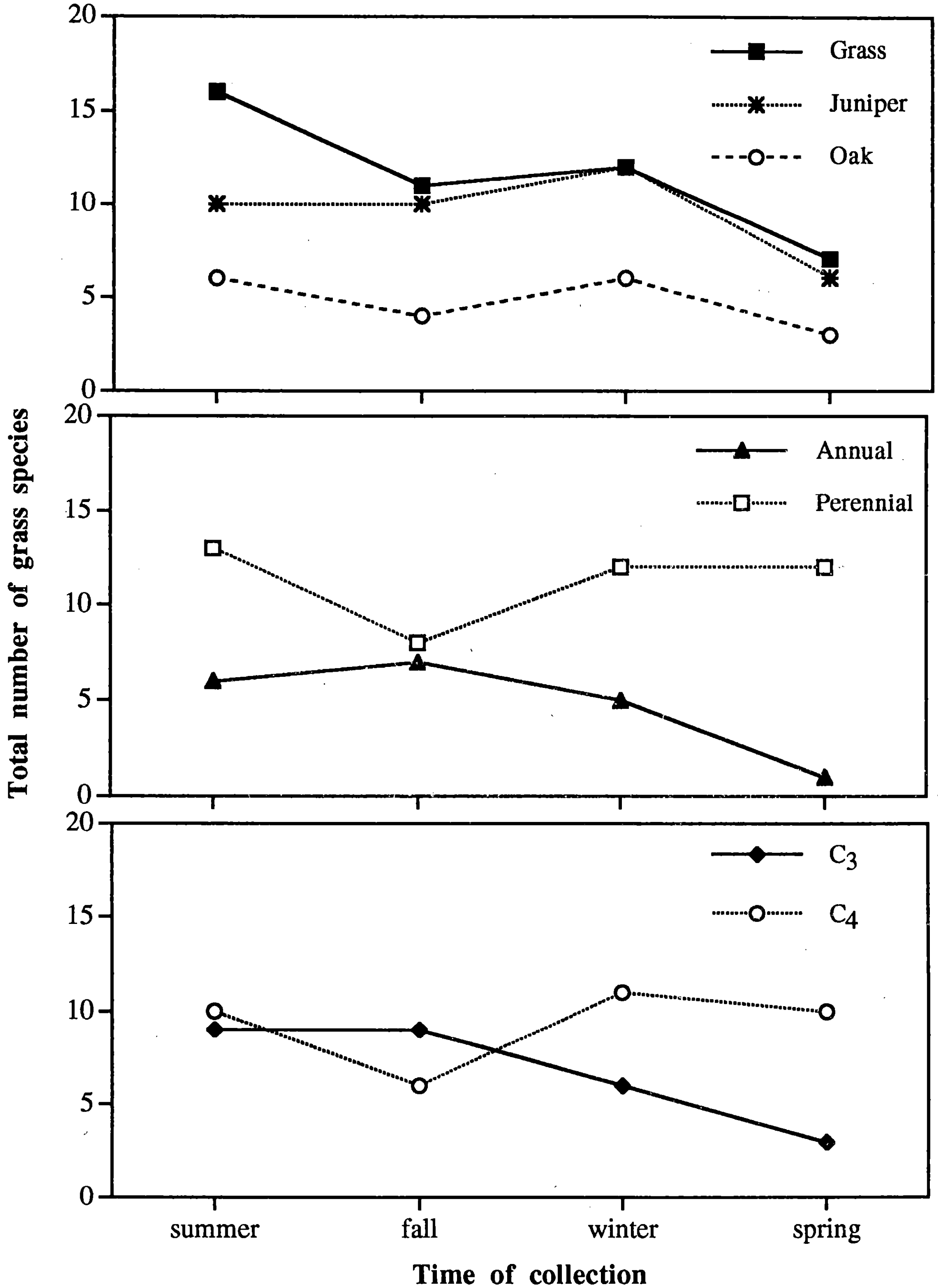


Figure 12. Total number of grass species for (a) grass, juniper, and oak habitats (n = 6), (b) annuals and perennials (n = 18), and (c) C_3 and C_4 grasses (n = 18) for different seasonal sampling dates.

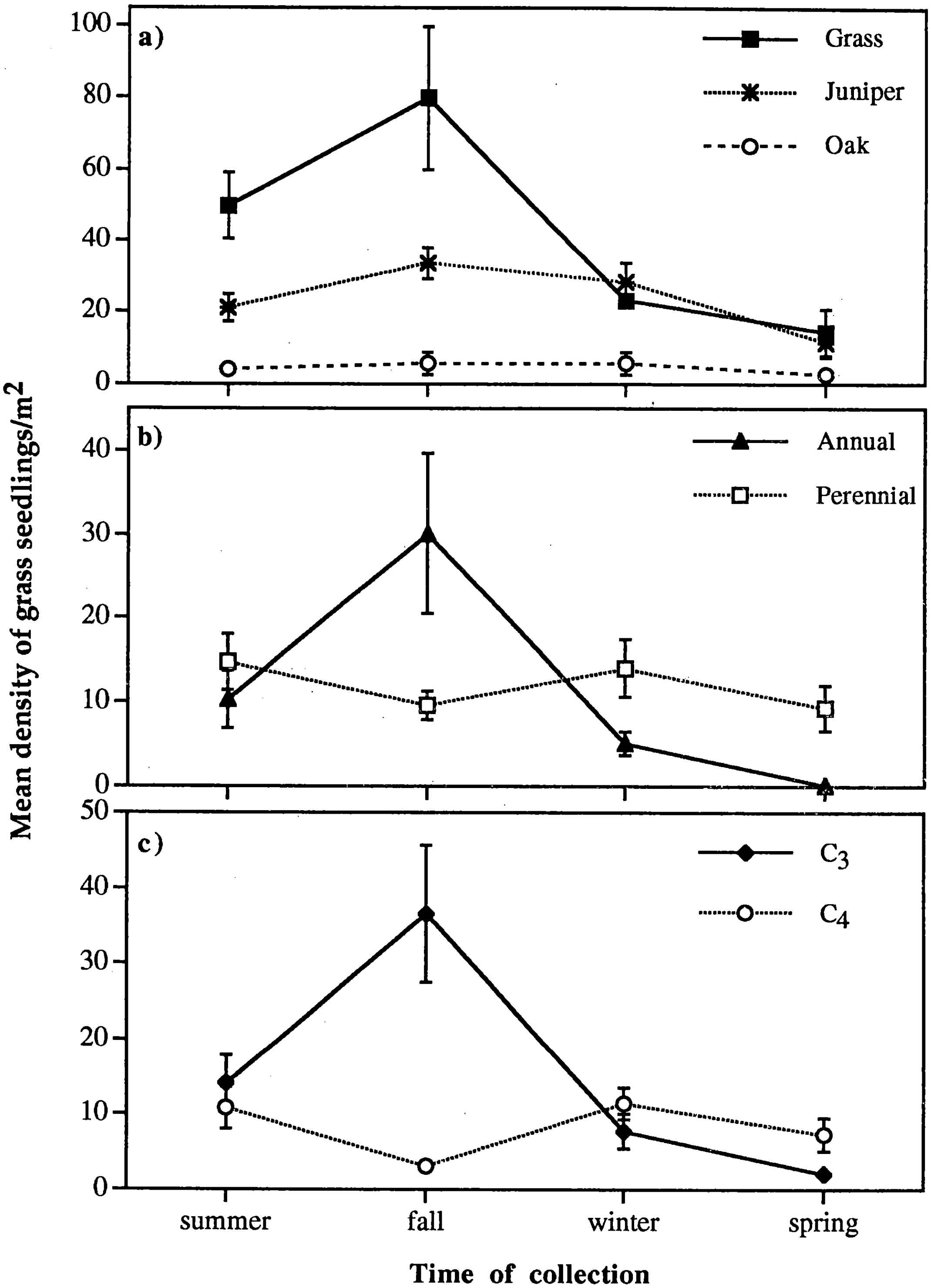


Figure 13. Mean (±SE) grass seedling density/m^2 for (a) grass, juniper, and oak habitats (n = 6), (b) annuals and perennials (n = 18), and (c) C_3 and C_4 grasses (n = 18) for different seasonal sampling dates.

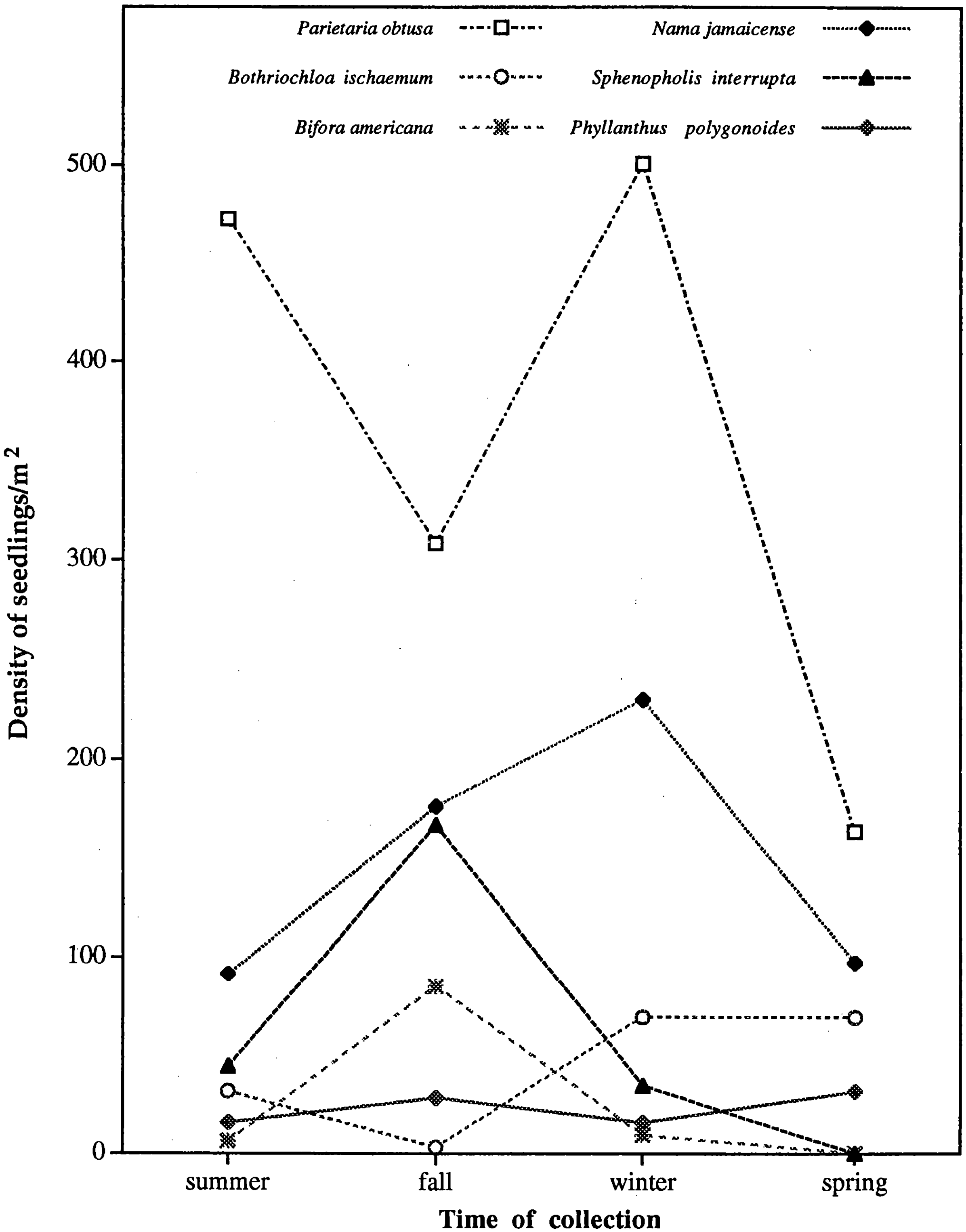


Figure 14. Density of various species of plants differing in seasonal peaks of seedling emergence found in the soil seed banks in all habitats for all sampling dates.

Table 6. Absolute and relative seedling density/m^2 of common seed bank species (>1%) for summer, fall, winter, and spring soil samples.

