

Structure of Isolated *Acer grandidentatum* (Bigtooth Maple) Communities and Potential Population Changes

Oscar W. Van Auken¹, Donna L. Taylor², Chen-chen Shen³, Janis K. Bush⁴

¹Department of Biology, University of Texas at San Antonio, San Antonio, Texas, USA

²Cisebsi Ltd. Co., Fair Oaks Ranch, Texas, USA

³Department of Forest, Rangeland, and Fire Sciences, University of Idaho, Idaho, USA

⁴Environmental Science Academic Programs, University of Texas at San Antonio, San Antonio, Texas, USA

Email: oscar.vanauken@utsa.edu, dltaylor3@me.com, shencc219@gmail.com, janis.bush@utsa.edu

How to cite this paper: Van Auken, O.W., Taylor, D.L., Shen, C.-C. and Bush, J.K. (2017) Structure of Isolated *Acer grandidentatum* (Bigtooth Maple) Communities and Potential Population Changes. *American Journal of Plant Sciences*, 8, 1368-1387. <https://doi.org/10.4236/ajps.2017.86093>

Received: April 3, 2017

Accepted: May 23, 2017

Published: May 26, 2017

Copyright © 2017 by authors and Scientific Research Publishing Inc. This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

Abstract

Isolated, relic populations of *Acer grandidentatum* (bigtooth maple, Sapindaceae) were found in deep canyons in central Texas. Associated with them on hilltops were communities of *Juniperus ashei* (ash juniper). We determined the structure of relic *A. grandidentatum* populations and compared them to adjacent *J. ashei* populations. The overstory and understory density was counted and basal area was determined for all woody species in both communities using the quadrat procedure. *Acer grandidentatum* was the highest density (788 ± 964 or 52%) and basal area (29 ± 35 or 52%) overstory species in the canyon communities while *J. ashei* had the highest density (1589 ± 146 or 92%) and basal area (51 ± 13 or 88%) in the hilltop communities. In the understory of the canyon communities, there were five juvenile tree species including *A. grandidentatum* which had the fourth highest density (13% or 176 ± 110 plants/ha). In the hilltop communities, *J. ashei* was the high density understory tree species (52% or 994 ± 400 plants/ha). There were no *A. grandidentatum* overstory or understory plants in the hilltop *Juniperus* communities. *Acer grandidentatum* had an inverse quadratic size distribution with few juveniles. Although we counted a number of seedlings, there was little recruitment over the last 16 years and very little potential recruitment in the previous 20 years. *Juniperus ashei* had an inverse exponential size distribution with many understory plants and considerable recruitment. Weibull age/size distributions showed one *A. grandidentatum* established in the 1670's and 2 in the 1760's, with peak establishment in the 1970's. Causes of the lack of recent recruitment are uncertain, but it could be episodic due to changes in herbivory, management or other environmental conditions.

Keywords

Age structure, Community Structure, Dendrochronology, Diameter Structure, Population Dynamics, Weibull Analyses

1. Introduction

Population dynamics of woodland or forest communities are not well understood [1]. Isolated or relic populations seem more multifaceted probably because of their low density and/or associated communities and species [2] [3]. In Texas and other private property states trying to determine species or community dynamics is difficult because as ownership changes management changes. Changing management strategies and effects are difficult to follow on long-lived species [4]. Three main factors caused changes in North American plant communities over the last 20,000 years including: 1) warming temperatures and glacial retreat [5] [6] [7] [8], 2) Native Americans [9] and 3) the appearance of Europeans and their animals [10]. Disturbances of all kinds are important to understanding population dynamics, including changing light, nutrient and water levels as well as competitors, herbivores and carnivores [11] [12] [13] [14].

Many studies examined encroachment in grasslands [11] [15] [16] [17], but replacement dynamics in woodlands and forests is more difficult [1] [18]. Factors that control recruitment into woodland and forest populations are also ambiguous [19] [20]. Establishment of early successional species requires disturbances [1] [18] [21] [22] [23]. Early species have high light (shade intolerant) and low nitrogen requirements, conditions that occur in forest or woodland gaps, but not below a closed canopy [23]. These early species would have a pulse of synchronous short-term establishment and an inverse or negative exponential diameter size-class population distribution [24]. Establishment of late successional species, that are tolerant of low light and requiring higher nitrogen levels are harder to explain; but appear to be a result of changes in competition intensity as a function of changing environmental resources [23] [25] [26] [27].

Models have been used to describe tree population distributions. Diameter distribution using the Weibull density function is a simple way to describe populations [28]. It is mathematically simple, flexible, and covers distributions that are normal and those that are strongly positively or negatively skewed [1] [12] [21] [28] [29].

Understanding patterns of variation of plant recruitment, as well as identifying processes that affect recruitment of adult plants into a population is a major conservation and management need [3] [30] [31]. A tree population that is expanding will have a negative exponential diameter distribution that is positively skewed [24] [32]. An established population will have a normal diameter distribution and as growth and mortality occur, the distribution becomes negatively skewed [24]. If there is no recruitment the population could become locally extinct [33].

Populations of many North American woodland and forest species are changing [34], with changes being widespread and species independent [12] [29] [35]. Changes include lack of replacement of various mature tree species [36]. The lack of recruitment does not seem to occur in the germination stage [34]; but rather in seed production, fruit consumption, browsing damage, decreased fire frequency, low-light, climatic variability or a combination of factors [37]. Based on evidence, seed production, germination and seedling recruitment was not a problem prior to European settlement in North America [38] [39] [40].

Lack of recruitment has been shown for many *Quercus* species that are being replaced by less palatable *Acer* species in northeastern North America [34] [35], but we have not found studies concerning population dynamics of *Acer grandidentatum* Nutt. (bigtooth maple). The distribution of the genus *Acer* is centered in China with 100 - 150 species. *Acer grandidentatum* is widespread in the mountains of the southwestern United States, including mountain ranges in New Mexico and western Texas (Figure 1) [41] [42] [43]. Native relict populations of *A. grandidentatum* are also found in central Texas [3] [14]. This species is a deciduous hardwood tree [43] [44] in the family Sapindaceae (Previously Aceraceae) [45].

There are anecdotal reports that populations of *A. grandidentatum* in central Texas are not being replaced [46] [47]. Causing the lack of recruitment or replacement in central Texas appears to be browsing of large populations of *Odocoileus virginianus* (white-tailed deer) [14]. Wolf and bear populations have been expatriated in central Texas for many years and white-tailed deer popula-

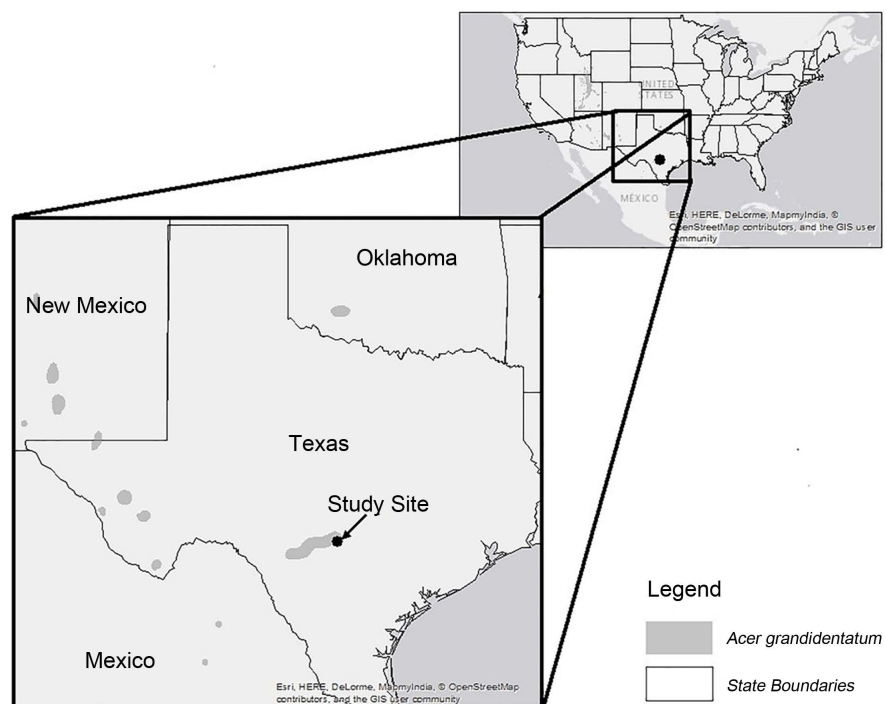


Figure 1. Map of distribution of *Acer grandidentatum* in the United States and the location of the study site in central Texas (arrow). Maps are from USGS and are slightly modified (see notation on map).

tions in this area are higher than other parts of North America [16] [48] [49] [50]. It is not known if this lack of recruitment is occurring in all populations of *A. grandidentatum* or if it occurred in the past. High abundance and browsing of Rocky Mountain Elk (Red deer, *Cervus elaphus*) in Yellowstone and other western national parks have caused a lack of recruitment of woody seedlings of other species [13] [51] [52] [53]. Reintroduction of the gray wolf in the American west has reversed some of these changes in population dynamics. Similar changes have not been shown for *A. grandidentatum*.

