JUNIPERUS ASHEI (CUPRESSACEAE): PHYSIOGNOMY AND AGE STRUCTURE IN THREE MATURE TEXAS STANDS

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ABSTRACT

Despite the abundance of *Juniperus ashei* Buchholz in Texas, mature, intact stands are relatively rare. This study compares structural patterns and growth dynamics among three mature stands on the Edwards Plateau and documents relationships between structural changes and temporal development of these forests. Each stand has varied physiognomic characteristics and age-related structure. By identifying and comparing these properties, this study provides information relevant to conservation and management decisions relating to *J. ashei*.

RESUMEN

A pesar de la abundancia de *Juniperus ashei* Buchholz en Texas, las agrupaciones maduras e intactas son relativamente raras. Este estudio compara los modelos estructurales y la dinámica de crecimiento entre tres agrupaciones maduras en el altiplano Edwards y se documentan las relaciones entre los cambios estructurales y el desarrollo temporal de estos bosques. Cada agrupación tiene diversas características fisonómicas y una estructura relacionada con su edad. Al identificar y comparar estas propiedades, este estudio provee información pertinente para la conservación y decisiones de supervisión relacionadas con *J. ashei*.

INTRODUCTION

Background

Juniperus ashei Buchholz (Ashe juniper), one of the nine Texas species of the genus *Juniperus* (Correll & Johnston 1970; Simpson 1999), has dense populations from the Ozark Mountains in Missouri and Arkansas, to the Arbuckle Mountains of northeastern Oklahoma, and is found throughout central Texas particularly on southern and eastern portions of the Edwards Plateau where it is the dominant woody species and forms a significant component of the state's vegetation (Van Auken 1988; Diamond et al. 1995; Jackson & Van Auken 1997; Smeins et al. 1997). It also occurs in northeastern Mexico (Little 1992). Although

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J. ashei has an overlapping distribution with both *J. virginiana* L. (eastern red cedar) and *J. pinchotii* Sudw. (redberry juniper), chemical analyses suggest that hybridization does not occur (Adams 1972, 1975; Kelley 1976; Flake et al. 1978).

Juniperus ashei is typically found on thin, calcareous limestone- or dolomite-derived soils (Vines 1960) and also grows in deeper, sandier soils often in association with *Quercus fusiformis* Small (plateau live oak), *Diospyros texana* Scheele (Texas persimmon), *Q. stellata* Wang. (post oak), *Q. sinuata* var. *breviloba* (Torr.) C.H. Müll. (scaly-bark oak) and *Q. buckleyi* Nixon & Dorr (Texas oak) (Van Auken et al. 1978; Riskind & Diamond 1986; Diggs et al. 1999). Co-occurrence of *J. ashei* with broadleaf trees constitutes prime habitat for *Dendroica crysoparia* (golden-cheeked warbler), an endangered species which nests solely in juniper/oak woodlands and uses the bark from mature (>30 yrs old) *J. ashei* trees as nesting material (Doughty & Parmenter 1989; Beardmore et al. 1995).

Mature, second-growth *J. ashei* stands are rapidly disappearing due to high rates of urban and suburban expansion (Doughty & Parmenter 1989; Diamond et al. 1995; Patoski 1999). Effective land and endangered species management must include an understanding and appreciation of *J. ashei*'s role in establishing and maintaining stable, mature communities (Diamond et al. 1995) and its importance to the endangered golden-cheeked warbler.

This study investigates the structure and dynamics of three mature *J. ashei* stands and provides information regarding the establishment and persistence of these stands. By identifying and comparing several structural and age-related characteristics, it provides information relevant to conservation and management decisions. Structural patterns and growth dynamics are compared among stands to document relationships between structural changes and temporal development of these forests.