Summer Season			Fall Season			Winter Season			Spring Season		
Species	Abs. density	Rel. (%)	Species	Abs. density	Rel. (%)	Species	Abs. density	Rel. (%)	Species	Abs. density	Rel. (%)
Parietaria obtusa	472.4	21.5	*Oxalis dillenii*	1102.3	26.0	*Oxalis dillenii*	541.7	19.7	*Oxalis dillenii*	296.0	21.1
Oxalis dillenii	340.1	15.5	*Parietaria obtusa*	308.6	7.3	*Parietaria obtusa*	500.8	18.2	*Bouchetia erecta*	163.8	11.7
Limnodea arkansana	107.1	4.9	*Limnodea arkansana*	252.0	5.9	*Nama jamaicense*	229.9	8.4	*Parietaria obtusa*	163.8	11.7
Nama jamaicense	91.3	4.2	*Nama jamaicense*	176.4	4.2	*Croton monanthogynus*	198.4	7.2	*Nama jamaicense*	97.6	6.9
Croton monanthogynus	81.9	3.7	*Sphenopholis interrupta*	166.9	3.9	*Calyptocarpus vialis*	129.1	4.7	*Cyperus* spp.	78.7	5.6
Nassella leucotricha	78.7	3.6	*Bouchetia erecta*	157.5	3.7	*Bothriochloa ischaemum*	69.3	2.5	*Bothriochloa ischaemum*	69.3	4.9
Bouchetia erecta	78.7	3.6	*Verbena halei*	151.2	3.6	*Verbena halei*	69.3	2.5	*Sida abutifolia*	63.0	4.5
Cyperus spp.	63.0	2.9	*Rudbeckia hirta*	126.0	3.0	*Cyperus* spp.	56.7	2.1	*Verbena halei*	59.8	4.3
Chaerophyllum tainturieri	53.5	2.4	*Croton monanthogynus*	110.2	2.6	*Bouchetia erecta*	50.4	1.8	*Calyptocarpus vialis*	34.6	2.5
Medicago minima	53.5	2.4	*Cyperus* spp.	103.9	2.5	*Plantago virginica*	47.2	1.7	*Phyllanthus polygonoides*	31.5	2.2
Sida abutifolia	53.5	2.4	*Nassella leucotricha*	103.9	2.5	*Limnodea arkansana*	47.2	1.7	*Medicago minima*	31.5	2.2
Sphenopholis interrupta	44.1	2.0	*Krigia cespitosa*	88.2	2.1	*Medicago minima*	44.1	1.6	*Vicia* sp.	28.3	2.0
Bouteloua rigidiseta	40.9	1.9	*Bifora americana*	85.0	2.0	*Eragrostis intermedia*	40.9	1.5	*Argythamnia humilis*	22.0	1.6
Eragrostis intermedia	34.6	1.6	*Calyptocarpus vialis*	78.7	1.9	*Nassella leucotricha*	40.9	1.5	*Nassella leucotricha*	18.9	1.3
Bothriochloa ischaemum	31.5	1.4	*Medicago minima*	75.6	1.8	*Opuntia engelmannii*	37.8	1.4	*Panicum hallii*	18.9	1.3
Arenaria benthamii	28.3	1.3	*Triodanis perfoliata*	66.1	1.6	*Evax* sp.	34.6	1.3	*Panicum oligosanthes*	44.1	3.1
Verbena canescens	28.3	1.3	*Arenaria benthamii*	63.0	1.5	*Sphenopholis interrupta*	34.6	1.3	*Galium* spp.	15.7	1.1
Hordeum pusillum	25.2	1.1	*Hordeum pusillum*	63.0	1.5	*Galium* spp.	34.6	1.3	*Solanum ptycanthum*	15.7	1.1
Panicum hallii	25.2	1.1	*Oxalis drummondii*	56.7	1.3	*Stachys crenata*	31.5	1.1			
Verbena halei	25.2	1.1	*Nuttallanthus texana*	56.7	1.3	*Nuttallanthus texana*	31.5	1.1			
Calyptocarpus vialis	22.0	1.0	*Stachys crenata*	50.4	1.2	*Rudbeckia hirta*	28.3	1.0			
Rudbeckia hirta	22.0	1.0	*Ambrosia psilostachya*	47.2	1.1	*Triodanis perfoliata*	28.3	1.0			
Euphorbia sp.	22.0	1.0	*Plantago virginica*	47.2	1.1	*Sida abutifolia*	28.3	1.0			
Vicia sp.	22.0	1.0				*Oxalis drummondi*	28.3	1.0			
Sporobolus compositus	22.0	1.0				*Digitaria cognata*	28.3	1.0			
Total (25 spp.)	**1867.0**	**84.9**	**Total (23 spp.)**	**3536.7**	**83.4**	**Total (25 spp.)**	**2412.0**	**87.7**	**Total (18 spp.)**	**1253.2**	**89.2**
Others (55 spp.)	**331.3**	**15.1**	**Others (44 spp.)**	**702.4**	**16.6**	**Others (47 spp.)**	**382.4**	**12.3**	**Others (35 spp.)**	**151.4**	**10.8**
TOTAL (80 spp.)	**2198.3**	**100**	**TOTAL (77 spp.)**	**4239.1**	**100**	**TOTAL (72 spp.)**	**2794.4**	**100**	**TOTAL (53 spp.)**	**1404.6**	**100**

species), while others (e.g., *Parietaria obtusa*) showed a distinctly bimodal pattern in abundance. Still other species (e.g., *Phyllanthus polygonoides*) showed little seasonal variation in abundance.

Habitat Comparisons: Species Richness and Seedling Densities

The seed banks of the three habitats (grassland, juniper and oak woodlands) showed significant variation in species richness and seedling densities. When data were combined over the four sampling periods, a total of 79, 87, and 64 species were recorded within the grassland, juniper, and oak habitats, respectively (Table 7; Fig. 15a). There were more annual species than perennial species in all habitats sampled, but these differences were greatest in the grassland and juniper habitats (Fig. 15b). Forbs were the most common growth form in all habitats and they were followed in importance by graminoids and woody species (Fig. 15c). Grassland habitats had the greatest number of graminoid species present (24) and juniper habitats had the greatest number of forb species present (67). Oak habitats had fewer graminoid and forb species (13 and 55 species, respectively) than either grassland or juniper habitats, but more woody species were present here (7) than in juniper habitats (5). No woody plant species were found in grassland habitats.

The number of annual graminoid species was higher in grasslands (8) than in either juniper (3) or oak (2) habitats (Fig. 16a). However, the number of perennial graminoid species was generally similar among habitat types. Annual forb species richness was highest in juniper habitats (49) and least in oak habitats (32). The number of perennial forb species was similar among all habitats. The number of both C_3 and C_4 grass species declined from grassland to juniper to oak habitats, but there were consistently more C_4 than C_3 graminoid species in all habitats. (Fig. 17b).

Mean seedling densities were not statistically different ($P > 0.05$) between juniper (535 seedlings/m^2) and grassland (319 seedlings/m^2) habitats and densities in both of these habitats were significantly greater than in the oak woodlands (169 seedlings/m^2)

Table 7. Number of seedlings/m^2 and relative density of each species found in seed banks sampled in grass, juniper, and oak habitats. Percent relative density was calculated by dividing the density for a species by the total density of all species and multiplying by 100.

Species	Grass	Juniper	Oak	Total	Rel. Density (%)
AGAVACEAE					
Nolina lindheimeriana	0.00	0.00	1.95	**0.65**	**0.03**
AMARANTHACEAE					
Amaranthus sp.	0.00	0.00	1.95	**0.65**	**0.03**
AMARYLLIDACEAE					
Habranthus texanus	0.00	1.95	0.00	**0.65**	**0.03**
ANACARDIACEAE					
Rhus lanceolata	0.00	0.00	1.95	**0.65**	**0.03**
APIACEAE					
Bifora americana	23.45	33.22	5.86	**20.85**	**0.95**
Chaerophyllum tainturieri	5.86	33.22	9.77	**16.29**	**0.74**
ASTERACEAE					
Ambrosia psilostachya	13.68	9.77	15.63	**13.03**	**0.59**
Baccharis neglecta	0.00	3.91	0.00	**1.30**	**0.06**
Calyptocarpus vialis	7.82	117.27	39.09	**54.73**	**2.50**
Centaurea melitensis	1.95	0.00	0.00	**0.65**	**0.03**
Cirsium texanum	0.00	9.77	15.63	**8.47**	**0.39**
Conzya sp.	3.91	3.91	0.00	**2.61**	**0.12**
Evax sp.	27.36	1.95	0.00	**9.77**	**0.45**
Gamochaeta purpurea	3.91	1.95	1.95	**2.61**	**0.12**
Gnaphalium sp.	1.95	0.00	0.00	**0.65**	**0.03**
Gutierrezia texana	15.63	5.86	0.00	**7.17**	**0.33**
Krigia cespitosa	41.04	15.63	1.95	**19.54**	**0.89**
Pyrrhopappus paucifloris	0.00	7.82	1.95	**3.26**	**0.15**
Rudbeckia hirta	66.45	39.09	5.86	**37.14**	**1.69**
Sonchus asper	0.00	5.86	0.00	**1.95**	**0.09**
Taraxacum officinale	3.91	1.95	0.00	**1.95**	**0.09**
Wedelia texana	1.95	7.82	3.91	**4.56**	**0.21**
BERBERIDACEAE					
Berberis trifoliolata	0.00	0.00	1.95	**0.65**	**0.03**
BRASSICACEAE					
Arabis petiolaris	0.00	1.95	0.00	**0.65**	**0.03**
Draba cuneifolia	0.00	7.82	0.00	**2.61**	**0.12**
Lepidium virginicum	13.68	17.59	0.00	**10.42**	**0.48**
Lesquerella sp.	0.00	1.95	0.00	**0.65**	**0.03**
CACTACEAE					
Opuntia engelmannii	0.00	7.82	31.27	**13.03**	**0.59**
CAMPANULACEAE					
Triodanis perfoliata	41.04	17.59	1.95	**20.20**	**0.92**
CARYOPHYLLACEAE					
Arenaria benthamii	33.22	31.27	0.00	**21.50**	**0.98**

Table 7. Continued

Species	**Grass**	**Juniper**	**Oak**	**Total**	**Rel. Density (%)**
Arenaria sp.	3.91	0.00	0.00	**1.30**	**0.06**
Cerastium sp.	1.95	1.95	0.00	**1.30**	**0.06**
Silene antirrhina	5.86	9.77	0.00	**5.21**	**0.24**
COMMELINACEAE					
Commelina erecta	0.00	11.73	1.95	**4.56**	**0.21**
CONVOLVULACEAE					
Dichondra carolinensis	11.73	7.82	7.82	**9.12**	**0.42**
Evolvulus sericeus	5.86	1.95	0.00	**2.61**	**0.12**
CYPERACEAE					
Cyperus spp.	23.45	66.45	97.72	**62.54**	**2.85**
EBENACEAE					
Diospyros texana	0.00	1.95	0.00	**0.65**	**0.03**
EUPHORBIACEAE					
Acalypha lindheimeri	0.00	3.91	3.91	**2.61**	**0.12**
Argythamnia humilis	11.73	29.32	0.00	**13.68**	**0.62**
Croton fruticulosus	0.00	1.95	3.91	**1.95**	**0.09**
Croton monanthogynus	158.31	87.95	1.95	**82.74**	**3.78**
Euphorbia cyathophora	0.00	3.91	0.00	**1.30**	**0.06**
Euphorbia dentata	0.00	5.86	1.95	**2.61**	**0.12**
Euphorbia sp.	0.00	21.50	5.86	**9.12**	**0.42**
Phyllanthus polygoniodes	13.68	41.04	1.95	**18.89**	**0.86**
Tragia sp.	0.00	1.95	0.00	**0.65**	**0.03**
FABACEAE					
Astragalus sp.	21.50	3.91	0.00	**8.47**	**0.39**
Desmanthus virgatus	1.95	0.00	0.00	**0.65**	**0.03**
Indigofera miniata	1.95	0.00	0.00	**0.65**	**0.03**
Medicago minima	86.00	31.27	9.77	**42.35**	**1.93**
Medicago polymorpha	0.00	1.95	1.95	**1.30**	**0.06**
Pediomelum rhombifolium	1.95	0.00	0.00	**0.65**	**0.03**
Senna lindheimeriana	1.95	1.95	0.00	**1.30**	**0.06**
Vicia sp.	19.54	39.09	1.95	**20.20**	**0.92**
GERANIACEAE					
Geranium carolinianum	0.00	3.91	0.00	**1.30**	**0.06**
HYDROPHYLLACEAE					
Nama jamaicense	138.77	201.31	29.32	**123.13**	**5.62**
Phacelia congesta	0.00	1.95	0.00	**0.65**	**0.03**
IRIDACEAE					
Sisyrinchium sp.	9.77	11.73	0.00	**7.17**	**0.33**
LAMIACEAE					
Brazoria scutellarioides	3.91	11.73	0.00	**5.21**	**0.24**
Hedeoma acinoides	1.95	3.91	3.91	**3.26**	**0.15**
Stachys crenata	17.59	25.41	23.45	**22.15**	**1.01**

Table 7. Continued

Species	**Grass**	**Juniper**	**Oak**	**Total**	**Rel. Density (%)**
LILIACEAE					
Nothoscordum bivalve	1.95	1.95	3.91	**2.61**	**0.12**
LINACEAE					
Linum hudsonioides	11.73	1.95	0.00	**4.56**	**0.21**
MALVACEAE					
Abutilon fruticosum	0.00	0.00	9.77	**3.26**	**0.15**
Sida abutilifolia	82.09	19.54	5.86	**35.83**	**1.64**
MOLLUGINACEAE					
Mollugo verticillata	3.91	0.00	1.95	**1.95**	**0.09**
ONAGRACEAE					
Gaura sp.	5.86	0.00	0.00	**1.95**	**0.09**
Oenothera triloba	0.00	5.86	0.00	**1.95**	**0.09**
OXALIDACEAE					
Oxalis dillenii	322.48	848.23	244.31	**471.67**	**21.53**
Oxalis drummondii	15.63	35.18	13.68	**21.50**	**0.98**
PLANTAGINACEAE					
Plantago patagonica	1.95	0.00	0.00	**0.65**	**0.03**
Plantago virginica	43.00	17.59	1.95	**20.85**	**0.95**
POACEAE					
Aristida oligantha	1.95	0.00	0.00	**0.65**	**0.03**
Bothriochloa ischaemum	60.59	35.18	11.73	**35.83**	**1.64**
Bouteloua rigidiseta	27.36	1.95	0.00	**9.77**	**0.45**
Bromus catharticus	0.00	0.00	7.82	**2.61**	**0.12**
Bromus japonicus	19.54	3.91	0.00	**7.82**	**0.36**
Buchloe dactyloides	7.82	1.95	0.00	**3.26**	**0.15**
Cenchrus spinifex	3.91	0.00	0.00	**1.30**	**0.06**
Cynodon dactylon	5.86	0.00	9.77	**5.21**	**0.24**
Desmazeria rigida	3.91	1.95	0.00	**1.95**	**0.09**
Digitaria cognata	5.86	17.59	1.95	**8.47**	**0.39**
Elymus virginicus	0.00	0.00	1.95	**0.65**	**0.03**
Eragrostis intermedia	21.50	35.18	7.82	**21.50**	**0.98**
Hilaria belangeri	1.95	0.00	0.00	**0.65**	**0.03**
Hordeum pusillum	58.63	0.00	0.00	**19.54**	**0.89**
Limnodea arkansana	162.22	87.95	1.95	**84.04**	**3.84**
Nassella leucotricha	33.22	89.90	27.36	**50.16**	**2.29**
Panicum hallii	31.27	5.86	1.95	**13.03**	**0.59**
Panicum oligosanthes	1.95	25.41	0.00	**9.12**	**0.42**
Paspalum dilatatum	1.95	0.00	1.95	**1.30**	**0.06**
Paspalum setaceum	25.41	7.82	0.00	**11.08**	**0.51**
Setaria scheelei	0.00	1.95	0.00	**0.65**	**0.03**
Sphenopholis interrupta	132.90	17.59	1.95	**50.82**	**2.32**
Sporobolus compositus	3.91	15.63	1.95	**7.17**	**0.33**
Vulpia octoflora	7.82	0.00	0.00	**2.61**	**0.12**