Acer grandidentatum is a shade tolerant woody plant, capable of growth in woodland or forest understories [54]. *Juniperus ashei*, an associated species, can survive and grow slowly for many years in the shade below a *Juniperus* canopy [19], but apparently not in deep shade below an *A. grandidentatum* canopy [54]. Shade tolerant plants utilize low levels of light to compensate for lost biomass more effectively than sun plants [55]. Photosynthetic characteristics affect a plant's inherent growth rate and thus its biomass, and therefore, understanding photosynthetic characteristics can help explain how an individual plant or population is able to compensate for episodes of herbivory or respond to disturbances [27]. In spite of reports of *Acer* species in low light understory environments [56] [57] [58] [59] [60], only one published paper concerning photosynthetic rates of *A. grandidentatum* has been found [54].

Because little is known about isolated relic populations of *A. grandidentatum*, including recruitment and population dynamics, we decided to determine the structure of several relic populations and to compare them to adjacent *J. ashei* populations. We examined and compared the density and basal area of the overstory and understory species in these populations. In addition, we examined the size-age distribution of *A. grandidentatum* and size distribution of *J. ashei* in the communities to see if new individuals were being recruited, if the populations were stable and to determine when the *Acer* communities first established.

2. Materials and Methods

The study sites were located in the 1520 ha (=3757 ac) Albert and Bessie Kronkosky State Natural Area, which is in the Edwards Plateau Physiographic region of central Texas (Figure 1, approximately 29°44'25"N, 98°50'18"W). The study sites were specifically in the "Tin Cup Canyon" and on associated hill tops [61]. Domestic grazing was the main industry of the general area, but in 1998 a 2.4 m high deer fence was constructed and domestic grazing was halted in the Natural Area [4]. The elevation of the study area is 484 - 614 m a. m. s. Canyon bottom *Acer grandidentatum* communities have relatively deep calcareous silty clay soil, a Mollisol overlying limestone bedrock [62]. The hill top *Juniperus ashei* community soils are shallow, calcareous, in the Eckrant-Rock outcrop association. Some of the upland, hill top communities are level while some are steep, but all soils are clayey-skeletal, smectitic, thermic lithic haplustolls [62]. Mean annual temperature in the study area is approximately 18.3°C, ranging from near 0.7°C in January to 34.1°C in August, and highly variable. Mean annual precipitation

is also highly variable but approximately 72.4 cm/year with very little in July and August with May and September being wettest [63].

The study areas were surveyed by conducting a reconnaissance flyover in November 2014 as the canyon deciduous canopy started to change color. This was followed by interviews in early 2015 with persons that had considerable field time in the Natural Area. Field conditions and site accessibility allowed surveying the *A. grandidentatum* community woody plant population in five woodland canyon sites and the *J. ashei* communities in three adjacent upland sites, beginning November 2015 and continuing from April through June of 2016.

The quadrat method was used in the quantitative surveys [64]. The number of 5×5 m quadrats varied in each of the *A. grandidentatum* communities due to site conditions and topography. There were 19 - 24, 5×5 m quadrats/transect in the *J. ashei* communities. Adequate sampling for each transect was determined by examining species and density stabilization curves (not presented). There were a total of 69 quadrats or 0.18 ha sampled in the upland *J. ashei* communities, while 217 quadrats or 0.543 ha were sampled in the *A. grandidentatum* communities. All plants greater than 137 cm in height and 3 cm basal diameter were considered trees, identified, counted and basal diameter measured. Five 1 m^2 sub-quadrats were established in each of the 25 m^2 quadrats. All woody plants less than 137 cm in height and/or 3 cm basal diameter were identified and counted as seedlings or juveniles. Density, relative density, basal area, and relative basal area were calculated for each overstory species within each community, then means were determined [64]. Mean density of all understory woody species was also determined. Shannon species diversity (H') and the Simpson Index (D) for the overstory were also calculated [32].

Light levels ($\text{PAR-}\mu\text{mol/m}^2/\text{s}$), soil depth (cm) and slope angle were measured at the center point of each 25 m^2 quadrat in each community. Light level was measured with a LI-COR®LI-188 integrating quantum sensor within ± 60 min of solar noon on clear, cloud-free days. Soil depth was measured with a piece of rebar (0.9 cm dia. and 36.4 cm

long) driven into the soil until it would not penetrate deeper [65]. The bar was extracted and the depth that the bar was driven into the soil was measured with a meter stick [66]. Slope angle was measured with an inclinometer placed on a meter stick on the surface of the soil.

Diameter of *A. grandidentatum* was converted to age using a previously established growth rate [61] and age class distributions were constructed. To compare the age class distributions of *A. grandidentatum*, a two-parameter Weibull function was fit to each distribution [28] [67]. Twenty-two “bins” were created for each plot. The largest diameter tree (86.5 cm) was divided by 22 to determine the range of the bins (3.93 cm) to construct the diameter distribution plots and for the Weibull analysis. The bars in the figures are positioned at the midpoint of 1.96 cm. Each bar in **Figure 2** is plotted at the midpoint and the bins in the figures are rounded to the nearest whole number. The following species characteristics are presented: species sample size (N), mean diameter \pm standard deviation

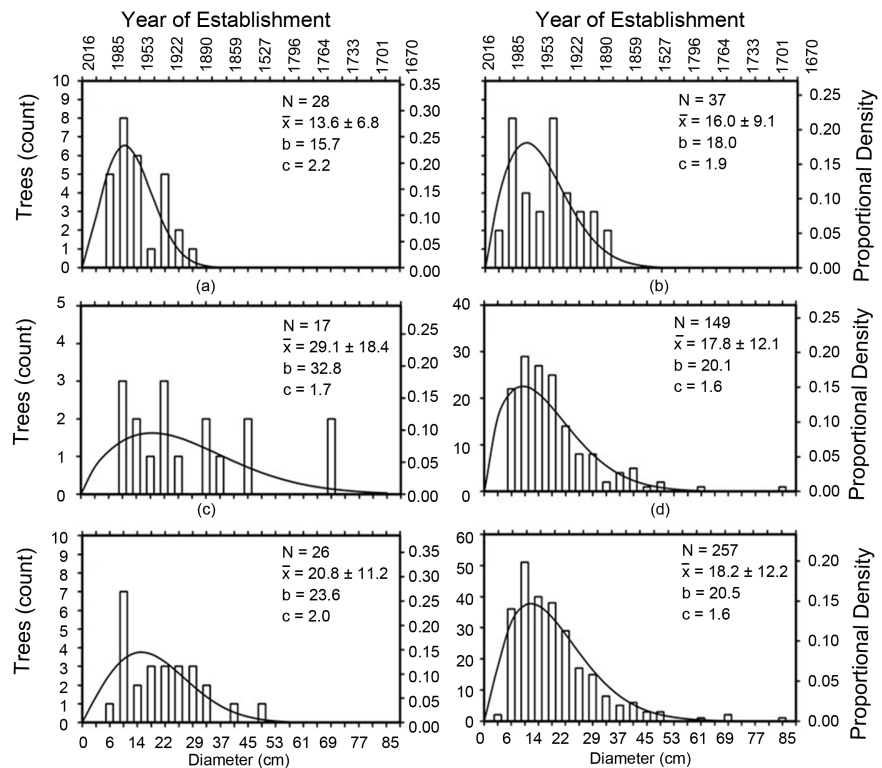


Figure 2. Diameter size class histograms and corresponding fitted Weibull distributions (solid lines) for five *Acer grandidentatum* communities and a summary plot. Communities were found in canyons of southcentral Texas. The top x-axis in panel (a) and (b) is uniform and each interval (tick) represents 15.5 years and is the year of plant establishment. The bottom, x-axis in panel (e) and (f) is uniform and 6 - 8 cm size intervals of diameter measured at ground level. Both the actual number of trees and the proportional frequency are shown on the y-axes. Sample size (N), mean diameter and standard deviation, Weibull scale statistic (b), and the Weibull shape statistic (c) are also included.

tion, and the shape statistic “c”. Diameter size class distributions for *J. ashei* trees were created and analyzed using a two parameter Weibull function, but a figure is not presented.