METHODS

Study Areas

The three study areas are on the Edwards Plateau of central Texas (Fig. 1) where eroded marine sandstones, limestones, shales, and dolomites are covered by thin soil deposits (Riskind & Diamond 1988) on upland areas deeply dissected by streams. Precipitation, which averages 85 cm per year in the region of the study sites (Riskind & Diamond 1988), percolates downward to the water table, expands fissures in the limestone, and forms the sinkholes, caves, and underground drainages characteristic of 'karst' topography (Spearing 1991).

Two study sites are in Guadalupe River State Park, a 769 ha park in Comal and Kendall counties. The first site (hereafter Guadalupe South) is located south of the Guadalupe River on a 35 ha 'karst dome' (elevation = 385 m; N 29° 51' W 98° 30'). The second site (hereafter Guadalupe North) is north of the Guadalupe River atop the river's escarpment (elevation = 342 m; N 29° 52' W 98° 28').

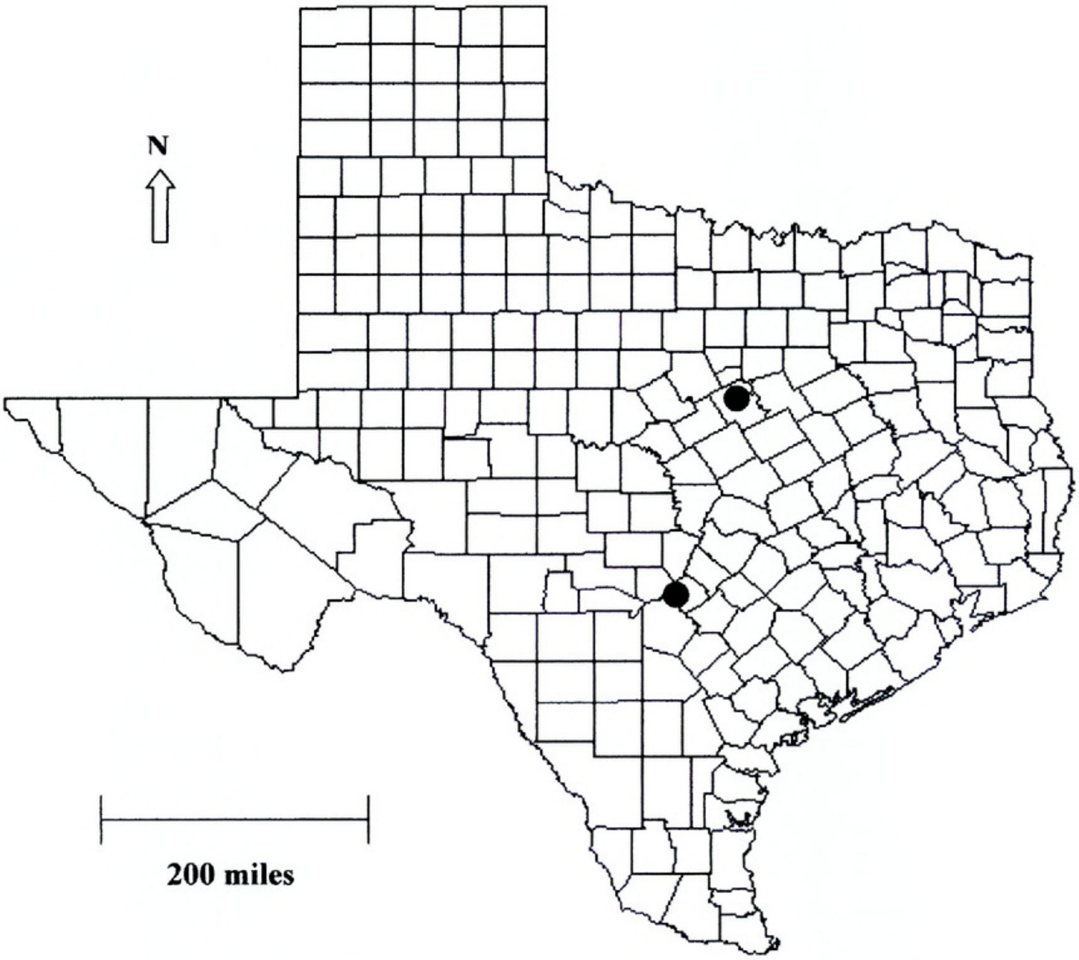

FIG. 1. Map of Texas with locations of study sites in Bosque and Comal counties.