Table 7. Continued

Species	Grass	Juniper	Oak	Total	Rel. Density (%)
POLEMONIACEAE					
Gilia incisa	1.95	11.73	1.95	**5.21**	**0.24**
PORTULACACEAE					
Portulaca pilosa	3.91	0.00	1.95	**1.95**	**0.09**
RUBIACEAE					
Galium aparine	0.00	0.00	1.95	**0.65**	**0.03**
Galium spp.	3.91	44.95	1.95	**16.94**	**0.77**
Richardia tricocca	3.91	0.00	3.91	**2.61**	**0.12**
SCROPHULARIACEAE					
Mecardonia procumbens	41.04	13.68	0.00	**18.24**	**0.83**
Nuttallanthus texanus	1.95	13.68	0.00	**5.21**	**0.24**
Verbascum thapsus	0.00	0.00	1.95	**0.65**	**0.03**
SMILACACEAE					
Smilax bona-nox	0.00	1.95	3.91	**1.95**	**0.09**
SOLANACEAE					
Bouchetia erecta	111.40	166.13	1.95	**93.16**	**4.25**
Physalis cinerascens	0.00	0.00	7.82	**2.61**	**0.12**
Solanum ptycanthum	0.00	1.95	9.77	**3.91**	**0.18**
ULMACEAE					
Celtis laevigata	0.00	0.00	1.95	**0.65**	**0.03**
URTICACEAE					
Parietaria obtusa	56.68	570.70	269.71	**299.03**	**13.65**
VERBENACEAE					
Glandularia bipinnatifida	0.00	1.95	0.00	**0.65**	**0.03**
Glandularia pumila	3.91	7.82	0.00	**3.91**	**0.18**
Verbena canescens	19.54	27.36	0.00	**15.64**	**0.71**
Verbena halei	138.77	46.91	3.91	**63.19**	**2.88**
VITACEAE					
Vitis sp.	0.00	0.00	1.95	**0.65**	**0.03**
Total	**16977.15**	**23286.80**	**7342.63**	**2190.96**	**100.00**
Mean/sample	**2829.53**	**3881.13**	**1223.77**	**365.16**	
Total species (116 species)	**79**	**87**	**64**	**116**	

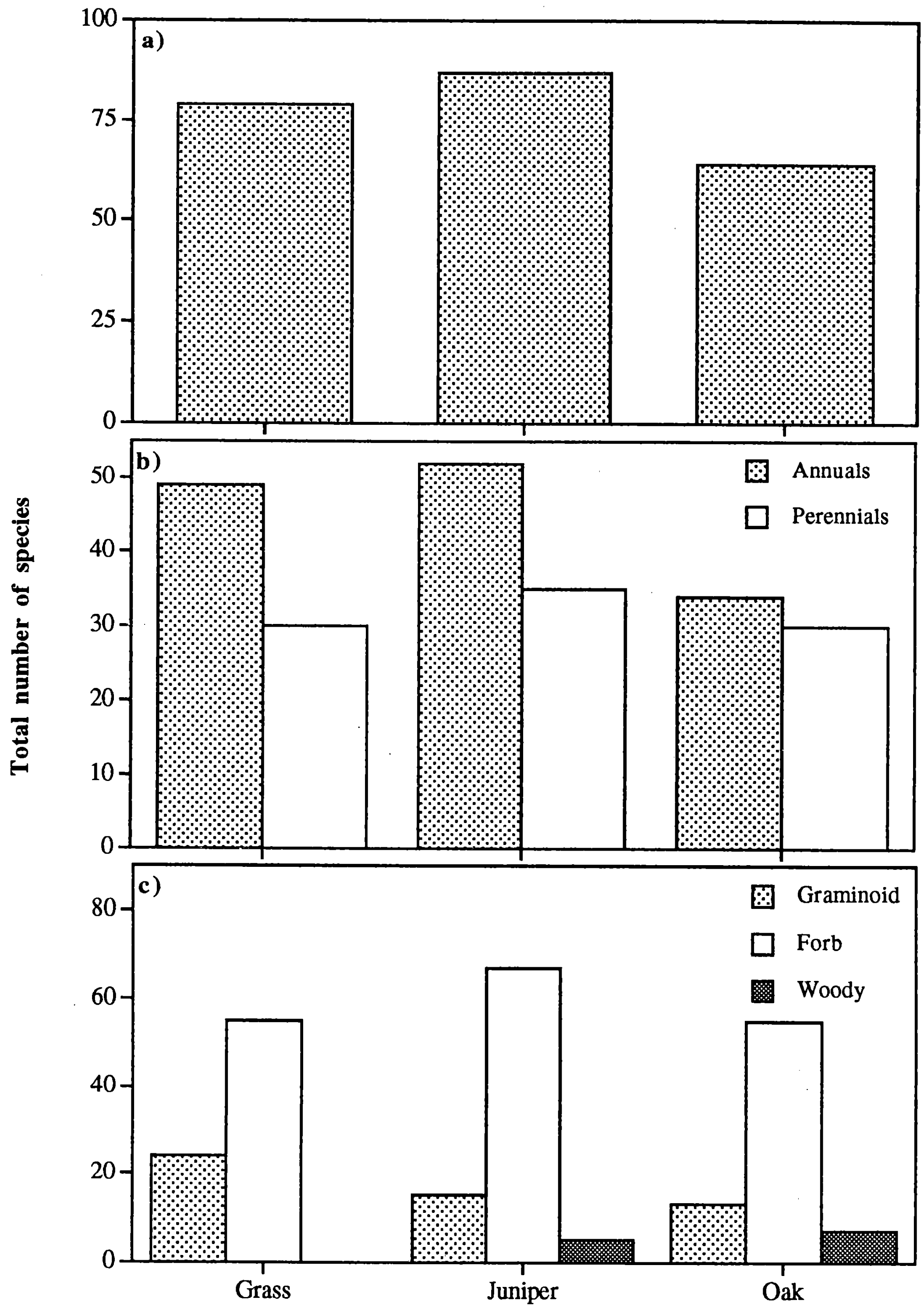


Figure 15. Number (n = 6) of (a) total, (b) annual and perennial, (c) and graminoid, forb, and woody species found in seed banks in grass, juniper, and oak habitats. Habitat data pooled for all seasons.

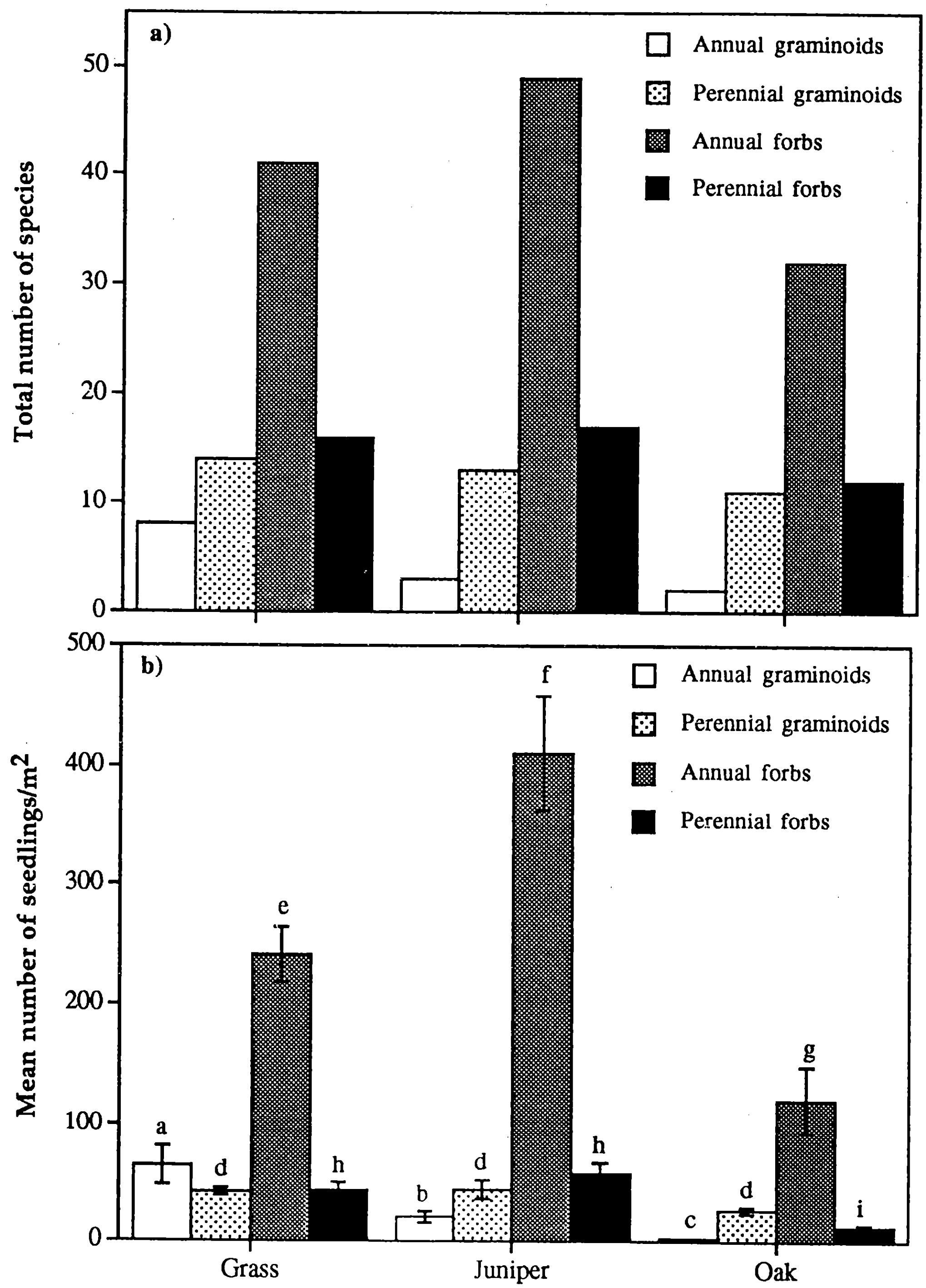


Figure 16. Total number (n = 6) of annual and perennial graminoid and forb (a) species and (b) mean number of individual seedlings/m^2 found in seed banks in grass, juniper, and oak habitats. Habitat data pooled for all seasons. Means (± 1 SE) within growth form with the same letter were not significantly different at $P > 0.05$ as determined by ANOVA.

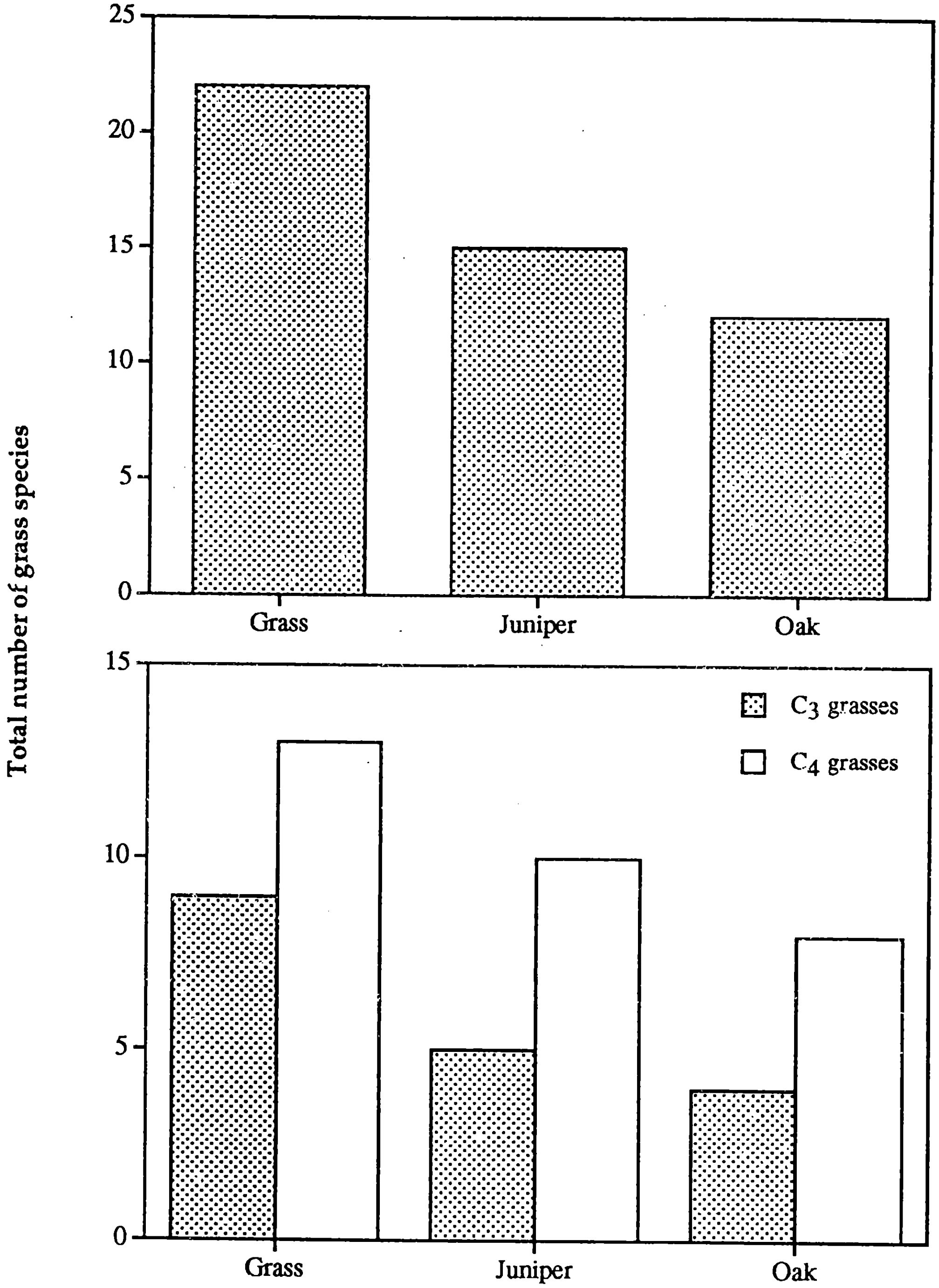


Figure 17. Total number (n = 6) of (a) grass species and (b) C_3 and C_4 grass species found in seed banks in grass, juniper, and oak habitats. Habitat data pooled for all seasons.