The shape parameter “c” of the Weibull distribution can produce a variety of forms. When $c < 1$, the distribution is a steeply descending monotonic function, a value of $c = 1$ is a negative exponential distribution, when $1 < c < 3.6$ the distribution is positively skewed, when $c = 3.6$ the distribution is normal, while a c value > 3.6 is a negatively skewed distribution [1] [12] [21] [28] [29]. Because it is difficult to evaluate the smallest size plants in the Weibull distributions, we examined the smallest sized plants in one cm size and age class distributions. In this plot (Figure 3) the bins are one cm and the midpoints are at 0.5 cm intervals.

Leaf samples were examined and compared [44] [68]. Once identified, scientific names and common species names were taken from Correll and Johnston [44] and confirmed in the USDA plants database [68]. Student’s-*t* test for unequal sample size was used to detect differences in chemical, physical and population data and a *p*-value of 0.05 was used in all cases [69].

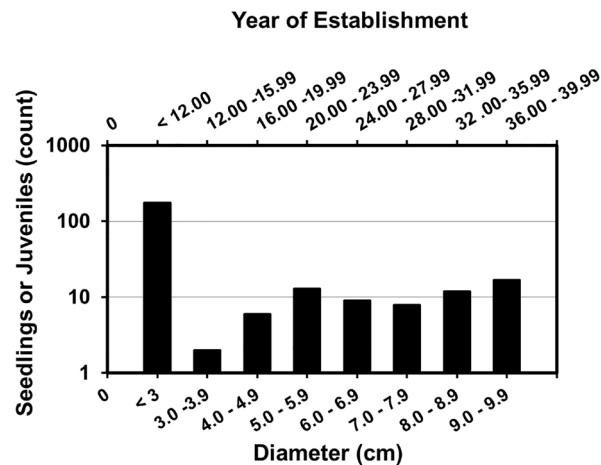


Figure 3. Bar graph (log y axis) of the number of seedlings and juvenile *Acer grandidentatum* plants found is presented. The bottom x-axis is the diameter range (cm) and the top x-axis is the age range (years).

3. Results

The upland *Juniperus* woodlands and the canyon *Acer* woodlands were physically very close together, less than 0.25 km apart, and separated by approximately 100 m in elevation, but structurally they were very different. There were significant differences in the slope angle and soil depth of the two communities (Student's t with unequal sample size, $p < 0.05$ for both). The *Juniperus* communities were level (slope = $1.3 \pm 0.4^\circ$ mean \pm SD) with shallow soil (10.8 ± 10.2 cm), while the *Acer* communities had mean slopes of $19.6 \pm 6.5^\circ$ and deeper soil (22.9 ± 18.2 cm). Light levels were very high in the open at 2014 ± 322 $\mu\text{moles/m}^2\cdot\text{sec}$ and significantly reduced below the canopies (Student's t with unequal sample size, $p < 0.0001$), and significantly different below the upland and canyon communities (Student's t with unequal sample size, $p < 0.05$). Light level was reduced by 83% to 339 ± 44 $\mu\text{moles/m}^2\cdot\text{sec}$ below the *Juniperus* canopy and reduced by 92% to 166 ± 49 $\mu\text{moles/m}^2\cdot\text{sec}$ below the *Acer* community canopy. Species richness for the understory woody species in the upland *Juniperus* community was 12 species and it was 22 species in the canyon *Acer* community (Table 1). Ten woody species were found in the understory of both communities, while two were exclusive in the upland *Juniperus* communities and 12 were exclusive to the canyon *Acer* communities.

The mean density and relative density of the understory woody plants in both upland and canyon communities with both scientific and common names in descending order of species found in the canyon *Acer* communities are presented (Table 1). Total understory mean density was significantly different between the two communities (Student's t with unequal sample size, $p < 0.001$). In the upland *Juniperus* communities density was 1928 plants/ha or 1.37 times the density in the canyon *Acer* community that was 1404 plants/ha. *Acer grandidentatum* in the canyon *Acer* communities had the fourth highest relative density of understory juvenile plants (13%, or density = 176 ± 110 plants/ha) behind

Table 1. Understory woody species found including scientific names, common names, density, standard deviation and relative

Scientific Name	Common Name	Understory Woody Plants			
		Canyon		Upland	
		Density	% Density	Density	% Density
<i>Quercus buckleyi</i>	Texas red oak	289 ± 288	21	28 ± 48	1
<i>Prunus serotina</i>	Black cherry	229 ± 201	16	0	0
<i>Quercus laceyi</i>	Lacey oak	227 ± 223	16	344 ± 59	18
<i>Acer grandidentatum</i>	Bigtooth maple	176 ± 110	13	0	0
<i>Smilax bona-nox</i> ^a	Saw greenbrier	140 ± 113	10	0	0
<i>Aesculus pavia</i>	Red buckeye	73 ± 76	5	0	0
<i>Juniperus ashei</i>	Ashe Juniper	65 ± 33	5	994 ± 40	52
<i>Diospyros texana</i>	Texas persimmon	46 ± 42	3	50 ± 33	3
<i>Sideroxylon lanuginosum</i>	Gum bumelia	35 ± 73	2	11 ± 10	1
<i>Toxicodendron radicans</i> ^a	Poison ivy	25 ± 57	2	0	0
<i>Vitis arizonica</i> ^a	Arizona grape	22 ± 23	2	0	0
<i>Rhamnus caroliniana</i>	Carolina buckthorn	18 ± 32	1	6 ± 10	--
<i>Cercis canadensis</i>	Texas redbud	15 ± 16	1	0	0
<i>Garrya ovate</i>	Mexican silkthassel	15 ± 33	1	6 ± 10	--
<i>Celtis laevigata</i>	Sugar hackberry	11 ± 12	1	0	0
<i>Ulmus crassifolia</i>	Cedar Elm	5 ± 10	--	0	0
<i>Sophora secundiflora</i>	Mountain laurel	5 ± 6	--	367 ± 473	19
<i>Juglans major</i>	Black walnut	3 ± 4	--	0	0
<i>Mahonia trifoliolata</i>	Agarita	3 ± 8	--	39 ± 19	2
<i>Rhus virens</i>	Evergreen sumac	2 ± 4	--	11 ± 10	1
<i>Platanus occidentalis</i>	Amer. sycamore	2 ± 5	--	0	0
<i>Parthenocissus quinquefolia</i> ^a	Virginia Creeper	2 ± 5	--	0	0
<i>Quercus fusiformis</i>	Live oak	0	0	67 ± 60	3
<i>Eysenhardtia texana</i>	Kidneywood	0	0	6 ± 10	--
TOTALS		1407	99	1928	100

Density. Plants were found in the canyon and upland communities of the ABK natural area in southcentral Texas. -- is < 1%. a. Woody vine.

Quercus buckleyi, *Prunus serotina* and *Q. laceyi* (Table 1). The understory *Acer* communities had four species of woody vines. The upland *Juniperus* communities had no *A. grandidentatum* plants or woody vines. *Juniperus ashei* juveniles in these upland communities had the highest relative density at 52% and density (994 ± 400 plants/ha), followed by *Sophora secundiflora* and *Q. laceyi* at 19% and 18% respectively.