Both stands are on undulating, well drained, cherty clay loam soils where chert and limestone cobbles cover >20 percent of the surface and subsoil layers below 15–20 cm are 75%, by volume, limestone fragments (U.S. Department of Agriculture 1984). Soils at both locations are typical of the region.

The third study site is on moderately deep, well-drained, loamy soil in Meridian State Park, a 204 ha reserve in Bosque County (elevation = 326 m; N 31° 53' W 97° 41'). Surface soil and subsoil layers are up to 38 and 94 cm deep, respectively, over a karst bedrock (U.S. Department of Agriculture 1980).

Sampling Procedures

Circular, 100 m^2 plots were established at 20 m intervals along transects in each stand. Transects differed in length according to stand dimensions. All trees were identified to species, mapped by their distance and bearing to the plot center, and their diameter breast height (dbh) recorded. Trees with dbh >8 cm were marked with individually numbered aluminum tags and cored at the base using a 4.3 mm diameter increment borer. Dead or unhealthy trees were not cored. Cores were glued to wooden mounting boards and sanded to a flat surface. Rings were counted under 37.5× magnification.

Because *J. ashei* forms false rings in response to environmental changes, ring number does not accurately reflect tree age. Therefore a formula for estimating age using ring counts was developed with cores from a separate set of trees of approximate known age from Meridian State Park. Photographs dating back to the park's development in 1933–34 were analyzed to isolate specific areas devoid of *J. ashei*. Trees now present in these areas were assumed to have germinated immediately after the park's establishment, giving them a maximum age (at the time of the study) of sixty-seven years. Cores from these trees were analyzed and a formula was derived by (1) counting rings of each tree, (2) dividing approximate age by ring count, and (3) pooling results and computing a mean. Approximate age of each *J. ashei* in this study was then calculated using the resulting formula: ring count × 0.67. Large rays and the diffuse porous nature of the deciduous hardwoods made it impossible to accurately determine ages of those trees. Ring count information was used to determine forest age structure.

Tree numbers, dbh, and height were used to determine mean height, mean basal area, size distribution, relative density (number of *J. ashei* as a proportion of the total number of individuals of all species), relative frequency (frequency of *J. ashei* as a proportion of the sum of the frequencies for all species), and relative basal area of each tree species. Importance values (Brower et al. 1998) were calculated.

Measurements for height, basal area, and age were tested for normality and homogeneity of variance (Sokal & Rohlf 1973) in order to determine the appropriate method of statistical analysis. All variables were normally distributed but displayed heterogeneity of variance, therefore non-parametric analysis of variance (ANOVA) was chosen to test for significant differences between stands.

RESULTS

Tree Species Identified and Importance Values

Table 1 provides numbers of each tree species found at each study site. Only *Juniperus ashei* was common to all three sites.

Relative density, frequency, and basal area of species may be summed to produce importance values (ranging from 0–3). Importance values integrate these separate measures to provide an indication of species influence in the community (Smith 1974). High importance values occurred for *J. ashei* at all three sites, with Guadalupe South at 2.70 and Meridian and Guadalupe North at 2.36 and 1.93, respectively (Table 2). These values indicate the dominance of this species in these communities.

TABLE 1. Summary counts of trees sampled.

Scientific Name	Common Name	Guadalupe South	Guadalupe North	Meridian
Juniperus ashei	Ashe juniper	138	131	86
Diospyros texana	Texas persimmon	3	38	0
Celtis laevigata	hackberry	0	5	0
Ulmus crassifolia	cedar elm	1	6	0
Quercus texana	Texas oak	1	0	2
Quercus fusiformis	plateau live oak	0	4	12
Quercus stellata	post oak	2	1	0
Quercus sinuata	scaly-bark oak	1	6	0
Fraxinus texensis	Texas ash	0	0	4
Sideroxylon lanuginosum	gum bumelia	0	0	1
Total Sampled		146	191	105

TABLE 2. Relative density, relative frequency, relative basal area and importance values.