(Fig. 18a). The mean number of annual and perennial seedlings was similar between grassland and juniper habitats, but both were significantly higher ($P < 0.0001$ and $P < 0.0004$) than oak habitats (Fig. 18b). Seedling densities of graminoid and forb seedlings differed significantly ($P < 0.003$ and $P < 0.0001$) among habitats (Fig. 18c). Grassland habitats displayed the highest graminoid seedling density (106 seedlings/m^2) and juniper habitats had the greatest number of forb seedlings present (468 seedlings/m^2). Oak habitats had fewer graminoid and forb seedlings (28 and 133 seedlings/m^2, respectively) than either grass or juniper habitats. However, woody plant seedling density was significantly higher in oak woodlands than in juniper habitats ($P < 0.001$).

Annual graminoid seedling density decreased ($P < 0.0001$) from grassland to juniper, and oak habitats (65, 20, and 2 seedlings/m^2, respectively), yet the densities of perennial graminoid seedlings were similar among all habitats (Fig. 16b). The density of annual forbs was highest in juniper (411 seedlings/m^2), intermediate in grasslands (241 seedlings/m^2) and lowest in oak habitats (122 seedlings/m^2). The seedling density of perennial forbs were similar between grassland (43 seedlings/m^2) and juniper habitats (58 seedlings/m^2) and lowest in the oak habitats (12 seedlings/m^2). In contrast to the patterns for species richness, the density of C_3 grass seedlings was significantly higher than that of C_4 grasses in all habitats, and no differences were found between grassland and juniper habitats with respect to C_3 and C_4 seedling densities (Fig. 19b).

Habitat Comparisons: Community Dominance and Diversity

Seed banks of all habitats were dominated by the annual forb, *Oxalis dillenii*. Another annual forb, *Parietaria obtusa* , also dominated the juniper and oak habitats (Table 8). Other common species found in the soil seed banks of all habitats included 2 annual forbs (*Nama jamaicense* and *Medicago minima*). *Limnodea arkansana* was the dominant grass in the grassy habitats were as *Nassella leucotricha* was the dominant grass in the juniper and oak habitats (Table 9).

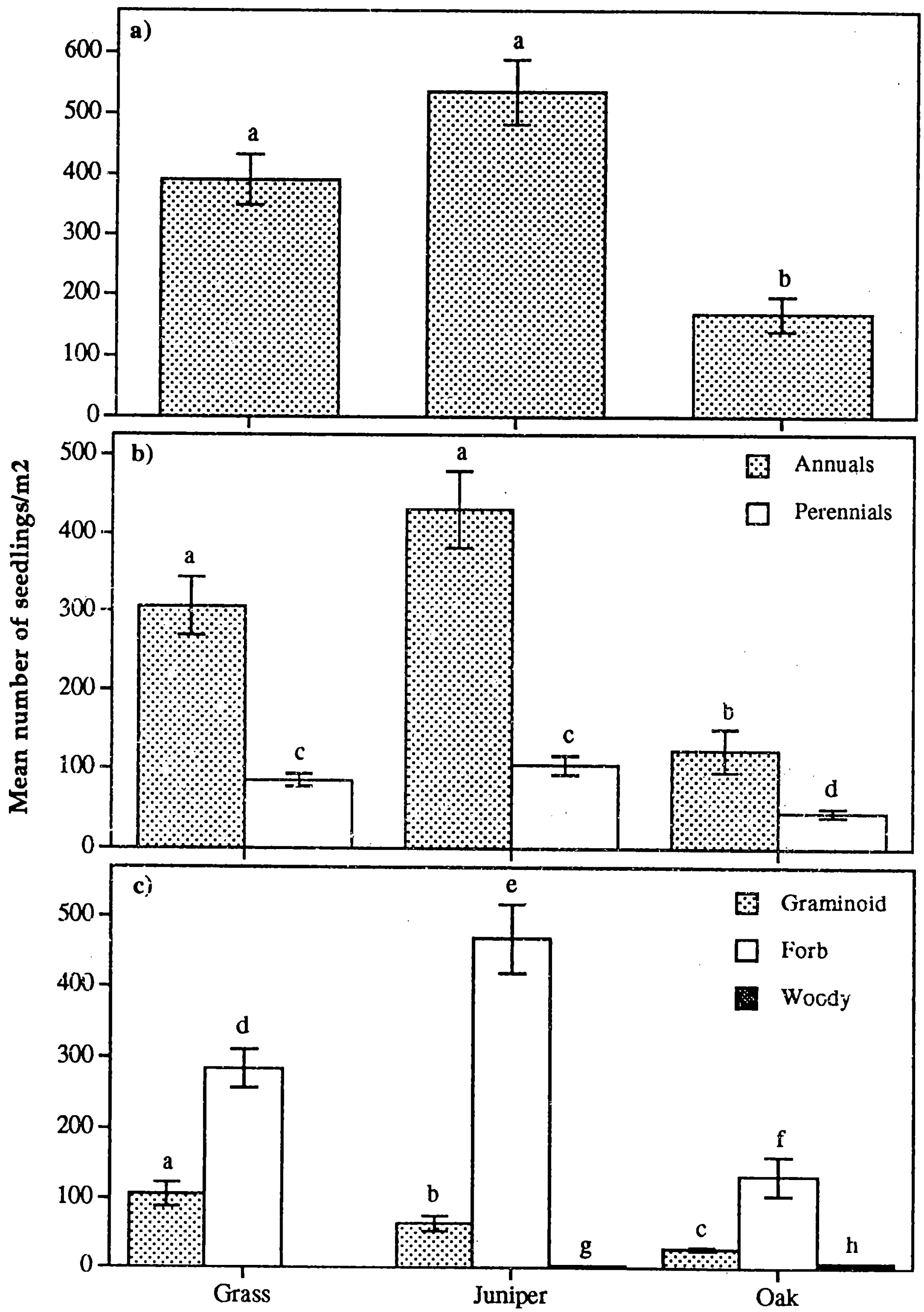


Figure 18. Mean number (n = 6) of (a) individual, (b) annual and perennial, and (c) graminiod, forb, and woody seedlings/m^2 found in seed banks in grass, juniper, and oak habitats. Habitat data pooled for all seasons. Means (± 1 SE) within growth form with the same letter were not significantly different at $P > 0.05$ as determined by Tukey.

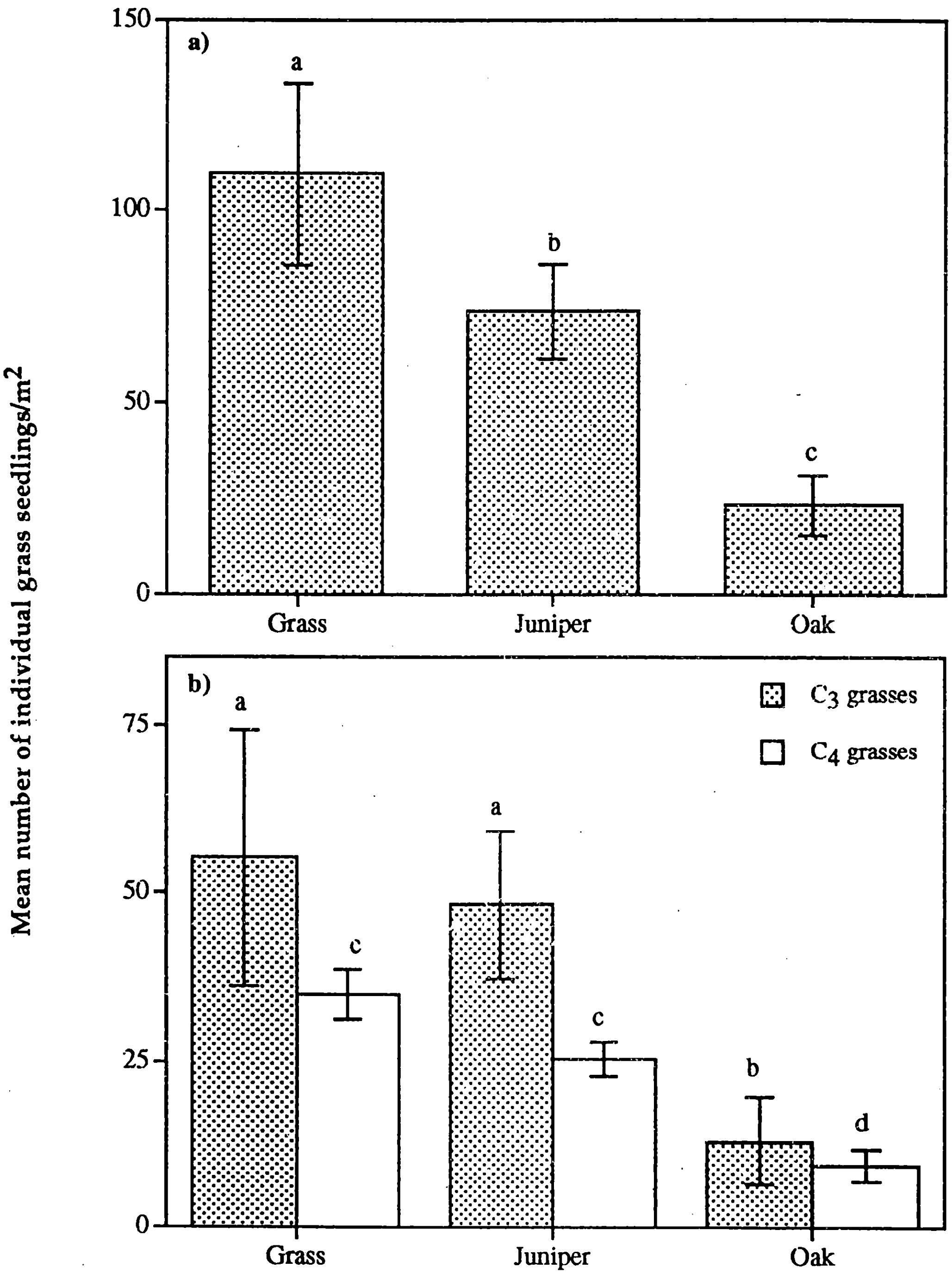


Figure 19. Mean number (n = 6) of (a) grass seedlings (b) and C_3 and C_4 grass seedlings/m^2 found in seed banks in grass, juniper, and oak habitats. Habitat data pooled for all seasons. Means ($\pm$1 SE) among habitats with the same letter were not significantly different at $P > 0.05$ as determined by Tukey.

Table 8. Absolute and relative seedling densities/m^2 of common seed bank species (>1%) found in the soil seed banks of grass, juniper and oak habitats. Relative density was calculated for each habitat by dividing each species density by the sum of the absolute density of all species.

Grassy Habitats			Juniper Habitats			Oak Habitats		
Species	Absolute density	Relative density %	Species	Absolute density	Relative density %	Species	Absolute density	Relative density %
*Oxalis dillenii**	322.5	13.8	*Oxalis dillenii**	848.2	26.4	*Parietaria obtusa**	269.7	26.6
Limnodea arkansana	162.2	6.9	*Parietaria obtusa* *	570.7	17.8	*Oxalis dillenii**	244.3	24.1
Croton monanthogynus	158.3	6.7	*Nama jamaicense**	201.3	6.3	*Cyperus* spp.*	97.7	9.6
*Nama jamaicense**	138.8	5.9	*Bouchetia erecta*	166.1	5.2	*Calyptocarpus vialis*	39.1	3.9
Verbena halei	138.8	5.9	*Calyptocarpus vialis*	117.3	3.7	*Opuntia engelmannii*	31.3	3.1
Sphenopholis interrupta	132.9	5.7	*Nassella leucotricha* *	89.9	2.8	*Nama jamaicense**	29.3	2.9
Bouchetia erecta	111.4	4.7	*Croton monanthogynus*	88.0	2.7	*Nassella leucotricha**	27.4	2.7
*Medicago minima**	86.0	3.7	*Limnodea arkansana*	87.9	2.7	*Stachys crenata*	23.5	2.3
Sida abutifolia	82.1	3.5	*Cyperus* spp.*	66.5	2.1	*Ambrosia psilostachya*	15.6	1.5
Rudbeckia hirta	66.5	2.8	*Verbena halei*	46.9	1.5	*Cirsium texanum*	15.6	1.5
*Bothriochloa ischaemum**	60.6	2.6	*Galium* spp.	45.0	1.4	*Oxalis drummondii*	13.7	1.3
Hordeum pusillum	58.6	2.5	*Phyllanthus polygonoides*	41.0	1.3	*Bothriochloa ischaemum**	11.7	1.2
*Parietaria obtusa**	56.7	2.4	*Rudbeckia hirta*	39.1	1.2	*Chaerophyllum tainturieri*	9.8	1.0
Plantago virginica	43.0	1.8	*Vicia* sp.	39.1	1.2	*Medicago minima**	9.8	1.0
Krigia cespitosa	41.0	1.7	*Oxalis drummondi*	35.2	1.1	*Abutilon fruticosum*	9.8	1.0
Triodanis perfoliata	41.0	1.7	*Bothriochloa ischaemum**	35.2	1.1	*Cynodon dactylon*	9.8	1.0
Nuttallanthus texana	41.0	1.7	*Eragrostis intermedia*	33.2	1.0	*Solanum ptycanthum*	9.8	1.0
Arenaria benthamii	33.2	1.4	*Bifora americana*	33.2	1.0			
*Nassella leucotricha**	33.2	1.4	*Chaerophyllum tainturieri*	33.2	1.0			
Panicum hallii	31.3	1.3	*Arenaria benthamii*	33.2	1.0			
Evax sp.	27.4	1.2	*Medicago minima**	31.3	1.0			
Bouteloua rigidiseta	27.4	1.2						
Paspalum setaceum	25.4	1.1						
Bifora americana	23.5	1.0						
Cyperus spp.*	23.5	1.0						
Total (25 species)	**1966.2**	**83.8**	**Total (21 species)**	**2681.4**	**83.5**	**Total (17 species)**	**867.7**	**85.5**
Others (54 species)	**379.2**	**16.2**	**Others (66 species)**	**531.7**	**16.5**	**Others (47 species)**	**146.7**	**14.5**
TOTAL (79 species)	**2345.4**	**100**	**TOTAL (87 species)**	**3213.1**	**100.0**	**TOTAL (64 species)**	**1014.4**	**100.0**

* Signifies species found in all habitats

Table 9. Absolute and relative seedling densities/m^2 of all grass species found in the soil seed banks of grass, juniper, and oak habitats. Relative density was calculated for each habitat by dividing each species density by the sum of the absolute density of all species.