Overstory species richness for the of the *Juniperus* communities was 5 woody species while the overstory of the canyon *Acer* communities had 14 species (Table 2). Two of the same species were found in both communities (*J. ashei* and *V. arizonica*), while 3 species were exclusive to the upland *Juniperus* communities

Table 2. Overstory mean density, standard deviation, relative density, basal area, standard deviation and relative basal area of woody plants found in the canyon and upland communities of the ABK natural area in southcentral Texas.

Scientific Name	Overstory Woody Plant							
	Canyon		Upland		Canyon		Upland	
	Density (plants/ha)	Relative Density (%)	Density (plants/ha)	Relative Density (%)	Basal Area (m ² /ha)	Relative Basal Area (%)	Basal Area (m ² /ha)	Relative Basal Area (%)
<i>Acer grandidentatum</i>	788 ± 964	52	0	0	29 ± 35	52	0	0
<i>Juniperus ashei</i>	299 ± 195	25	1589 ± 146	92	4 ± 4	10	51 ± 13	88
<i>Prunus serotina</i>	76 ± 70	6	0	0	7 ± 6	16	0	0
<i>Quercus laceyi</i>	58 ± 27	6	0	0	4 ± 2	11	0	0
<i>Aesculus pavia</i>	32 ± 48	4	0	0	--	--	0	0
<i>Tilia caroliniana</i>	23 ± 52	1	0	0	5 ± 10	4	0	0
<i>Quercus buckleyi</i>	18 ± 22	1	0	0	1 ± 2	2	0	0
<i>Vitis arizonica</i>	11 ± 14	1	6 ± 10	--	--	--	0	0
<i>Garrya ovata</i>	11 ± 24	1	0	0	--	--	0	0
<i>Juglans major</i>	9 ± 9	1	0	0	--	1	0	0
<i>Cercis canadensis</i>	7 ± 16	1	0	0	--	--	0	0
<i>Ilex decidua</i>	5 ± 7	1	0	0	--	--	0	0
<i>Sideroxylon lanuginosum</i>	4 ± 8	--	0	0	--	--	0	0
<i>Ungnadia speciosa</i>	2 ± 4	--	0	0	1 ± 2	4	0	0
<i>Sophora secundiflora</i>	0	0	100 ± 109	5	0	0	7 ± 9	12
<i>Quercus fusiformis</i>	0	0	22 ± 38	1	0	0	--	--
<i>Diospyros texana</i>	0	0	6 ± 10	--	0	0	0	0
TOTALS	1343 ± 987	100	1723 ± 294	99	51 ± 44	100	58 ± 10	100

-- is < 1%.

and 12 were found exclusively in the canyon *Acer* communities (Table 2). Overstory Shannon diversity and Simpson diversity for the upland *Juniperus* community were 0.145 and 1.170 respectively and for the canyon *Acer* community they were 0.587 and 2.502. The *Acer* community was almost exclusively composed of deciduous species and the *Juniperus* community was almost exclusively evergreen species.

Total density of the overstory of the two communities was significantly different (Student's *t* with unequal sample size, $p < 0.001$). In the overstory of the *Acer* canyon communities, *A. grandidentatum* had the highest mean relative density at 52% and an actual mean overstory density of 788 ± 964 plants/ha followed by *J. ashei* at 25% with a mean density of 299 ± 195 plants/ha (Table 2). Other lower density woody species in the overstory of these canyon communi-

ties were *P. serotina*, *Q. laceyi*, *Aesculus pavia* (a shrub), *Tilia caroliniana*, *Q. buckleyi*, *Vitis arizonica* (a woody vine), *Garrya ovata* and *Juglans major*. In the upland *Juniperus* communities, the main overstory woody species was *J. ashei* at a mean relative density of 92% and density of 1589 ± 146 plants/ha and total community density of 1723 ± 294 plants/ha. *Sophora secundiflora* was the species with the second highest relative density at 5%. The overstory woody plant density in the upland *Juniperus* community was 1.28 times the total density of the *Acer* canyon communities. *Juniperus ashei* density in the upland communities was 5.31 times its density in the canyon *Acer* communities.

Total overstory basal area in the two communities was not significantly different (Student's *t* with unequal sample size, $p > 0.05$). Total overstory basal area in the *Acer* community was 51 ± 44 m²/ha or 88% of the *Juniper* communities total basal area that was 58 ± 10 m²/ha (Table 2). Relative basal area of *A. grandidentatum* was 52 % of the total basal area in the canyon communities or 29 ± 35 m²/ha. The species with the second highest relative basal area at 16% was *Prunus serotina* followed by *Quercus laceyi* at 11% and then *Tilia caroliniana* at 4%, but no juveniles were found for this species. In the upland *Juniperus* community, *J. ashei* basal area was 51 ± 13 m²/ ha and was 88% of the total basal area. Although *J. ashei* had the second highest relatively density in the *Acer* canyon communities its mean basal area there was fairly low at 4 ± 4 m²/ha or 10% of the total, indicating the *Juniperus* plants present in the canyon communities were small. In addition, 90% of the basal area in the *Acer* communities consisted of deciduous plants and 100% of the *Juniperus* communities were evergreen.

The diameter size class distributions and the year of establishment of each of the *A. grandidentatum* plants in each community and the summery plot for these populations are presented (Figure 2). Based on the Weibull analysis, all five of the size class histograms and the summery plot of the *A. grandidentatum* populations are unimodal (Figure 2). Sample sizes were 17 - 149 plants with the sample size for the summery plot being 257 total plants. Mean diameter values ranged from 13.6 to 29.1 cm with standard deviations from 6.8 to 18.4 cm. Weibull analyses demonstrated that all of the values for the scale parameter “*b*” approximate the distribution diameter mean value as one would expect. The shape statistic “*c*” for all of the *Acer* populations was 1.6 - 2.2, which indicated the populations all were unimodal and had a positively skew ($1 < c < 3.6$). The summery plot showed 2 trees out of 257 individuals in the smallest size class plotted (Figure 2(f)). Only one of the five populations had any trees in the smallest size class (Figure 2(b)). The two individual plants indicated by the first bar in the figure (Figure 2(b) and Figure 2(f)) were > 3 cm in diameter, the smallest trees measured. It is difficult to see and estimate the age and number of plants in each bar in the smallest bins or size classes in all of the plots in Figure 2.

Consequently, for the smallest categories, they were re-plotted in one cm size classes (Figure 3). There were 175 seedlings or juveniles < 3 cm in diameter and

< 12 years old. None of these plants were tall enough or large enough to be considered trees (> 137 cm tall and >3 cm in basal diameter). There were 2 saplings 3.0 - 3.9 cm basal diameter and 12.00 - 15.99 years of age. There were 65 saplings between 4.0 and 9.9 cm in basal diameter and between 16 and 39.99 years of age. The age and number of the oldest trees are more easily determined (**Figure 2**), one started growth in the 1670's and 2 in the 1760's. The majority of trees began growth in the 1970's. The youngest tree sized plants found were in the smallest size class (3.0 - 3.9 cm in diameter) or 12.00 - 15.99 years old and there were only two plants.

Each of the diameter size class distributions for the *J. ashei* populations and associated Weibull plots were prepared but not presented. Three *J. ashei* populations growing with the *A. grandidentatum* populations in the canyons and three *J. ashei* hill tops populations were examined. The *J. ashei* populations growing on the hilltop upland sites have some large individuals and larger population density and size (mostly) than those present in the canyons. Based on the Weibull analysis, all of the size class histograms for the *J. ashei* populations were unimodal with sample sizes of 66-93 for the upland and 22 - 35 for the canyon populations. Mean diameter values ranged from 15.2 to 18.0 cm upland and 8.4 - 19.1 cm canyon. The shape statistic "*c*" for the upland populations was 1.5 - 1.6 and for the canyons was 1.4 - 2.5 which indicated they were unimodal and all had a positive skew ($1 < c < 3.6$).