	Relative Density	Relative Frequency	Relative Basal Area	Importance Values
Guadalupe South				
Juniperus ashei	.95	.79	.96	2.70
Diospyros texana	.02	.07	.01	.10
Ulmus crassifolia	.01	.03	.01	.05
Quercus texana	.01	.03	.02	.06
Quercus stellata	.01	.03	.01	.06
Quercus sinuata	.01	.03	.003	.04
Guadalupe North				
Juniperus ashei	.69	.39	.85	1.93
Diospyros texana	.20	.27	.01	.48
Ulmus crassifolia	.03	.06	.04	.13
Quercus sinuata	.03	.04	.003	.07
Celtis laevigata	.03	.10	.01	.14
Quercus fusiformis	.02	.12	.07	.21
Quercus stellata	.01	.02	.01	.04
Meridian				
Juniperus ashei	.82	.62	.92	2.36
Quercus fusiformis	.11	.19	.07	.37
Fraxinus texensis	.04	.10	.003	.14
Quercus texana	.02	.05	.01	.08
Sideroxylon lanuginosum	.01	.05	.001	.06

Basal Area and Size Class Distribution

Mean basal area of *J. ashei* was calculated for each site. Data indicate 29.58 m^2ha^{-1} ($\pm$11.41), 33.89 m^2ha^{-1} ($\pm$12.13), and 39.30 m^2ha^{-1} ($\pm$10.63) for Guadalupe South, Guadalupe North, and Meridian, respectively. Analysis of variance (Table 3) showed no significant differences between basal area of the three stands.

TABLE 3. Kruskal-Wallace one-way multisample non-parametric ANOVA with ties correction and χ^2 approximation for tree basal area, height, and age at three sites. Mean sums of ranked scores are shown. Letters indicate significant differences at p<0.05 via Student-Newman-Keuls Multiple Range Test.

	Guadalupe South (n=84)	Guadalupe North (n=77)	Meridian (n=66)	
Basal Area (cm^2)	111.42 (a)	108.73 (a)	123.43 (a)	$\chi^2 = 1.99_{(2)}$, $p<0.3704$
Age (yrs)	128.2 (a)	134.5 (a)	72.0 (b)	$\chi^2 = 38.53_{(2)}$, $p<0.0001$
Height (m)	71.89 (a)	154.03 (b)	120.89 (c)	$\chi^2 = 63.89_{(2)}$, $p<0.0001$

Highest percentages of *J. ashei* at each site were in the smallest size class category (>30-300 cm^2) with Guadalupe South at 45.3%, Guadalupe North at 48.5%, and Meridian at 36.5% (Fig. 2). Fewer than 5% of *J. ashei* at each site were in each of the four largest size class categories.

Age Structure

Ages of cored *J. ashei* were calculated and divided into five equal groups, 27–56 years, 57–86 years, 87–116 years, 117–146, and 147–177 years. At all sites most trees were younger than 86 years and few were over 147 years (Fig. 3).

Mean ages for the stands ranged from 80.4 years at Guadalupe North to 55.5 years at Meridian (Table 4), and these differences were statistically significant (Table 3). There was no significant difference in mean ages between Guadalupe North and Guadalupe South. However, this result is believed to be due to the inability to determine ages of the many dead trees at Guadalupe North. Pattern for mean ages was reflected in the pattern for oldest trees (Table 4). The oldest trees at Guadalupe North and Guadalupe South sites were >150 years old. The oldest tree at Meridian was about the same age as the mean trees at both Guadalupe sites and was less than half the age of Guadalupe North's oldest tree.