Grassy Habitats			**Juniper Habitats**			**Oak Habitats**		
Grass species	**Absolute Density**	**Relative Density**	*Grass species*	**Absolute Density**	**Relative Density**	*Grass species*	**Absolute Density**	**Relative Density**
*Limnodea arkansana**	162.2	26.2	*Nassella leucotricha**	89.9	25.7	*Nassella leuchotricha**	27.4	35.0
*Sphenopholis interrupta**	132.9	21.5	*Limnodea arkansana**	88.0	25.1	*Bothriochloa ischaemum**	11.7	15.0
*Bothriochloa ischaemum**	60.6	9.8	*Bothriochloa ischaemum**	35.2	10.1	*Cynodon dactylon*	9.8	12.5
Hordeum pusillum	58.6	9.5	*Eragrostis intermedia**	35.2	10.0	*Eragrostis intermedia**	7.8	10.0
*Nassella leucotricha**	33.2	5.4	*Panicum oligosanthes*	25.4	7.3	*Bromus catharticus*	7.8	10.0
Panicum hallii	31.3	5.0	*Sphenopholis interrupta**	17.6	5.0	*Limnodea arkansana**	2.0	2.5
Bouteloua rigidiseta	27.4	4.4	*Digitaria cognata**	17.6	5.0	*Sphenopholis interrupta**	2.0	2.5
Paspalum setaceum	25.4	4.1	*Sporobolus compositus**	15.6	4.5	*Panicum hallii**	2.0	2.5
*Eragrostis intermedia**	21.5	3.5	*Paspalum setaceum*	7.8	2.2	*Digitaria cognata**	2.0	2.5
Bromus japonicus	19.5	3.2	*Panicum hallii**	5.9	1.7	*Sporobolus compositus**	2.0	2.5
Vulpia octoflora	7.8	1.3	*Bromus japonicus*	3.9	1.1	*Paspalum dilatatum*	2.0	2.5
Buchloe dactyloides	7.8	1.3	*Bouteloua rigidiseta*	2.0	0.6	*Elymus canadensis*	1.9	2.5
*Digitaria cognata**	5.9	0.9	*Buchloe dactyloides*	2.0	0.6			
Cynodon dactylon	5.9	0.9	*Desmazeria rigidum*	2.0	0.6			
*Sporobolus compositus**	3.9	0.6	*Setaria scheelei*	2.0	0.6			
Desmazeria rigidum	3.9	0.6						
Cenchrus spinifex	3.9	0.6						
Panicum oligosanthes	2.0	0.3						
Paspalum dilatatum	2.0	0.3						
Aristida oligantha	2.0	0.3						
Hilaria belangeri	2.0	0.3						
Total seedlings/m^2	**619.5**	**100.0**	**Total seedlings/m^2**	**349.8**	**100.0**	**Total seedlings/m^2**	**78.1**	**100.0**
Total species	**21**	**100.0**	**Total species**	**15**	**100.0**	**Total species**	**12**	**100.0**

*Signifies species found in all habitats

Overall, there were 18 plant species that were common to the soil seed banks of the three habitats, and these species were therefore considered habitat generalists (Table 10). In contrast to the above species, there were a number of species that were found in only one habitat type and may, therefore, be good indicators of the seed banks for these habitats. Four species were unique to the grassland habitat: three of these species were grasses (*Hordeum pusillum*, *Vulpia octoflora*, and *Cenchrus spinifex*) and one was an annual forb (*Arenaria* sp.). Six species were unique to the juniper habitats (all forbs) and 3 species were found only in the oak habitats (2 forbs and one grass, *Bromus catharticus).*

Heterogeneity, or evenness of the seed bank species differed significantly ($P < 0.0488$) among habitat (Fig. 20). Oak habitats had the greatest concentration of dominance of seed bank species and grassland sites were the most diverse. Seed banks from juniper habitats were similar to both grassland and oak . Analysis of seed bank species diversity (Shannon-Wiener Diversity Index (H')) indicated that species diversity also varied significantly among habitat ($P< .0002$) (Fig. 21). Grassland habitats exhibited the most diverse seed bank ($H' = 3.0$), juniper habitats were intermediate in diversity ($H' = 2.7$) and oak habitats displayed the least diverse seed banks ($H' = 2.3$). Interestingly, even though juniper habitats had a greater number of species and seedlings present, the majority of the seedlings were from a relatively few species and therefore the habitat had a lower diversity than grasslands.

Table 10. Number of seedlings/m^2 of each species found in the soil seed banks on more than one occasion in grass, juniper, and oak habitats.

Species	Grass	Juniper	Oak	Total
Habitat Generalist				
Oxalis dillenii	389.7	1025.1	295.3	**1710.1**
Parietaria obtusa	68.5	689.7	326.0	**1084.2**
Nama jamaicense	167.7	243.3	35.4	**446.4**
Verbena halei	167.7	56.7	4.7	**229.1**
Cyperus spp.	28.3	80.3	118.1	**226.7**
Calyptocarpus vialis	9.4	141.7	47.2	**198.3**
Nassella leucotricha	40.2	108.7	33.1	**182.0**
Medicago minima	103.9	37.8	11.8	**153.5**
Rudbeckia hirta	80.3	47.2	7.1	**134.6**
Sida abutifolia	99.2	23.6	7.1	**129.9**
Bothriochloa ischaemum	73.2	42.5	14.2	**129.9**
Stachys crenata	21.3	30.7	28.3	**80.3**
Oxalis drummondii	18.9	42.5	16.5	**77.9**
Eragrostis intermedia	26.0	42.5	9.4	**77.9**
Bifora americana	28.3	40.2	7.1	**75.6**
Chaerophyllum tainturieri	7.1	40.2	11.8	**59.1**
Ambrosia psilostachya	16.5	11.8	18.9	**47.2**
Dichondra carolinensis	14.2	9.4	9.4	**33.0**
Predominantly Grassland				
Hordeum pusillum	70.9			**70.9**
Vulpia octiflora	9.4			**9.4**
Arenaria sp.	4.7			**4.7**
Cenchrus spinifex	4.7			**4.7**
Predominantly Juniper				
Draba cuneifolia		9.4		**9.4**
Sonchus asper		7.1		**7.1**
Oenothera triloba		7.1		**7.1**
Geranium carolinianum		4.7		**4.7**
Euphorbia cyanthophora		4.7		**4.7**
Baccharis neglecta		4.7		**4.7**
Predominantly Oak				
Abutilon fruticosum			11.8	**11.8**
Bromus cartharticus			9.4	**9.4**
Physalis cinerascens			9.4	**9.4**

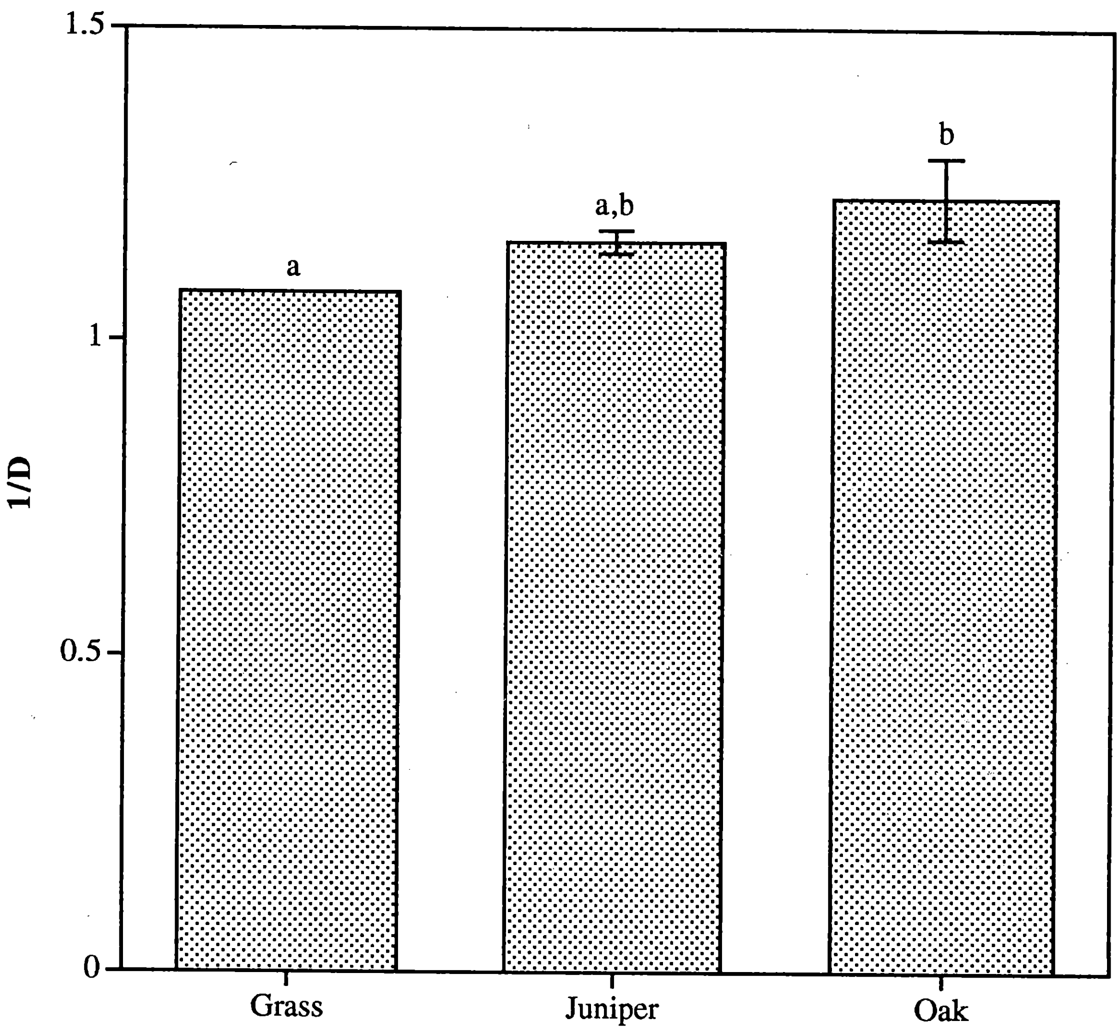


Figure 20. Simpson's Index values (1/D) for soil seed bank concentration of dominance or heterogeneity of grass, juniper, and oak habitats. Values represent the mean (±1 SE) for each habitat (n = 6). Habitat means with the same letter were not significantly different at $P > 0.05$ as determined by Tukey.

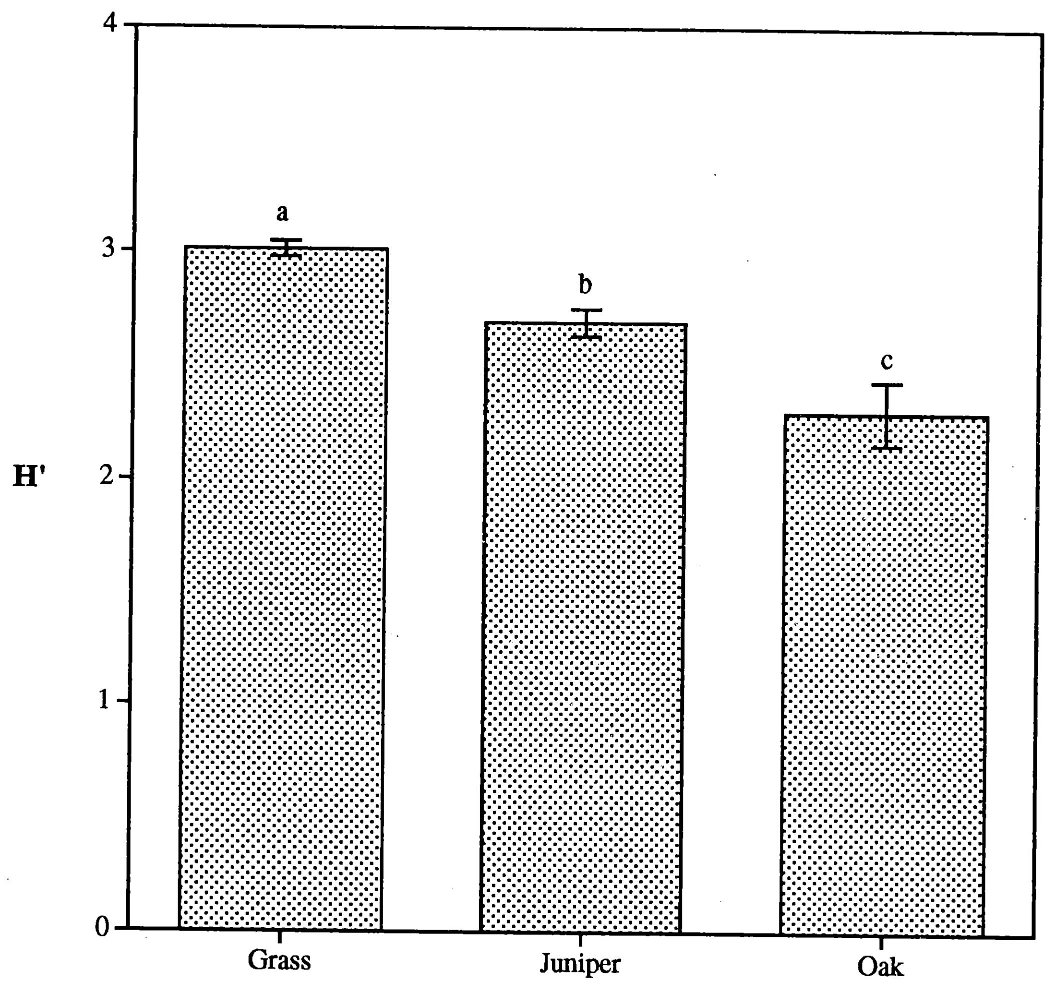


Figure 21. Shannon-Wiener's Index values (H') for soil seed bank diversity of grass, juniper, and oak habitats. Values represent the mean (±1 SE) for each habitat (n = 6). Habitat means with the same letter were not significantly different at P > 0.05 as determined by Tukey.