4. Discussion

Density of understory or juvenile *Acer grandidentatum* plants in deep canyons in central Texas was fairly high but not as high as the juvenile density of some of the other overstory trees (**Table 1**). Examining the smallest diameter size classes, it was clear that there was little recruitment of *A. grandidentatum* juvenile plants into the mature communities (**Figure 2** and **Figure 3**). When Weibull analyses were examined, all of the *Acer* communities had unimodal positive skewed distributions with only two individuals in the smallest size class, suggesting a declining population [28]. This lack of recruitment could be caused by high juvenile mortality or growth suppression of the juveniles or herbivory, but is difficult to conclude from one visit to the populations [14]. Consequently, marking juveniles and monitoring over time is warranted [12] [29]. We showed in an earlier study that *A. grandidentatum* had moderate growth but older plants mostly had heart rot and age was difficult to determine [61]. Diameter growth rate for *A. grandidentatum* plants was a significant linear function (2.50 mm/year, $N = 26$; $y = 0.40x$; $r^2 = 0.85$; $P < 0.0001$) and comparable to other deciduous species.

Composition and structure of the hilltop *Juniperus* communities were similar to other reports, except species richness and diversity was lower in the present study [30] [66] [70] [71] [72] [73]. The canyon *A. grandidentatum* phytosociological characteristics in the present study are similar to one other *A. grandidentatum* community described in the literature [14], but ages were not determined in that study and size class distributions were limited, as was recruitment

potential. In addition, no *A. grandidentatum* plants have been reported from area riparian communities [74].

It is difficult to determine if recruitment is occurring in populations with only one temporal datum as in these *A. grandidentatum* communities. Nevertheless, it appears that the current rate of recruitment in these communities is below the level needed to maintain the existing adult population because there are numerous seedlings in the communities but few saplings and individuals in the community midstory. A bottleneck appears to be present, but does not look as if it is due to seed production or germination because of the numerous seedlings or small *A. grandidentatum* plants in the understory. A lack of recruitment has been demonstrated for woody species in many communities across North America [12] [29] [34] [53] [75], including various species in central Texas [30] [70] [72] [73] [76] [77]. These small individuals appear to be suppressed and not recruited into the mature population, but the cause of mortality of the smallest individuals in the current study is only suspected. A previous investigation demonstrated 60% survival of protected *A. grandidentatum* plants for at least one year compared to 0% survival of unprotected plants [14]. In other areas, changes in diameter distributions were associated with community succession or early development, including high mortality of seedlings [33] and recruitment could be episodic or irregular [32].

Pinus, *Quercus* and seedlings of other species establish in grasslands when there is a reduction in fire frequency [9] [16] [17] [18] [39]. However, there is considerable debate over the frequency of fire necessary to maintain grasslands, woodlands and forests [9]. Herds of domestic livestock increased with an associated reduction in fire frequency in the late 1800's in southwestern North America [78] [79]. A reduction in fire frequency could have allowed or maintained various *Acer* communities in the American west and southwest at that time.

Fire and domestic grazing no doubt play a significant role in these woodlands and forests by shifting the rate and direction of succession [23] [53] [72]. Light levels may be reduced by the canopy so juveniles of shade-intolerant species are growth suppressed as shade-tolerant species are stimulated [23] [72] [80]. Consequently, as forest or woodland conditions change, so does community composition. Without fire, many species which are more shade-tolerant and fire intolerant, establish and increase in basal area. This includes species in the genera *Acer*, *Betula*, *Fagus*, *Quercus* and *Tsuga* [18] [39] [81] [82].

While reduced light levels may influence the recruitment of juveniles of various forest species [83] [84], other studies indicate that herbivory is more important in determining community composition [14] [53] [85]-[90]. Browsing pressure has resulted in pronounced reductions in seedling survival and scarcity of saplings of various species in savannahs, woodlands and forests throughout North America [14] [53] [88] [89] [91] [92] [93]. In the present study, we were able to establish through evaluation of community structure, size and age class analysis that there is a bottleneck in the recruitment of juvenile *A. grandidenta-*

tum; however, we could not determine if factors such as light levels below the canopy, herbivory or a combination were the cause.

Seed production, dispersal and seed germination are undoubtedly important in the establishment phase for *Acer* populations in new areas. In addition, production of fruit is highly erratic for most woody species probably because of available moisture [94], and losses due to birds and mammals [95]-[102]. However, juvenile growth may be limited to vegetative growth below the *A. grandidentatum* canopy [73]. If this is true, it may be caused by arbuscular mycorrhizal fungi and negative growth feedback to conspecific seedlings below the mature trees, which has been shown for other North American *Acer* species [106]. This is similar to reports of juvenile density below various species of *Populus* and *Quercus* [12] [29] [103] [104] [105]. Vegetative growth following disturbance suggests successful regeneration below a canopy may depend on abiotic factors such as soil resources, light levels, temperature and even wind-throw or biotic factors including competition, herbivory and soil biota. All of these factors could play a role in determining mature woodland and forest community structure by shifting resource availability [1] [23] [91] [106].

Density and size-age class distributions have been used to show bottlenecks of recruitment in other species [12] [29] [82]. The underrepresentation of *A. grandidentatum* juveniles in these central Texas communities suggests a lack of recruitment into the adult population. Recruitment may be below the replacement rate necessary for these populations, suggesting adult density may be decreasing. However, the future structure of these *A. grandidentatum* communities is difficult to know and predicting the future is hard to do. Twenty-four woody species were found in the understory, four were woody vines, five were shrubs and 15 were trees with a chance of replacing some of the overstory species. Nevertheless, prediction of the replacement of the current overstory apparently will require further investigations.

Weibull shape statistics for *A. grandidentatum* were positively skewed unimodal functions. Some of the *A. grandidentatum* trees were present in these canyons over 300 years ago, but populations present at or before that time are not known. This early time corresponds with increases in the human population and their grazing animals. These anthropogenic factors could have led to a decrease in fire frequency and plant community changes [16]. The structure of these canyon *A. grandidentatum* communities will change in the future, but the direction and rate of change and the future community structure are not known. Because of the apparent lack of juvenile recruitment, a decrease in *A. grandidentatum* adult density is suggested, but the rate of change of these *A. grandidentatum* populations is difficult to predict because of plant longevity and lack of comparable community data in the literature.

Acknowledgements

We thank James Rice superintendent of the Albert and Bessie Kronkosky State Natural Area for permission to study isolated *Acer grandidentatum* communi-

ties and for supplies needed to set up the study. Both James Rice and Tom Rior-dan helped us with transportation needed to get to the remote study sites. Thanks also to Tom Denyer for help getting some clear sections of old, down, *Acer grandidentatum* stems. The authors also thank Julian Chavez for preparing the *A. grandidentatum* distribution map.