Height

Mean heights were calculated for each tree species comprising >3 percent of each community. *Juniperus ashei* occupied the canopy at all three sites. At Guadalupe South and Guadalupe North, where the canopy was shared with other species, only *Ulmus crassifolia* (cedar elm) at Guadalupe North was taller than *J. ashei* (Table 5). Mean heights of *J. ashei* differed significantly among all sites with the greatest heights at Guadalupe North and the least at Guadalupe South (Table 3). Meridian had the highest rate of height increase (cm yr^{-1}), growing approximately 35% faster than Guadalupe South over the lifetime of the two stands (Table 6).

DISCUSSION

Mature *Juniperus ashei* dominated all three sites in this study; however, each stand had varied physiognomic characteristics and age-related structure.

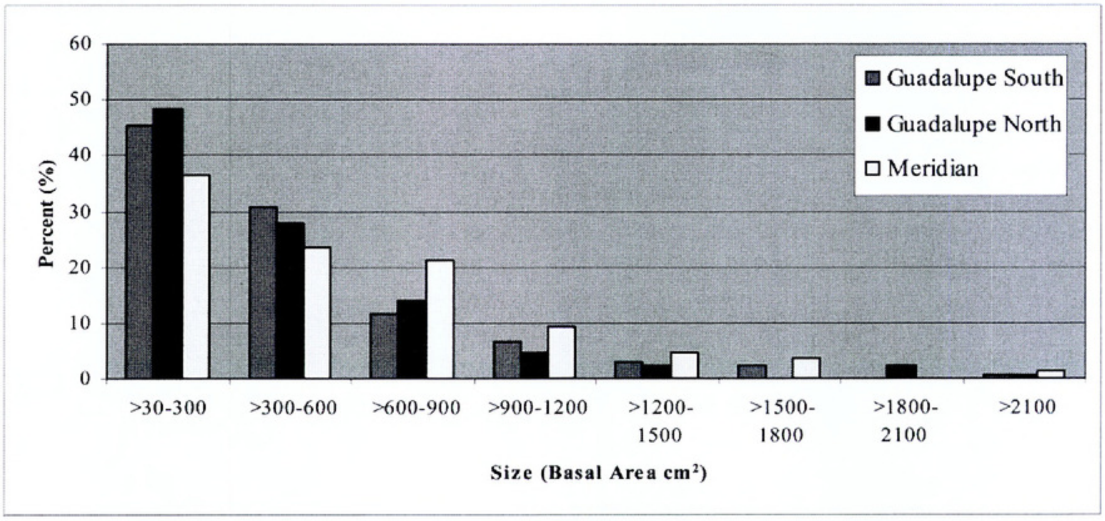

Fig. 2. Size class distribution of *Juniperus ashei* based on basal area.