DISCUSSION

Habitat Differences

In this study three different habitats (grassland, recently-established junipers, and long-established live oak clusters) in a savanna ecosystem were compared to determine the effects of different above-ground plant communities on the soil seed bank. Because the seed bank is derived from both present and past seed production of the above-ground plant community, it was hypothesized that different types and compositions of soil seed banks would be found in grassland and woody habitats. The results from this study indicate that long-established grassland and oak sites were indeed, very dissimilar in seed bank species composition. Overall, grasslands displayed a greater species richness and diversity than the oak sites. These results are in agreement with findings from other studies that have shown that the seed banks of woodlands and forests generally have fewer species and lower seed densities than grassland seed banks (Roberts 1984).

It was also hypothesized that the seed banks beneath recently-established Ashe juniper trees would differ from those in adjacent grasslands. My findings support this hypothesis. For example, although seed banks of recently-established juniper habitats were similar in species richness and seedling density to those of grassland habitats, the species composition of these two habitats differed considerably (i.e., juniper sites were composed of more forbs and fewer grass seedlings than grassland habitats). The greater forb seedling density and diversity of seed banks in juniper habitats may reflect increased numbers of pioneer species that occur during early succession of woody species

(Thompson 1992). These pioneer species peak early in succession but then decrease with time. Interestingly, a decline of grass species and grass seedlings occurred in the juniper habitats. Thus, these results indicate that grassland seed banks can be altered after a very short time following juniper invasion. Similar results have been found in seed banks studies examining successional gradients. Donelan and Thompson (1980) found a decline in the density of seeds during succession of a grazed pasture to a mature oak woodland in England. Bakker et al. (1996) reported in their study in dry alvar grasslands that after 80 years of abandonment and shrub encroachment that the majority of grassland species had disappeared from the seed bank.

Growth Form Composition of the Seed Bank

Mean seedling density was 2643 seedling/m ^{2} with a range from 1224 seedlings/m ^{2} in the oak sites to 2830 seedling/m^2 in the grassland sites. These results are similar to some previous studies (2252–4320 seedlings/m^2 (Kunican and Smeins 1992), 2834–4320 seedlings/m^2 (O'Conner and Pickett 1992) and 2932–3304 seedlings/m^2 (Milberg 1995)) in other savanna ecosystems. However, a large range in seedling density occurs in semi-arid and temperate ecosystems (lows of 783–1144 seedling/m ^{2} (Coffin and Lauenroth 1989) with highs of 7988 seedlings/m^2 (Lunt 1997)). Roberts (1984) cites other published accounts with a greater range of seedling densities from approximately 400/m^2 in a permanent grassland to 70,000/m ^{2} in a grassland that was formerly cultivated.

Annual plants accounted for the majority of the species and seedlings present in the soil seed banks. Moveover, most of the annuals were forbs, and when perennials were found they were mostly graminoids. In this study 6 annual species constituted over 50% of the seedling density and included 5 dicot species (*Oxalis dillenii, Parietaria obtusa, Nama jamaicense*, *Bouchetia erecta* , and *Croton monanthogynus*) and 1 monocot species (*Limnodea arkansanas*). Similar to previous studies in a grassland-to-woodland successional series, dominant woody plant species had the fewest seedlings in the seed bank (Donelan and Thompson 1980). A high density of annual seeds is commonly observed in the seed banks of grazed grassland and savanna ecosystems (Kunican and Smeins 1992; Lunt 1997). This abundance of annuals has been attributed to the long seed longevity that is often characteristic of annuals and species of disturbed habitats (i.e, ruderal species; Grime 1979). Since our study site has a history of chronic disturbance (i.e., overgrazing) the overall abundance of ruderal species in the seed bank is not unexpected.

Seasonal Changes in Seed Bank Composition

Temporal or seasonal factors can have a major effect on the composition of the soil seed bank (Thompson and Grime 1979; Coffin and Lauenroth 1989). Thompson and Grime (1979) found seasonal variation in the seed bank composition and density and recognized four types of seed banks from various vegetation types in northern England. Types I and II were transient seed banks with fewer, larger seeds. Type I consisted mostly of grasses that were present in the summer and would germinate in the fall. These seed banks function to exploit trampled areas or seasonal damage from drought. Type II were present in winter, but were dormant and germinated in spring when conditions were more favorable. Types III and IV were persistent seed banks with many small seeds. Types III and IV seeds either germinated in the fall or formed a seed bank. Type III differed from type IV since most of seeds germinated after dispersal, while the majority of seeds of type IV persisted in the soil. However, rigid distinctions between these groups were not clear, and they may be found to be similar.

This study found seasonal differences in patterns seed bank composition, yet the patterns were similar between species richness and seedling density. In general, the fall soil samples exhibited the greatest abundance of species and seedlings, summer and winter samples were intermediate, and spring had the lowest abundance values. Low numbers of species and seedling densities of spring habitats may be due to a shorter observation time of samples. Annual grass and forb species richness and seedling densities peaked in fall, but perennial plants showed little seasonal variation.

The majority of the seed species that peaked in fall were also present during all the other seasons which suggests that the seeds are persistent in the soil. Seed bank Types III and IV are persistent and closely resemble the majority of my seed banks. Longevity of these seeds can be attributed to their small size and high quantities that tend to bury more easily and have lower amounts of predation (Thompson 1992). Five annual forbs dominated the soil seed bank at the Freeman Ranch. *Oxalis dillenii* and *Bouchetia erecta* have seed banks which resembled Type III, and *Parietaria obtusa*, *Croton monanthogynus*, and *Nama jamaicense* have seed banks that resemble Type IV.

Some species found in our study peaked in the fall and had fewer seeds present during other seasons. This may be a result of freshly dispersed seeds that have germinated soon after their release. This type of strategy is used by seed banks Types I and III and functions to exploit seasonal disturbance caused by drought and livestock grazing (Thompson and Grime 1979). Type I seed banks are transient and are usually composed of perennial grasses and a few annual grasses. Type I seed banks are further characterized by larger seeds with elongated structure, often with awns present. Three annual grass species found in my study, *Limnodea arkansana*, *Sphenopholis interrupta*, and *Hordeum pusillum*, fit the morphological characteristics for the Type I seed bank.

It was observed that the germinating and flowering patterns of the study plants in the glasshouse were similar to what occurred in the field despite differences in availability of water and nutrients. This suggests that physiological processes such as enforced seed dormancy may be playing an important role in the dynamics of the seed bank. Seed dormancy can be difficult to quantify but is important to consider in a seed bank study.

Grazing and Restoration Implications

Grazing is a disturbance that can alter the vegetation of an area and is known to affect the seed bank (Kunican and Smeins 1992; O'Conner and Pickett 1992; Bakker et al. 1996). O'Connor and Pickett (1992) found differences in the vegetation from different grazing regimes (long-lived perennial grasses with light grazing vs. short-lived perennial grasses and forbs with heavy grazing) and found that plant species that form small seed banks could be eliminated with grazing. In other studies, grazing was found to alter the species composition of the seed bank by reducing the number of perennial grass species and increasing the number of annual dicot species (Kunican and Smeins 1992). My study found the soil seed bank of Freeman Ranch to be dominated by annual dicots, which is likely a result of long-term, overgrazing of this site.

Although this particular study did not address grazing *per se*, it is important to understand how this widespread practice can potentially affect the grassland vegetation on the Edwards Plateau. Low representation of mid- and tallgrasses is common in other areas on the plateau where long-term overgrazing has occurred (Kunican and Smeins 1992). These highly palatable grasses are usually replaced with less palatable, more grazing tolerant, shortgrass species when heavy or prolonged grazing occurs. It is important to note that in my study the species present in the soil seed bank are not representative of the grasses on the range. Also, many late successional mid-tall grass species (e.g., *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Bouteloua curtipendula*) are absent from soil seed bank and are either not present in the current vegetation or are poorly represented.

A failure of perennial grasses to form persistent seed banks is well documented (Champness and Morris 1948) and is of great importance for rangeland management and restoration (Thompson and Grime 1979). Many species of grasses have transient seeds that either germinate directly after dispersal or die. Some species have no dormancy and this is important since failure to form a seed bank gives an advantage to species that do form persistent seed banks, especially after disturbance. Many studies (Johnson and Anderson 1986; Graham and Hutchings 1988; Kunican and Smeins 1992; O'Conner and Pickett 1992; Milberg 1995; Bakker et al. 1996), including this one, have found that in grassland ecosystems the above-ground and below-ground floras are often very different, which is usually attributed to differences in seed longevity.

Natural regeneration or restoration of the plant community following disturbance is largely dependent on local and outside seed dispersal and the soil seed bank. The soil seed bank can only be successful at revegetating the land if the desirable species are present and unwanted species are not present or are uncommon (van der Valk and Pederson 1989). Many important late-successional grasses are present on the Freeman Ranch, but are very limited in numbers. Although most of these grass species are absent from the seed bank, many of these species can reproduce vegetatively. Vegetative regeneration can be slow and unpredictable, but if the grazing pressure is not reduced many species could become locally lost from the vegetation and the soil seed bank. Based on my results, many of the species that are needed for restoration are either absent from the seed bank or are present in very low numbers. Thus, if the long-term goal is to restore the vegetation to pre-settlement conditions, it appears that grazing pressure would have to be reduced. Moreover, my results suggest that juniper removal alone will not be sufficient to restore these grasslands to climax conditions.

Appendix A: Species List

Plant species found in seed banks with longevity, growth habit, and voucher number.

Family/Species	**Plant Longevity**	**Growth Habit**	**Voucher Number**
AGAVACEAE			
Nolina lindheimeriana (Scheele) Wats.	Perennial	Herb	120
AMARANTHACEAE			
Amaranthus sp.	Annual	Herb	17
AMARYLLIDACEAE			
Habranthus texanus (Herb.) Steud.	Perennial	Herb	110
ANACARDIACEAE			
Rhus lanceolata (Gray) Britt.	Perennial	Shrub/Tree	91
APIACEAE			
Bifora americana (DC.) Benth. & Hook.	Annual	Herb	53
Chaerophyllum tainturieri Hook.	Annual	Herb	48
ASTERACEAE			
Ambrosia psilostachya DC.	Perennial	Herb	102
Baccharis neglecta Britt.	Perennial	Shrub	105
Calyptocarpus vialis Less.	Annual	Herb	33
Centaurea melitensis L.	Annual	Herb	93
Cirsium texanum Buckl.	Annual	Herb	70
Conzya sp.	Annual	Herb	83
Evax sp.	Annual	Herb	63
Gamochaeta purpurea (L.) Cabrera	Annual	Herb	82
Gnaphalium sp.	Annual	Herb	80
Gutierrezia texana (DC.) T. & G.	Annual	Herb	23
Krigia cespitosa (Rafin.-Schm.) Chambers (sy = *K. oppositifolia*)	Annual	Herb	59
Pyrrhopappus paucifloris (Don) A.P. de Candolle (sy = *P. multicaulis*)	Annual	Herb	86
Rudbeckia hirta L.	Annual	Herb	38
Sonchus asper (L.) Hill	Annual	Herb	65
Taraxacum officinale Wiggers	Annual	Herb	94
Wedelia texana (Gray) Turner	Perennial	Herb	25
BERBERIDACEAE			
Berberis trifoliolata Moric.	Perennial	Shrub	112
BRASSICACEAE			
Arabis petiolaris Gray	Annual	Herb	79
Draba cuneifolia Nutt.ex Torr. & Gray	Annual	Herb	58
Lepidium virginicum L.	Annual	Herb	77
Lesquerella sp.	Annual	Herb	89
CACTACEAE			
Opuntia engelmannii Salm-Reiff.-Dyck var. *engelmannii*	Perennial	Shrub	66
CAMPANULACEAE			
Triodanis perfoliata (L.) Neiuw.	Annual	Herb	60