References

- [1] Baker, P.J., Bunyavejchewin, S., Oliver, C.D. and Ashton, P.S. (2005) Disturbance History and Historical Stand Dynamics of a Seasonal Tropical Forest in Western Thailand. *Ecological Monographs*, **75**, 317-343. <https://doi.org/10.1890/04-0488>
- [2] Van Auken, O.W. (1997) Species Rareness and Commonness along Spatial and Temporal Gradients. *Southwestern Naturalist*, **42**, 369-377.
- [3] Pool, J.M., Carr, W.R., Price, D.M. and Singhurst, J.R. (2007) Rare Plants of Texas. Texas A&M Nature Guides. Texas Parks and Wildlife. Everbest Printing Louisville, Kentucky.
- [4] Carpenter, J. and Brandimarte, C. (2014) The Albert and Bessie Kronksky State Natural Area: A History of Lands and people. Historic Sites and Structures Program, State Parks Division, Texas Parks and Wildlife Department (Available on Line TPWD as a Draft).
- [5] Delcourt, P.A., Delcourt, H.R. and Webb, T. (1983) Dynamic Plant Ecology: The Spectrum of Vegetation Change in Space and Time. *Quaternary Science Review*, **1**, 153-175.
- [6] Betancourt, J.L., Van Devender, T.R. and Martin, P.S. (1990) Synthesis and Prospectus. In: Betancourt, J.L., Van Devender, T.R. and Martin, P.S., Eds., *Packrat Middens: The Last 40,000 Years of Biotic Change*, University of Arizona Press, Tucson, 435-447.
- [7] Miller, R.F. and Wigand, P.E. (1994) Holocene Changes in Semiarid Pinyon-Juniper Woodlands: Response to Climate, Fire, and Human Activities in the Great Basin. *Bioscience*, **44**, 465-474. <https://doi.org/10.2307/1312298>
- [8] Van Devender, T.R. (1995) Desert Grassland History: Changing Climates, Evolution, Biography, and Community Dynamics. In: McClaran, M.P. and Van Devender, T.R. Eds., *The Desert Grassland*, University Arizona Press, Tucson.
- [9] Collins, S.L. and Wallace, L.L. (1990) Fire in North American Tallgrass Prairie. University of Oklahoma Press, Norman.
- [10] Inglis, J.M. (1964) A History of Vegetation on the Rio Grande Plain. Texas Parks and Wildlife, Austin.
- [11] Archer, S., Schimel, D.S. and Holland, E.A. (1995) Mechanisms of Shrubland Expansion: Land Use, Climate or CO₂. *Climate Change*, **29**, 91-99. <https://doi.org/10.1007/BF01091640>
- [12] Ryniker, K.A., Bush, J.K. and Van Auken, O.W. (2006) Structure of *Quercus gambelii* Communities in the Lincoln National Forest, New Mexico, USA. *Forest Ecology and Management*, **233**, 69-77.
- [13] Beschta, R.L., Painter, L.E., Levi, T. and Ripple, W.J. (2016) Long-Term Aspen Dynamics, Trophic Cascades, and Climate in Northern Yellowstone National Park. *Canadian Journal of Forest Research*, **46**, 548-556. <https://doi.org/10.1139/cjfr-2015-0301>
- [14] Nelson-Dickerson, T. and Van Auken, O.W. (2016) Survival, Growth and Recruitment of Bigtooth Maple (*Acer grandidentatum*) in Central Texas Relict Communi-

- ties. *Natural Areas Journal*, **36**, 174-180. <https://doi.org/10.3375/043.036.0209>
- [15] Bond, W.J. (2008) What Limits Trees in C₄ Grasslands and Savannas? *Annual Review of Ecology, Evolution and Systematics*, **39**, 641-659. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173411>
- [16] Van Auken, O.W. (2000) Shrub Invasions of Semiarid Grasslands. *Annual Review of Ecology and Systematics*, **31**, 197-216. <https://doi.org/10.1146/annurev.ecolsys.31.1.197>
- [17] Van Auken, O.W. (2009) Causes and Consequences of Woody Plant Encroachment into Western North American Grasslands. *Journal of Environmental Management*, **90**, 2931-2942.
- [18] Foster, D.R., Orwig, D.A. and McLachlan, J.S. (1996) Ecological and Conservation Insights from Reconstructive Studies of Temperate Old-Growth Forests. *Tree*, **11**, 419-423.
- [19] Van Auken, O.W., Jackson, J.T. and Jurena, P.N. (2004) Survival and Growth of *Juniperus* Seedlings in *Juniperus* Woodlands. *Plant Ecology*, **175**, 245-257. <https://doi.org/10.1007/s11258-005-0022-z>
- [20] McKinley, D.C. and Van Auken, O.W. (2005) Influence of Interacting Factors on the Growth and Mortality of *Juniperus ashei* Seedlings. *American Midland Naturalist*, **154**, 320-330. [https://doi.org/10.1674/0003-0031\(2005\)154\[0320:IOIFOT\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2005)154[0320:IOIFOT]2.0.CO;2)
- [21] Lorimer, C.G. and Krug, A.G. (1983) Diameter Distributions in Even-Aged Stands of Shade-Tolerant and Midtolerant Tree Species. *American Midland Naturalist*, **109**, 331-345. <https://doi.org/10.2307/2425414>
- [22] Abrams, M.D. and Orwig, D.A. (1996) A 300-Year History of Disturbance and Canopy Recruitment for Co-Occurring White Pine and Hemlock on the Allegheny Plateau, USA. *Journal of Ecology*, **84**, 353-363. <https://doi.org/10.2307/2261198>
- [23] Van Auken, O.W. and Bush, J.K. (2013) Invasion of Woody Legumes. Springer Briefs in Ecology, Springer, New York. <https://doi.org/10.1007/978-1-4614-7199-8>
- [24] Mohler, C.L., Marks, P.L. and Sprugel, D.G. (1978) Stand Structure and Allometry of Trees during Self-Thinning of Pure Stands. *Journal of Ecology*, **66**, 599-614. <https://doi.org/10.2307/2259153>
- [25] Tilman, D. (1988) Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton.
- [26] Grace, J.B. and Tilman, D. (1990) Perspectives on Plant Competition. Academic Press, New York.
- [27] Valladares, F. and Niinemets, U. (2008) Shade Tolerance, a Key Plant Feature of Complex Nature and Consequence. *Annual Review of Ecology and Systematics*, **39**, 237-257. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173506>
- [28] Bailey, R.L. and Dell, T.R. (1973) Quantifying Diameter Distributions with the Weibull Function. *Forest Science*, **19**, 97-104.
- [29] Van Auken, O.W., Bush, J.K., Richter, F.A. and Karges, J. (2007) Structure of Isolated Populations of *Populus tremuloides* (Quaking Aspen) in the Davis Mountains of Far-West Texas. *Natural Areas Journal*, **27**, 302-312. [https://doi.org/10.3375/0885-8608\(2007\)27\[302:SOIPOP\]2.0.CO;2](https://doi.org/10.3375/0885-8608(2007)27[302:SOIPOP]2.0.CO;2)
- [30] Russell, F.L. and Fowler, N.L. (2002) Failure of Adult Recruitment in *Quercus buckleyi* Populations on the Eastern Edwards Plateau, Texas. *American Midland Naturalist*, **148**, 201-217. [https://doi.org/10.1674/0003-0031\(2002\)148\[0201:FOARIQ\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2002)148[0201:FOARIQ]2.0.CO;2)

- [31] Galatowitsch, S.M. (2012) Ecological Restoration. Sinauer Associates, Sunderland.
- [32] Whittaker, R.H. (1975) Communities and Ecosystems. MacMillan, New York.
- [33] Knox, R.G., Peet, R.K. and Christensen, N.L. (1989) Population Dynamics in Loblolly Pine Stands: Changes in Skewness and Size Inequality. *Ecology*, **70**, 1153-1167. <https://doi.org/10.2307/1941383>
- [34] Lorimer, C.G. (1992) Causes of the Oak Regeneration Problem. In: Loftis, D.L. and McGee, C.E., Eds., *Oak Regeneration: Serious problems, Practical Recommendations*, USDA Southeastern Forest Experiment Station, Knoxville.
- [35] Loftis, D.L. and McGee, C.E. (1992) Oak Regeneration: Serious Problems, Practical Recommendations. USDA Southeastern Forest Experiment Station, Knoxville.
- [36] Shumway, D.L., Abrams, M.D. and Ruffner, C.M. (2001) A 400-Year History of Fire and Oak Recruitment in an Old-Growth Oak Forest in Western Maryland, USA. *Canadian Journal of Forest Research*, **31**, 1437-1443. <https://doi.org/10.1139/x01-079>
- [37] Begon, M., Townsend, C.R. and Harper, J.L. (2006) Ecology: From Individuals to Ecosystems. Blackwell Publishing, Malden.
- [38] Mensing, S.A. (1992) The Impact of European Settlement on Blue Oak (*Quercus douglasii*) Regeneration and Recruitment in the Tehachapi Mountains, California. *Madrono*, **39**, 36-46.
- [39] Abrams, M.D., Orwig, D.A. and Demeo, T.E. (1995) Dendroecological Analysis of Successional Dynamics for a Presettlement-Origin White-Pine-Mixed-Oak Forest in the Southern Appalachians, USA. *Journal of Ecology*, **83**, 133-143. <https://doi.org/10.2307/2261156>
- [40] Ruffner, C.M. and Abrams, M.D. (1998) Relating Land-Use History and Climate to the Dendroecology of a 326-Year Old *Quercus prinus* Talus Slope Forest. *Canadian Journal of Forest Research*, **28**, 347-358. <https://doi.org/10.1139/x97-220>
- [41] Hanks, J.P. and Dick-Peddie, W.A. (1974) Vegetation Patterns of the White Mountains, New Mexico. *Southwestern Naturalist*, **18**, 371-382. <https://doi.org/10.2307/3670295>
- [42] Alexander, B.G. Jr., Ronco, F. Jr., Fitzhugh, E.L. and Ludwig, J.A. (1984) A Classification of Forest Habitat Types of the Lincoln National Forest, New Mexico. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, General Technical Report RM-104, Fort Collins.
- [43] Tollefson, J.E. (2006) *Acer grandidentatum*. In: *Fire Effects Information System*, USDA, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. <http://www.fs.fed.us/database/feis/>
- [44] Correll, D.S. and Johnston, M.C. (1979) Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner.
- [45] Buerki, S., *et al.* (2009) Plastid and Nuclear DNA Markers Reveal Intricate Relationships at Subfamilial and Tribal Levels in the Soapberry Family (Sapindaceae). *Molecular Phylogeny and Evolution*, **51**, 238-258.
- [46] BCNPSOT (2010) Bigtooth Maples for Boerne, Texas. <http://npsot.org/wp/boerne/maples-for-boerne/>
- [47] Heidemann, R.E. (2011) Lost Maples State Natural Area. Handbook of Texas Online. <http://www.tshaonline.org/handbook/online/articles/gil01>
- [48] Doughty, R.W. (1983) Wildlife and Man in Texas: Environmental Change and Conservation. Texas A&M University Press, College Station.
- [49] Fulbright, T.E. and Ortega-S, J.A. (2008) White-Tailed Deer Habitat: Ecology and