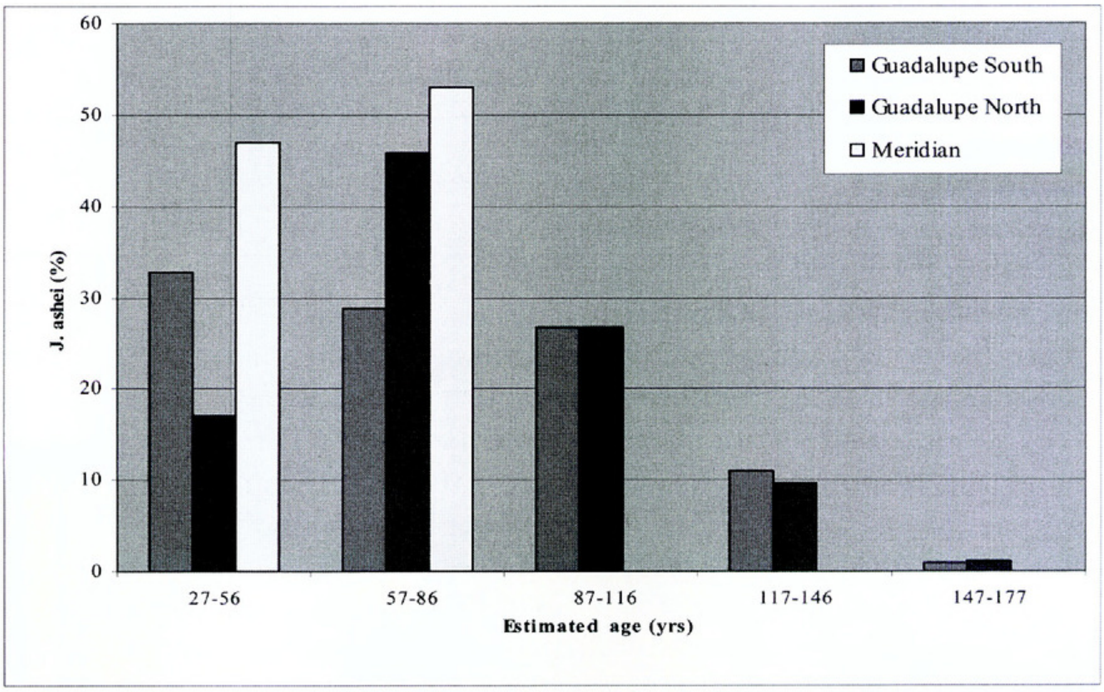

Fig. 3. *Juniperus ashei* estimated age class distribution.

Table 4. Mean *Juniperus ashei* ages and oldest trees.

Location	Mean Age *J. ashei* (yrs)	S.D.	Oldest *J. ashei* (yrs)
Guadalupe South	77.3	± 29.6	158
Guadalupe North	80.4	± 27.7	177
Meridian	55.5	± 12.4	82

TABLE 5. Mean heights (m) of trees comprising >3 percent of each stand.

	Mean Height (m)	Standard Deviation
Guadalupe South		
Juniperus ashei	6.19	±1.37
Guadalupe North		
Juniperus ashei	7.93	±2.10
Diospyros texana	3.71	±0.50
Ulmus crassifolia	10.47	±3.45
Quercus sinuata	4.97	±0.53
Meridian		
Juniperus ashei	7.19	±1.11
Quercus fusiformis	6.79	±2.36
Fraxinus texensis	6.23	±1.92

TABLE 6. *Juniperus ashei* mean height increase (cm yr^{-1}).

Location	Mean Increase (cm yr^{-1})	S.D.
Guadalupe South	9.05	±4.17
Guadalupe North	11.57	±4.99
Meridian	13.81	±3.23

Tree Species Identified and Importance Values

Importance values were determined at all three locations (Table 2). The lowest *J. ashei* value occurs at Guadalupe North. Also present at this site is *Diospyros texana* (Texas persimmon), a small tree usually less than 12 m tall (Little 1992). *Diospyros texana* is exclusively an understory tree at this location, with the tallest individual measuring 4.7 m. At Guadalupe South, with the highest *J. ashei* importance value, *D. texana* is rare (Table 1). Shading conditions make no significant difference in germination rates of *D. texana* (Everitt 1984). However, *Diospyros* species are reported to require full sun for optimum growth (Crockett 1972). At Guadalupe North these trees are often found clustered near dead *J. ashei*. These gaps in the canopy appear to provide ideal locations for the continued growth of this species. Few *D. texana* occur under the canopy at Guadalupe South, but may become more abundant as the stand ages and gaps are opened by tree death.

Basal Area and Size Class Distribution

Van Auken (1988) reported *J. ashei* mean basal areas of 38.6, 21.4, 43.2, and 18.4 $m^2 ha^{-1}$ in four mature, undisturbed, woodlands computed from diameters measured at 0.1 m above ground surface. These results are consistent with those for this study where mean basal areas of 29.6 (±11.4), 33.9 (±12.1), and 39.3 (±10.6)

m^2 ha^{-1} for *J. ashei* were measured at the Guadalupe South, Guadalupe North, and Meridian sites, respectively.