Appendix A: Species List continued

Family/Species	**Plant Longevity**	**Growth Habit**	**Voucher Number**
CARYOPHYLLACEAE			
Arenaria benthamii Fenzl.	Annual	Herb	62
Arenaria sp.	Annual	Herb	90
Cerastium sp.	Annual	Herb	88
Silene antirrhina L.	Annual	Herb	87
COMMELINACEAE			
Commelina erecta L.	Perennial	Herb	4
CONVOLVULACEAE			
Dichondra carolinensis Michx.	Perennial	Herb	14
Evolvulus sericeus Sw.	Perennial	Herb	109
CYPERACEAE			
Cyperus spp.	Perennial	Herb	18
EBENACEAE			
Diospyros texana Scheele	Perennial	Shrub/Tree	111
EUPHORBIACEAE			
Acalypha lindheimeri Muell.	Perennial	Herb	22
Argythamnia humilis (Engelm. & Gray) Muell.	Annual	Herb	31
Croton fruticulosus Torr.	Perennial	Shrub/Tree	36
Croton monanthogynus Michx.	Annual	Herb	7
Euphorbia cyathophora Murr.	Annual	Herb	67
Euphorbia dentata Michx.	Annual	Herb	5
Euphorbia sp. (sy = *Chamaesyce* sp.)	Annual	Herb	2
Phyllanthus polygonoides	Perennial	Herb	15
Tragia sp.	Perennial	Herb	101
FABACEAE			
Astragalus sp.	Annual	Herb	32
Desmanthus virgatus (L.) Willd. var. *acuminatus* (Benth.) Isely	Perennial	Herb	84
Indigofera miniata Ort.	Perennial	Herb	113
Medicago minima (L.) L.	Annual	Herb	13
Medicago polymorpha L.	Annual	Herb	43
Pediomelum rhombifolium (T. & G.) Rydb. (Sy = *Psorlea rhombifolium*)	Perennial	Herb	99
Senna lindheimeriana (Scheele.) Irwin & Barne.	Perennial	Herb	98
Vicia sp.	Annual	Herb	46
GERANIACEAE			
Geranium carolinianum L.	Annual	Herb	44
HYDROPHYLLACEAE			
Nama jamaicense L.	Annual	Herb	35
Phacelia congesta Hook.	Annual	Herb	126
IRIDACEAE			
Sisyrinchium sp.	Perennial	Herb	75
LAMIACEAE			
Brazoria scutellarioides Engelm. & Gray	Annual	Herb	78

Appendix A: Species List continued

Family/Species	Plant Longevity	Growth Habit	Voucher Number
Hedeoma acinoides Scheele	Annual	Herb	72
Stachys crenata Raf.	Annual	Herb	42
LILIACEAE			
Nothoscordum bivalve (L.) Britt.	Perennial	Herb	97
LINACEAE			
Linum hudsonioides Planch.	Annual	Herb	81
MALVACEAE			
Abutilon fruticosum Guill. & Perr.	Annual	Herb	16
Sida abutifolia Miller	Perennial	Herb	6
MOLLUGINACEAE			
Mollugo verticillata L.	Annual	Herb	3
ONAGRACEAE			
Gaura sp.	Annual	Herb	85
Oenothera triloba Nutt.	Annual	Herb	52
OXALIDACEAE			
Oxalis dillennii Jacq.	Annual	Herb	24
Oxalis drummondii Gray	Annual	Herb	10
PLANTAGINACEAE			
Plantago patagonica Jacq.	Annual	Herb	128
Plantago virginica L.	Annual	Herb	54
POACEAE			
Aristida oligantha Michx.	Annual	Grass	21
Bothriochloa ischaemum L.	Perennial	Grass	29
Bouteloua rigidiseta (Steud.) Hitchc.	Perennial	Grass	20
Bromus catharticus Vahl (sy = *B. unioloides*)	Annual	Grass	71
Bromus japonicus L.	Annual	Grass	37
Buchloe dactyloides (Nutt.) Engelm.	Perennial	Grass	26
Cenchrus spinifex Cavanilles (sy = *C. incertus*)	Perennial	Grass	9
Cynodon dactylon (L.) Pers.	Perennial	Grass	92
Desmazeria rigida (L.) Tutin (sy = *Catapodium rigidum*)	Annual	Grass	50
Digitaria cognata (Schultz) Pilger	Perennial	Grass	28
Elymus virginicus L.	Perennial	Grass	69
Eragrostis intermedia Hitchc.	Perennial	Grass	11
Hilaria belangeri (Steud.) Nash.	Perennial	Grass	108
Hordeum pusillum Nutt.	Annual	Grass	55
Limnodea arkansana (Nutt.) Dewey	Annual	Grass	49
Nassella leucotricha (Trin. & Rupr.) Pohl (sy = *Stipa leucotricha*)	Perennial	Grass	68
Panicum hallii Vasey	Perennial	Grass	1
Panicum oligosanthes Schult. var. *oligosanthes* (sy = *Dichanthelium oligosanthes*)	Perennial	Grass	27
Paspalum dilatatum Poir	Perennial	Grass	127
Paspalum setaceum Michx.	Perennial	Grass	12
Setaria scheelei (Steud.) Hitchc.	Perennial	Grass	103

Appendix A: Species List continued

Family/Species	**Plant Longevity**	**Growth Habit**	**Voucher Number**
Sphenopholis interrupta (Buckl.) Lamson-Scribner (sy = *Trisetum interruptum*)	Annual	Grass	56
Sporobolus compositus (Poir.) Merrill. var. *clandestinus* (sy = *S. asper*)	Perennial	Grass	34
Vulpia octoflora (Walt.) Rydb.	Annual	Grass	74
POLEMONIACEAE			
Gilia incisa Benth.	Annual	Herb	76
PORTULACACEAE			
Portulaca pilosa L.	Annual	Herb	8
RUBIACEAE			
Galium aparine L.	Annual	Herb	64
Galium spp.	Perennial	Herb	57
Richardia tricocca (T. & G.) Standley (sy = *Diodia tricocca*)	Perennial	Herb	41
SCROPHULARACEAE			
Mecardonia procumbens (Miller) Small	Perennial	Herb	116
Nuttallanthus texanus (Scheele) Sutton *(sy = Linaria texanus)*	Annual	Herb	61
Verbascum thapsus L.	Annual	Herb	40
SMILACACEAE			
Smilax bona-nox L.	Perennial	Vine	95
SOLANACEAE			
Bouchetia erecta D.C.	Perennial	Herb	39
Physalis cinerascens (Dunal) Hitchc. var. *cinerascens* (sy = *P. viscosa*)	Perennial	Herb	115
Solanum ptycanthum Dunal	Annual	Herb	104
ULMACEAE			
Celtis laevigata Willd. var. *reticulata* (Torr.) Benson	Perennial	Shrub/Tree	125
URTICACEAE			
Parietaria obtusa Rydb.	Annual	Herb	30
VERBENACEAE			
Glandularia bipinnatifida (Nutt.) Nutt. var. *bipinatifida* (sy = *Verbena bipinnatifida*)	Perennial	Herb	114
Glandularia pumila (Rydb.) Umber (sy = *Verbena pumila*)	Annual	Herb	47
Verbena halei Small (sy = *V. officinalis*)	Annual	Herb	51
Verbena canescens H.B.K.	Annual	Herb	45
VITACEAE			
Vitis sp.	Perennial	Vine	73

Appendix B: Seasonal Raw Data

Absolute number of emerged seedlings found for each species for each season in the soil seed bank.

Species	Summer	Fall	Winter	Spring	Average	Rel. Density
AGAVACEAE						
Nolina lindheimeriana	0	1	0	0	**0.25**	**0.03**
AMARANTHACEAE						
Amaranthus sp.	0	1	0	0	**0.25**	**0.03**
AMARYLLIDACEAE						
Habranthus texanus	1	0	0	0	**0.25**	**0.03**
ANACARDIACEAE						
Rhus lanceolata	0	0	1	0	**0.25**	**0.03**
APIACEAE						
Bifora americana	2	27	3	0	**8.00**	**0.95**
Chaerophyllum tainturieri	17	8	0	0	**6.25**	**0.74**
ASTERACEAE						
Ambrosia psilostachya	0	15	4	1	**5.00**	**0.59**
Baccharis neglecta	1	1	0	0	**0.50**	**0.06**
Calyptocarpus vialis	7	25	41	11	**21.00**	**2.50**
Centaurea melitensis	0	0	1	0	**0.25**	**0.03**
Cirsium texanum	1	10	1	1	**3.25**	**0.39**
Conzya sp.	1	2	1	0	**1.00**	**0.12**
Evax sp.	1	3	11	0	**3.75**	**0.45**
Gamochaeta purpurea	1	0	3	0	**1.00**	**0.12**
Gnaphalium sp.	0	0	1	0	**0.25**	**0.03**
Gutierrezia texana	0	7	4	0	**2.75**	**0.33**
Krigia cespitosa	1	28	1	0	**7.50**	**0.89**
Pyrrhopappus paucifloris	0	3	2	0	**1.25**	**0.15**
Rudbeckia hirta	7	40	9	1	**14.25**	**1.69**
Sonchus asper	3	0	0	0	**0.75**	**0.09**
Taraxacum officinale	1	2	0	0	**0.75**	**0.09**
Wedelia texana	3	0	3	1	**1.75**	**0.21**
BERBERIDACEAE						
Berberis trifoliolata	0	0	0	1	**0.25**	**0.03**
BRASSICACEAE						
Arabis petiolaris	0	1	0	0	**0.25**	**0.03**
Draba cuneifolia	3	0	1	0	**1.00**	**0.12**
Lepidium virginicum	2	11	2	1	**4.00**	**0.48**
Lesquerella sp.	0	1	0	0	**0.25**	**0.03**
CACTACEAE						
Opuntia engelmannii	2	3	12	3	**5.00**	**0.59**
CAMPANULACEAE						
Triodanis perfoliata	1	21	9	0	**7.75**	**0.92**

Appendix B: Seasonal Raw Data continued

Species	Summer	Fall	Winter	Spring	Total	Rel. Density
CARYOPHYLLACEAE						
Arenaria benthamii	9	20	3	1	**8.25**	**0.98**
Arenaria sp.	0	0	2	0	**0.50**	**0.06**
Cerastium sp.	0	0	2	0	**0.50**	**0.06**
Silene antirrhina	0	8	0	0	**2.00**	**0.24**
COMMELINACEAE						
Commelina erecta	1	0	6	0	**1.75**	**0.21**
CONVOLVULACEAE						
Dichondra carolinensis	1	3	5	5	**3.50**	**0.42**
Evolvulus sericeus	1	3	0	0	**1.00**	**0.12**
CYPERACEAE						
Cyperus spp.	20	33	18	25	**24.00**	**2.85**
EBENACEAE						
Diospyros texana	1	0	0	0	**0.25**	**0.03**
EUPHORBIACEAE						
Acalypha lindheimeri	3	0	0	1	**1.00**	**0.12**
Argythamnia humilis	6	7	1	7	**5.25**	**0.62**
Croton fruticulosus	2	0	1	0	**0.75**	**0.09**
Croton monanthogynus	26	35	63	3	**31.75**	**3.78**
Euphorbia cyathophora	1	0	1	0	**0.50**	**0.06**
Euphorbia dentata	2	0	1	1	**1.00**	**0.12**
Euphorbia sp.	7	3	2	2	**3.50**	**0.42**
Phyllanthus sp.	5	9	5	10	**7.25**	**0.86**
Tragia sp.	0	1	0	0	**0.25**	**0.03**
FABACEAE						
Astragalus sp.	4	6	2	1	**3.25**	**0.39**
Desmanthus virgatus	1	0	0	0	**0.25**	**0.03**
Indigofera miniata	0	0	0	1	**0.25**	**0.03**
Medicago minima	17	24	14	10	**16.25**	**1.93**
Medicago polymorpha	0	1	0	1	**0.50**	**0.06**
Pediomelum rhombifolium	0	0	0	1	**0.25**	**0.03**
Senna lindheimeriana	1	0	1	0	**0.50**	**0.06**
Vicia sp.	7	11	4	9	**7.75**	**0.92**
GERANIACEAE						
Geranium carolinianum	0	1	1	0	**0.50**	**0.06**
HYDROPHYLLACEAE						
Nama jamaicense	29	56	73	31	**47.25**	**5.62**
Phacelia congesta	0	0	0	1	**0.25**	**0.03**
IRIDACEAE						
Sisyrinchium sp.	1	9	1	0	**2.75**	**0.33**
LAMIACEAE						
Brazoria scutellarioides	2	6	0	0	**2.00**	**0.24**

Appendix B: Seasonal Raw Data continued

Species	Summer	Fall	Winter	Spring	Total	Rel. Density
Hedeoma acinoides	1	4	0	0	**1.25**	**0.15**
Stachys crenata	5	16	10	3	**8.50**	**1.01**
LILIACEAE						
Nothoscordum bivalve	3	1	0	0	**1.00**	**0.12**
LINACEAE						
Linum hudsonioides	1	5	0	1	**1.75**	**0.21**
MALVACEAE						
Abutilon fruticosum	3	1	0	1	**1.25**	**0.15**
Sida abutilifolia	17	9	9	20	**13.75**	**1.64**
MOLLUGINACEAE						
Mollugo verticillata	2	0	0	1	**0.75**	**0.09**
ONAGRACEAE						
Gaura sp.	1	2	0	0	**0.75**	**0.09**
Oenothera triloba	0	0	3	0	**0.75**	**0.09**
OXALIDACEAE						
Oxalis dillenii	108	350	172	94	**181.00**	**21.53**
Oxalis drummondii	3	18	9	3	**8.25**	**0.98**
PLANTAGINACEAE						
Plantago patagonica	0	1	0	0	**0.25**	**0.03**
Plantago virginica	2	15	15	0	**8.00**	**0.95**
POACEAE						
Aristida oligantha	0	0	1	0	**0.25**	**0.03**
Bothriochloa ischaemum	10	1	22	22	**13.75**	**1.64**
Bouteloua rigidiseta	13	0	2	0	**3.75**	**0.45**
Bromus catharticus	1	3	0	0	**1.00**	**0.12**
Bromus japonicus	1	11	0	0	**3.00**	**0.36**
Buchloe dactyloides	4	0	1	0	**1.25**	**0.15**
Cenchrus spinifex	1	0	0	1	**0.50**	**0.06**
Cynodon dactylon	1	2	2	3	**2.00**	**0.24**
Desmazeria rigida	1	2	0	0	**0.75**	**0.09**
Digitaria cognata	3	0	9	1	**3.25**	**0.39**
Elymus virginicus	1	0	0	0	**0.25**	**0.03**
Eragrostis intermedia	11	5	13	4	**8.25**	**0.98**
Hilaria belangeri	0	0	0	1	**0.25**	**0.03**
Hordeum pusillum	8	20	1	1	**7.50**	**0.89**
Limnodea arkansana	34	80	15	0	**32.25**	**3.84**
Nassella leucotricha	25	33	13	6	**19.25**	**2.29**
Panicum hallii	8	3	3	6	**5.00**	**0.59**
Panicum oligosanthes	1	5	3	5	**3.50**	**0.42**
Paspalum dilatatum	0	0	0	2	**0.50**	**0.06**
Paspalum setaceum	4	4	8	1	**4.25**	**0.51**
Setaria scheelei	0	0	1	0	**0.25**	**0.03**