Management on Rangelands. Texas A&M University Press, College Station.

- [50] Wolverton, S., Kennedy, J.H. and Cornelius, J.D. (2007) A Paleozoological Perspective on White-Tailed Deer (*Odocoileus virginianus texana*) Population Density and Body Size in Central Texas. *Environmental Management*, **39**, 545-552.
<https://doi.org/10.1007/s00267-006-0240-8>
- [51] Ripple, W.J., Beschta, R.L. and Painter, L.E. (2015) Trophic Cascades from Wolves to Alders in Yellowstone. *Forest Ecology and Management*, **354**, 254-260.
- [52] Beschta, R.L. and Ripple, W.J. (2016) Riparian Vegetation Recovery in Yellowstone: Two Decades after Wolf Reintroduction. *Biological Conservation*, **198**, 93-103.
- [53] Beschta, R.L. and Ripple, W.J. (2009) Large Predators and Trophic Cascades in Terrestrial Ecosystems in the Western United States. *Biological Conservation*, **143**, 2401-2414.
- [54] Nelson-Dickerson, T. and Van Auken, O.W. (2017) Seedling Growth and Photosynthesis of *Acer grandidentatum* (Bigtooth maple, Sapindaceae) from Isolated Central Texas Populations. *Phytologia*, **99**, 11-21.
- [55] Jones, R.H. and McLeod, K.W. (1989) Shade Tolerance in Seedlings of Chinese Tallow Tree, American Sycamore, and Cherrybark Oak. *Bulletin of the Torrey Botanical Club*, **116**, 371-377. <https://doi.org/10.2307/2996627>
- [56] Christensen, E.M. (1958) Growth Rates and Vegetation Change in the Oak-Maple Brush in Lower Provo Canyon, Utah. *Proceedings of the Utah Academy of Sciences, Arts and Letters*, **35**, 167-168.
- [57] Logan, K.T. and Krotkov, G. (1968) Adaptations of the Photosynthetic Mechanism of Sugar Maple (*Acer saccharum*) Seedlings Grown in Various Light Intensities. *Physiology Planetarium*, **22**, 104-116.
<https://doi.org/10.1111/j.1399-3054.1969.tb07846.x>
- [58] Bazzaz, F.A. and Carlson, R.W. (1982) Photosynthetic Acclimation to Variability in the Light Environment of Early and Late Successional Plants. *Oecologia*, **54**, 313-316. <https://doi.org/10.1007/BF00379999>
- [59] Augspurger, C.K. (2008) Early Spring Leaf out Enhances Growth and Survival of Saplings in a Temperate Deciduous Forest. *Oecologia*, **156**, 281-286.
<https://doi.org/10.1007/s00442-008-1000-7>
- [60] Kwit, M.C., Rigg, L.S. and Goldblum, D. (2010) Sugar Maple Seedling Carbon Assimilation at the Northern Limit of Its Range: The Importance of Seasonal Light. *Canadian Journal of Forest Research*, **40**, 385-393. <https://doi.org/10.1139/X09-196>
- [61] Van Auken, O.W., Taylor, D.L. and Shen, C. (2016) Diameter Growth of *Acer grandidentatum* (Bigtooth Maple) in Isolated Central Texas Populations. *Phytologia*, **98**, 232-240.
- [62] Hensell, J.L., Dittmar, G.W. and Taylor, F. (1977) Soil Survey of Bandera County, Texas. USDA Soil Conservation Service, Washington, D.C.
http://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/texas/TX019/0/Bandera.pdf
- [63] World Climate (2011) Climate Data for 29 N 98 W.
<http://www.worldclimate.com/cgi-bin/grid.pl?gr=N29W099>
- [64] Van Auken, O.W., Bush, J.K. and Elliott, S.A. (2005) Ecology-Laboratory Manual. Pearson Custom Publishing, Boston.
- [65] Larcher, W. (2003) Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups. Springer-Verlag, New York.
<https://doi.org/10.1007/978-3-662-05214-3>

- [66] Van Auken, O.W., Ford, A.L. and Allen, J.L. (1981) An Ecological Comparison of Upland Deciduous and Evergreen Forests of Central Texas. *American Journal of Botany*, **68**, 1249-1256. <https://doi.org/10.2307/2443048>
- [67] Cohen, A.C. (1965) Maximum Likelihood Estimation in the Weibull Distribution Based on Complete and on Censored Samples. *Technometrics*, **7**, 579-588. <https://doi.org/10.1080/00401706.1965.10490300>
- [68] USDA (2016) Plants Database, USDA Natural Resources Conservation Service. <http://plants.usda.gov/java/profile?symbol>
- [69] Sall, J., Creighton, L. and Lehman, A. (2005) JMP Start Statistics. SAS Institute Inc., Toronto.
- [70] Van Auken, O.W. (1988) Woody Vegetation of the Southeastern Escarpment and Plateau. In: Amos, B.B. and Gehlbach, F.R., Eds., *Edward's Plateau Vegetation: Plant Ecological Studies in Central Texas*, Baylor University Press, Waco.
- [71] Amos, B.B. and Gehlbach, F.R. (1988) Edwards Plateau Vegetation: Plant Ecological Studies in Central Texas. Baylor University Press, Waco.
- [72] Russell, F.L. and Fowler, N.L. (1999) Rarity of Oak Saplings in Savannahs and Woodlands of the Eastern Edwards Plateau, Texas. *Southwestern Naturalist*, **44**, 31-41.
- [73] Russell, F.L. and Fowler, N.L. (2004) Effects of White-Tailed Deer on Population Dynamics of Acorns, Seedlings, and Saplings of *Quercus buckleyi*. *Plant Ecology*, **173**, 59-72. <https://doi.org/10.1023/B:VEGE.0000026329.47461.99>
- [74] Ford, A.L. and Van Auken, O.W. (1982) Distribution of Woody Species in the Guadalupe River Flood Plain in the Edwards Plateau of Texas. *Southwestern Naturalist*, **27**, 383-392. <https://doi.org/10.2307/3670713>
- [75] Abrams, M.D. and Johnson, S.E. (2012) Long-Term Impacts of Deer Exlosures on Mixed-Oak Forest Composition at the Valley Forge National Historical Park, Pennsylvania, USA. *Journal of the Torrey Botanical Society*, **139**, 167-180. <https://doi.org/10.3159/TORREY-D-11-00075.1>
- [76] Bush, J.K. and Van Auken, O.W. (1986) Light Requirements of *Acacia smallii* and *Celtis laevigata* in Relation to Secondary Succession. *American Midland Naturalist*, **115**, 118-122. <https://doi.org/10.2307/2425841>
- [77] Van Auken, O.W. (1993) Size Distribution Patterns and Potential Population Change of Some Dominant Woody Species of the Edwards Plateau Region of Texas. *Texas Journal of Science*, **45**, 199-209.
- [78] Savage, M. and Swetnam, T.W. (1990) Early 19th-Century Fire Decline Following Sheep Pasturing in a Navajo Ponderosa Pine Forest. *Ecology*, **71**, 2374-2378. <https://doi.org/10.2307/1938649>
- [79] Swetnam, T.W., Allen, C.D. and Betancourt, J.L. (1999) Applied Historical Ecology: Using the Past to Manage for the Future. *Ecological Applications*, **9**, 1189-1206. [https://doi.org/10.1890/1051-0761\(1999\)009\[1189:AHEUTP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2)
- [80] Abrams, M.D. (1992) Fire and the Development of Oak Forests. *BioScience*, **42**, 346-353. <https://doi.org/10.2307/1311781>
- [81] Lorimer, C.G., Chapman, J.W. and Lambert, W.D. (1994) Tall Understory Vegetation as a Factor in the Poor Development of Oak Seedlings Beneath Mature Stands. *Journal of Ecology*, **82**, 227-237. <https://doi.org/10.2307/2261291>
- [82] Abrams, M.D. (2003) Where Has All the White Oak Gone? *BioScience*, **53**, 927-939. [https://doi.org/10.1641/0006-3568\(2003\)053\[0927:WHATWO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2003)053[0927:WHATWO]2.0.CO;2)
- [83] Griffin, J.R. (1976) Regeneration in *Quercus lobata* Savannahs, Santa Lucia Moun-