Analysis of variance (Table 3) showed no significant differences between basal areas of the three stands. However, since Meridian is a significantly younger stand (Table 4), this indicates a faster basal growth rate at that location. Some of this difference may be accounted for by the faster growth rate of younger trees. However, deeper surface soil with its associated greater moisture-holding capacity is probably the most important factor (Bockheim 1982) influencing tree growth and may have led to a faster growth rate at Meridian than at the two Guadalupe River State Park locations where soils are thinner and rockier.

Highest percentages of *J. ashei* were in the smallest size class category (>30-300 cm^2) at all three locations with Guadalupe South at 45.3%, Guadalupe North at 48.5%, and Meridian at 36.5% (Fig. 2). Less than 5% of *J. ashei* at each site were in each of the four largest size class categories. This arrangement results in a negative exponential size distribution, usually representing relatively early successional establishment (Van Auken 1993). However, size distribution does not necessarily reflect age distribution in forest age class studies. A generalization may be made that larger trees are likely to be old. However, it cannot be assumed that a small tree is young (Harper 1977). Many of the smaller *J. ashei* in this study were older than expected and size class distributions, in this case, do not indicate early successional stages, expanding populations, or relative youth of the majority of trees.

However, size class distribution is useful in describing the condition of a population in terms of its future and may offer insights into reproductive performance. While reproduction is often analyzed in terms of age structure, quite often it is a function of size and can best be studied using size distributions (Harper 1977). *Juniperus ashei* cone production is partially determined by environmental conditions, particularly rainfall, but is also dependent on tree size with trees reaching reproductive maturity at about 1.5 m height and about 50 cm^2 basal area. Results from this study indicate the majority of trees are reproductively mature and playing an important role in the reproductive dynamics of the population.

Age Structure

False rings formed by many species of *Juniperus* (Panshin & Dezeeuw 1964) cause considerable difficulty in age determination. Van Auken (1993) believes it is impossible to accurately determine ages of junipers from growth rings due to formation of several rings each year in response to fluctuating rainfall. Fuhlendorf (1992; pers. comm.) reported an inability to differentiate true and false annual rings while determining *J. ashei* ages from ring counts. Adams (pers. comm.) expressed doubt concerning dating method accuracy for *J. ashei* (Adams et al. 1998).

Methodology devised for age determination of *J. ashei* in this study is a novel approach based on ring counts of trees of known age. Although some conifers have a propensity to produce relatively more false rings when young and fewer when old, Grissino-Mayer has found no indication that Juniperus species have a tendency to do this (pers. comm.). Therefore, although the trees from Meridian were only 67 years old, the rate of false ring production should be similar to that of even the oldest trees in Guadalupe North. Although the trees were sampled at Meridian State Park, similar precipitation patterns at both parks also help validate use of the same formula constant for all three sites.

Forest populations often progress as a sequence of even-aged cohorts initiated by disturbance. However, the mixed-aged structure characterized in this study (Fig. 3) indicates rarity of disturbance and infers continuous recruitment over the life of the stands (Kelly & Larson 1997). These stands appear to have escaped the relatively frequent fires that historically occurred in Texas at the time of their establishment (Smeins et al. 1997) and apparently have been fire-free throughout their existence.

Interpreting age structure is complicated by the fact that there is no way to determine past mortality rates of a population. Age structure determination usually considers only survivors (as in this study) and does not utilize recruitment and mortality data (Harper 1977). However, accurate determination of stand age is dependent on mortality, as the oldest trees may be dead. This difficulty played a major role in determining the true age of Guadalupe North, where much of the forest was composed of dead trees. Despite these limitations, generalizations can be made concerning age structure of these stands.

Analysis of variance (Table 3) results indicated no significant differences between the ages of the two stands at Guadalupe River State Park. However, the stand at Meridian was significantly younger with a mean tree age of 55.5 years and no tree sampled older than 82 years (Table 4). All *J. ashei* at Meridian were in the two youngest age categories (Fig. 3). Stand age broadly corresponds to the establishment of the park in 1934. Much of the area now occupied by this stand was historically midgrass prairie (Riskind, pers. comm.), and the woodland's presence demonstrates the ability of *J. ashei* to colonize many terrain types in the absence of fire.