Appendix B: Seasonal Raw Data continued

Species	Summer	Fall	Winter	Spring	Total	Rel. Density
Sphenopholis interrupta	14	53	11	0	**19.50**	**2.32**
Sporobolus compositus	7	2	1	1	**2.75**	**0.33**
Vulpia octoflora	0	3	1	0	**1.00**	**0.12**
POLEMONIACEAE						
Gilia incisa	0	3	4	1	**2.00**	**0.24**
PORTULACACEAE						
Portulaca pilosa	2	0	0	1	**0.75**	**0.09**
RUBIACEAE						
Galium aparine	0	1	0	0	**0.25**	**0.03**
Galium spp.	4	6	11	5	**6.50**	**0.77**
Richardia tricocca	1	0	0	3	**1.00**	**0.12**
SCROPHULARACEAE						
Mecardonia procumbens	0	18	10	0	**7.00**	**0.83**
Nuttallanthus texanus	0	4	4	0	**2.00**	**0.24**
Verbascum thapsus	1	0	0	0	**0.25**	**0.03**
SMILACACEAE						
Smilax bona-nox	0	2	0	1	**0.75**	**0.09**
SOLANACEAE						
Bouchetia erecta	25	50	16	52	**35.75**	**4.25**
Physalis cinerascens	0	4	0	0	**1.00**	**0.12**
Solanum ptycanthum	0	0	1	5	**1.50**	**0.18**
ULMACEAE						
Celtis laevigata var. reticulata	0	1	0	0	**0.25**	**0.03**
URTICACEAE						
Parietaria obtusa	150	98	159	52	**114.75**	**13.65**
VERBENACEAE						
Glandularia bipinnatifida	1	0	0	0	**0.25**	**0.03**
Glandularia pumila	1	5	0	0	**1.50**	**0.18**
Verbena canescens	9	11	4	0	**6.00**	**0.71**
Verbena halei	8	48	22	19	**24.25**	**2.88**
VITACEAE						
Vitis sp.	0	0	1	0	**0.25**	**0.03**
Total	**698**	**1346**	**873**	**446**	**840.75**	**100.00**
Mean/sample	**116**	**224**	**146**	**74**	**140**	
Total species (116 species)	**80**	**77**	**72**	**53**	**116**	

Appendix C: Habitat Raw Data

Absolute number of emerged seedlings found for each species for each habitat in the soil seed bank.

Species	Grass	Juniper	Oak	Average	Rel. Density (%)
AGAVACEAE					
Nolina lindheimeriana	0.00	0.00	1.00	**0.33**	**0.03**
AMARANTHACEAE					
Amaranthus sp.	0.00	0.00	1.00	**0.33**	**0.03**
AMARYLLIDACEAE					
Habranthus texanus	0.00	1.00	0.00	**0.33**	**0.03**
ANACARDIACEAE					
Rhus lanceolata	0.00	0.00	1.00	**0.33**	**0.03**
APIACEAE					
Bifora americana	12.00	17.00	3.00	**10.66**	**0.95**
Chaerophyllum tainturieri	3.00	17.00	5.00	**8.33**	**0.74**
ASTERACEAE					
Ambrosia psilostachya	7.00	5.00	8.00	**6.66**	**0.59**
Baccharis neglecta	0.00	2.00	0.00	**0.67**	**0.06**
Calyptocarpus vialis	4.00	59.99	20.00	**28.00**	**2.50**
Centaurea melitensis	1.00	0.00	0.00	**0.33**	**0.03**
Cirsium texanum	0.00	5.00	8.00	**4.33**	**0.39**
Conzya sp.	2.00	2.00	0.00	**1.33**	**0.12**
Evax sp.	14.00	1.00	0.00	**5.00**	**0.45**
Gamochaeta purpurea	2.00	1.00	1.00	**1.33**	**0.12**
Gnaphalium sp.	1.00	0.00	0.00	**0.33**	**0.03**
Gutierrezia texana	8.00	3.00	0.00	**3.67**	**0.33**
Krigia cespitosa	21.00	8.00	1.00	**10.00**	**0.89**
Pyrrhopappus paucifloris	0.00	4.00	1.00	**1.67**	**0.15**
Rudbeckia hirta	33.99	20.00	3.00	**19.00**	**1.69**
Sonchus asper	0.00	3.00	0.00	**1.00**	**0.09**
Taraxacum officinale	2.00	1.00	0.00	**1.00**	**0.09**
Wedelia texana	1.00	4.00	2.00	**2.33**	**0.21**
BERBERIDACEAE					
Berberis trifoliolata	0.00	0.00	1.00	**0.33**	**0.03**
BRASSICACEAE					
Arabis petiolaris	0.00	1.00	0.00	**0.33**	**0.03**
Draba cuneifolia	0.00	4.00	0.00	**1.33**	**0.12**
Lepidium virginicum	7.00	9.00	0.00	**5.33**	**0.48**
Lesquerella sp.	0.00	1.00	0.00	**0.33**	**0.03**
CACTACEAE					
Opuntia engelmannii	0.00	4.00	16.00	**6.67**	**0.59**
CAMPANULACEAE					
Triodansis perfoliata	21.00	9.00	1.00	**10.33**	**0.92**
CARYOPHYLLACEAE					
Arenaria benthamii	17.00	16.00	0.00	**11.00**	**0.98**

Appendix C continued

Species	**Grass**	**Juniper**	**Oak**	**Average**	**Rel. Density (%)**
Arenaria sp.	2.00	0.00	0.00	**0.67**	**0.06**
Cerastium sp.	1.00	1.00	0.00	**0.67**	**0.06**
Silene antirrhina	3.00	5.00	0.00	**2.67**	**0.24**
COMMELINACEAE					
Commelina erecta	0.00	6.00	1.00	**2.33**	**0.21**
CONVOLVULACEAE					
Dichondra carolinensis	6.00	4.00	4.00	**4.67**	**0.42**
Evolvulus sericeus	3.00	1.00	0.00	**1.33**	**0.12**
CYPERACEAE					
Cyperus spp.	12.00	33.99	49.99	**31.99**	**2.85**
EBENACEAE					
Diospyros texana	0.00	1.00	0.00	**0.33**	**0.03**
EUPHORBIACEAE					
Acalypha lindheimeri	0.00	2.00	2.00	**1.33**	**0.12**
Argythamnia humilis	6.00	15.00	0.00	**7.00**	**0.62**
Croton fruticulosus	0.00	1.00	2.00	**1.00**	**0.09**
Croton monanthogynus	80.99	44.99	1.00	**42.33**	**3.78**
Euphorbia cyathophora	0.00	2.00	0.00	**0.67**	**0.06**
Euphorbia dentata	0.00	3.00	1.00	**1.33**	**0.12**
Euphorbia sp.	0.00	11.00	3.00	**4.67**	**0.42**
Phyllanthus polygoniodes	7.00	21.00	1.00	**9.66**	**0.86**
Tragia sp.	0.00	1.00	0.00	**0.33**	**0.03**
FABACEAE					
Astragalus sp.	11.00	2.00	0.00	**4.33**	**0.39**
Desmanthus virgatus	1.00	0.00	0.00	**0.33**	**0.03**
Indigofera miniata	1.00	0.00	0.00	**0.33**	**0.03**
Medicago minima	43.99	16.00	5.00	**21.66**	**1.93**
Medicago polymorpha	0.00	1.00	1.00	**0.67**	**0.06**
Pediomelum rhombifolium	1.00	0.00	0.00	**0.33**	**0.03**
Senna lindheimeriana	1.00	1.00	0.00	**0.67**	**0.06**
Vicia sp.	10.00	20.00	1.00	**10.33**	**0.92**
GERANIACEAE					
Geranium carolinianum	0.00	2.00	0.00	**0.67**	**0.06**
HYDROPHYLLACEAE					
Nama jamaicense	70.99	102.98	15.00	**62.99**	**5.62**
Phacelia congesta	0.00	1.00	0.00	**0.33**	**0.03**
IRIDACEAE					
Sisyrinchium sp.	5.00	6.00	0.00	**3.67**	**0.33**
LAMIACEAE					
Brazoria scutellarioides	2.00	6.00	0.00	**2.67**	**0.24**
Hedeoma acinoides	1.00	2.00	2.00	**1.67**	**0.15**
Stachys crenata	9.00	13.00	12.00	**11.33**	**1.01**

Appendix C continued

Species	**Grass**	**Juniper**	**Oak**	**Average**	**Rel. Density (%)**
LILIACEAE					
Nothoscordum bivalve	1.00	1.00	2.00	**1.33**	**0.12**
LINACEAE					
Linum hudsonioides	6.00	1.00	0.00	**2.33**	**0.21**
MALVACEAE					
Abutilon fruticosum	0.00	0.00	5.00	**1.67**	**0.15**
Sida abutilifolia	41.99	10.00	3.00	**18.33**	**1.64**
MOLLUGINACEAE					
Mollugo verticillata	2.00	0.00	1.00	**1.00**	**0.09**
ONAGRACEAE					
Gaura sp.	3.00	0.00	0.00	**1.00**	**0.09**
Oenothera triloba	0.00	3.00	0.00	**1.00**	**0.09**
OXALIDACEAE					
Oxalis dillenii	164.97	433.92	124.98	**241.29**	**21.53**
Oxalis drummondii	8.00	18.00	7.00	**11.00**	**0.98**
PLANTAGINACEAE					
Plantago patagonica	1.00	0.00	0.00	**0.33**	**0.03**
Plantago virginica	22.00	9.00	1.00	**10.66**	**0.95**
POACEAE					
Aristida oligantha	1.00	0.00	0.00	**0.33**	**0.03**
Bothriochloa ischaemum	30.99	18.00	6.00	**18.33**	**1.64**
Bouteloua rigidiseta	14.00	1.00	0.00	**5.00**	**0.45**
Bromus catharticus	0.00	0.00	4.00	**1.33**	**0.12**
Bromus japonicus	10.00	2.00	0.00	**4.00**	**0.36**
Buchloe dactyloides	4.00	1.00	0.00	**1.67**	**0.15**
Cenchrus spinifex	2.00	0.00	0.00	**0.67**	**0.06**
Cynodon dactylon	3.00	0.00	5.00	**2.67**	**0.24**
Desmazeria rigida	2.00	1.00	0.00	**1.00**	**0.09**
Digitaria cognata	3.00	9.00	1.00	**4.33**	**0.39**
Elymus virginicus	0.00	0.00	1.00	**0.33**	**0.03**
Eragrostis intermedia	11.00	18.00	4.00	**11.00**	**0.98**
Hilaria belangeri	1.00	0.00	0.00	**0.33**	**0.03**
Hordeum pusillum	29.99	0.00	0.00	**10.00**	**0.89**
Limnodea arkansana	82.99	44.99	1.00	**42.99**	**3.84**
Nassella leucotricha	17.00	45.99	14.00	**25.66**	**2.29**
Panicum hallii	16.00	3.00	1.00	**6.67**	**0.59**
Panicum oligosanthes	1.00	13.00	0.00	**4.67**	**0.42**
Paspalum dilatatum	1.00	0.00	1.00	**0.67**	**0.06**
Paspalum setaceum	13.00	4.00	0.00	**5.67**	**0.51**
Setaria scheelei	0.00	1.00	0.00	**0.33**	**0.03**
Sphenopholis interrupta	67.99	9.00	1.00	**26.00**	**2.32**
Sporobolus compositus	2.00	8.00	1.00	**3.67**	**0.33**
Vulpia octoflora	4.00	0.00	0.00	**1.33**	**0.12**

Appendix C continued

Species	Grass	Juniper	Oak	Average	Rel. Density (%)
POLEMONIACEAE					
Gilia incisa	1.00	6.00	1.00	**2.67**	**0.24**
PORTULACACEAE					
Portulaca pilosa	2.00	0.00	1.00	**1.00**	**0.09**
RUBIACEAE					
Galium aparine	0.00	0.00	1.00	**0.33**	**0.03**
Galium spp.	2.00	23.00	1.00	**8.67**	**0.77**
Richardia tricocca	2.00	0.00	2.00	**1.33**	**0.12**
SCROPHULARIACEAE					
Mecardonia procumbens	21.00	7.00	0.00	**9.33**	**0.83**
Nuttallanthus texanus	1.00	7.00	0.00	**2.67**	**0.24**
Verbascum thapsus	0.00	0.00	1.00	**0.33**	**0.03**
SMILACACEAE					
Smilax bona-nox	0.00	1.00	2.00	**1.00**	**0.09**
SOLANACEAE					
Bouchetia erecta	56.99	84.98	1.00	**47.66**	**4.25**
Physalis cinerascens	0.00	0.00	4.00	**1.33**	**0.12**
Solanum ptycanthum	0.00	1.00	5.00	**2.00**	**0.18**
ULMACEAE					
Celtis laevigata	0.00	0.00	1.00	**0.33**	**0.03**
URTICACEAE					
Parietaria obtusa	28.99	291.95	137.98	**152.97**	**13.65**
VERBENACEAE					
Glandularia bipinnatifida	0.00	1.00	0.00	**0.33**	**0.03**
Glandularia pumila	2.00	4.00	0.00	**2.00**	**0.18**
Verbena canescens	10.00	14.00	0.00	**8.00**	**0.71**
Verbena halei	70.99	24.00	2.00	**32.33**	**2.88**
VITACEAE					
Vitis sp.	0.00	0.00	1.00	**0.33**	**0.03**
Total	**1199.80**	**1643.71**	**518.91**	**1120.81**	**100.00**
Mean/sample	**2829.53**	**3881.13**	**1223.77**	**186.80**	
Total species (116 species)	**79**	**87**	**64**	**116**	

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