- tains, California. *American Midland Naturalist*, **95**, 422-435.
<https://doi.org/10.2307/2424405>
- [84] Cierjacks, A. and Hensen, I. (2004) Variation of Stand Structure and Regeneration of Mediterranean Holm Oak along a Grazing Intensity Gradient. *Plant Ecology*, **173**, 215-233. <https://doi.org/10.1023/B:VEGE.0000029322.75004.ad>
- [85] Strole, T.A. and Anderson, R.C. (1992) White-Tailed Deer Browsing-Species Preferences and Implications for Central Illinois Forests. *Natural Areas Journal*, **12**, 139-144.
- [86] Boerner, R.E.J. and Brinkman, J.A. (1996) Ten Years of Tree Seedling Establishment and Mortality in an Ohio Deciduous Forest Complex. *Bulletin of the Torrey Botanical Club*, **123**, 309-317. <https://doi.org/10.2307/2996780>
- [87] Didier, K.A. and Porter, W.F. (2003) Relating Spatial Patterns of Sugar Maple Reproductive Success and Relative Deer Density in Northern New York State. *Forest Ecology and Management*, **181**, 253-266.
- [88] Rooney, T.P. (2003) Direct and Indirect Effects of White-Tailed Deer in Forest Ecosystems. *Forest Ecology and Management*, **181**, 165-176.
- [89] Rossell, C.R. Jr., Gorsira, B. and Patch, S. (2005) Effects of White-Tailed Deer on Vegetation Structure and Woody Seedling Composition in Three Forest Types on the Piedmont Plateau. *Forest Ecology and Management*, **210**, 415-424.
- [90] Kain, M., Battaglia, L., Royo, A. and Carson, W.P. (2011) Over-Browsing in Pennsylvania Creates a Depauperate Forest Dominated by an Understory Tree: Results from a 60-Year-Old Deer Exclosure. *Journal of the Torrey Botanical Society*, **138**, 322-326. <https://doi.org/10.3159/TORREY-D-11-00018.1>
- [91] Allen-Diaz, B.H. and Bartolome, J.W. (1992) Survival of *Quercus douglasii* (Fagaceae) Seedlings under the Influence of Fire and Grazing. *Madrono*, **39**, 47-53.
- [92] McPherson, G.R. (1993) Effects of Herbivory and Herb Interference on Oak Establishment in a Semi-Arid Temperate Savannah. *Journal of Vegetation Science*, **4**, 687-692. <https://doi.org/10.2307/3236134>
- [93] Bonfil, C. (1998) The Effects of Seed Size, Cotyledon Reserves, and Herbivory on Seedling Survival and Growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). *American Journal of Botany*, **85**, 79-87. <https://doi.org/10.2307/2446557>
- [94] Reynolds, H.G., Warren, P.C. and Ffolliott, P.F. (1970) Gambel Oak for Southwestern Wildlife. *Journal of Forestry*, **68**, 545-547.
- [95] Shaw, M.W. (1968) Factors Affecting the Natural Regeneration of Sessile Oak (*Quercus petraea*) in North Wales: II. Acorn Losses and Germination under Field Conditions. *Journal of Ecology*, **56**, 647-660. <https://doi.org/10.2307/2258097>
- [96] Bock, C.E. and Bock, J.H. (1974) Geographical Ecology of Acorn Woodpeckers: Diversity versus Abundance of Resources. *American Naturalist*, **108**, 694-698.
<https://doi.org/10.1086/282945>
- [97] Barnett, R.J. (1977) The Effect of Burial by Squirrels on Germination and Survival of Oak and Hickory nuts. *American Midland Naturalist*, **98**, 319-330.
<https://doi.org/10.2307/2424983>
- [98] Smith, C.C. and Reichman, O.J. (1984) The Evolution of Food Caching by Birds and Mammals. *Annual Review of Ecology and Systematics*, **15**, 329-351.
<https://doi.org/10.1146/annurev.es.15.110184.001553>
- [99] Sork, V.L. (1984) Examination of Seed Dispersal and Survival in Red Oak (*Quercus rubra* Fagaceae), Using Metal-Tagged Acorns. *Ecology*, **65**, 1020-1022.
<https://doi.org/10.2307/1938075>

- [100] Borchert, M.I., Davis, F.W., Michaelsen, J. and Oyler, L.D. (1989) Interaction of Factors Affecting Seedling Recruitment of Blue Oak (*Quercus douglasii*) in California. *Ecology*, **70**, 389-404. <https://doi.org/10.2307/1937544>
- [101] DeGrange, A.R., Fitzpatrick, J.W., Layne, J.N. and Woolfenden, G.E. (1989) Acorn Harvesting by Florida Scrub Jays. *Ecology*, **70**, 348-356. <https://doi.org/10.2307/1937539>
- [102] Johnson, W.C. and Webb, T.I. (1989) The Role of Blue Jays (*Cyanocitta cristata* L.) in the Postglacial Dispersal of Fagaceous Trees in Eastern North America. *Journal of Biogeography*, **16**, 561-571. <https://doi.org/10.2307/2845211>
- [103] Herrera, J. (1995) Acorn Predation and Seedling Production in a Low-Density Population of Cork Oak (*Quercus suber* L.). *Forest Ecology and Management*, **76**, 197-201.
- [104] Iida, S. (1996) Quantitative Analysis of Acorn Transportation by Rodents Using Magnetic Locator. *Vegetatio*, **124**, 39-43. <https://doi.org/10.1007/BF00045142>
- [105] Anderson, L.J., Brumbaugh, S.M. and Jackson, R.B. (2001) Water and Tree-Understory Interactions: A Natural Experiment in a Savanna with Oak Wilt. *Ecology*, **82**, 33-39.
- [106] Bennett, J.A., *et al.* (2017) Plant-Soil Feedbacks and Mycorrhizal Type Influence Temperate Forest Population Dynamics. *Science*, **355**, 181-184. <https://doi.org/10.1126/science.aai8212>



Scientific Research Publishing

Submit or recommend next manuscript to SCIRP and we will provide best service for you:

Accepting pre-submission inquiries through Email, Facebook, LinkedIn, Twitter, etc.

A wide selection of journals (inclusive of 9 subjects, more than 200 journals)

Providing 24-hour high-quality service

User-friendly online submission system

Fair and swift peer-review system

Efficient typesetting and proofreading procedure

Display of the result of downloads and visits, as well as the number of cited articles

Maximum dissemination of your research work

Submit your manuscript at: <http://papersubmission.scirp.org/>

Or contact ajps@scirp.org