Mean ages for *J. ashei* were similar for Guadalupe South and Guadalupe North, with Guadalupe North results indicating a slightly (but not significantly) older stand (Table 4). Guadalupe South's age distribution is typical of an aging population, with trees in age categories of 27–56 yr, 57–86 yr, and 87–116 yr almost equally distributed (Fig. 3). Guadalupe North is the oldest stand with its establishment dating back to at least 170 years ago. Its greater age is reflected in the shift toward older trees (Fig. 3). It appears to be a declining population with relatively few individuals in the youngest 27–56 yr age category. Field observations indicated many large, old, dead trees for which ages could not be determined. This difficulty caused an underestimate of the stand's true age. Therefore, despite ANOVA results, Guadalupe North is believed to be older than Guadalupe South. Both Guadalupe North and Guadalupe South met some criteria for old-growth *J. ashei* stands as proposed by Diamond (1997) and perhaps could serve in refining the definition.

Height

Although *J. ashei* was the most abundant tree and dominated the canopy structure, other species, notably *Ulmus crassifolia*, *Quercus fusiformis*, and *Fraxinus texensis* were present in the canopy. At Guadalupe North the *J. ashei* canopy, at 7.93 m, is overtopped by a number of *U. crassifolia* (Table 5). Whether the taller *U. crassifolia* are older or whether they grow more quickly than *J. ashei* could not be determined. Presence of *Diospyros texana* is also significant at Guadalupe North. This species is primarily an understory tree as indicated by its mean height that is approximately half that of *J. ashei*.

Quercus fusiformis and *Fraxinus texensis* have mean heights shorter than *J. ashei* but still share the canopy at Meridian (Table 5). This stand developed in a grassland or savanna environment and records indicate that the area was a cotton field prior to establishment of the park (Riskind, pers. comm.). Therefore, trees sharing the canopy with *J. ashei* probably established concurrently.

ANOVA results indicated significantly different canopy heights between sites (Table 3). Although younger, Meridian had a greater mean height (7.19 m) than Guadalupe South (6.19 m). Reasons for this pattern are not known. However, deeper soils with greater moisture-holding capacity at Meridian could be one explanation for the observed height differences (Table 6). Tallest mean *J. ashei* height (7.93 m) is at Guadalupe North and differences between that site and Guadalupe South may be due to Guadalupe North's greater proportion of older trees.

Information is lacking concerning height growth rates of *J. ashei* but it is historically considered slow-growing (Blomquist 1990). Based on tree ring analysis, *J. pinchotii* grows in height an average of 6.01 cm yr^{-1} for the first thirty years (McPherson & Wright 1989; Ueckert 1997). *Juniperus ashei* height growth rates may be expected to be similar to those of *J. pinchotii* but data from this study indicated greater mean height increases at 9.05, 11.57, and 13.81 cm yr^{-1} for Guadalupe South, Guadalupe North, and Meridian, respectively (Table 6). If *J. ashei* height growth rates are similar to those of *J. pinchotii*, discrepancies may be due, in part, to previous studies overestimating tree age from faulty interpretation of annual ring counts.

Jackson and Van Auken (1997) recorded that *J. ashei* seedlings in edge habitats grow an average of 13.98 cm yr^{-1}. Their data are similar to height growth rates reported for Meridian. Deeper soils and the high light environment of open grassland during stand establishment may have resulted in relatively high rates of increase at this location.

Guadalupe South and Guadalupe North receive similar amounts of precipitation and have similar soil depths. Growth rate discrepancies between the two sites are probably due to underestimating the true age of Guadalupe North. If the Guadalupe North stand is older than data from this study indicate, an adjustment downward in height growth rate would result, giving Guadalupe North a growth rate more similar to that obtained for Guadalupe South.

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