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Creosote Bush, an Arid Zone Survivor in Southwestern U.S.: 1. Identification of Morphological and Environmental Factors that Affect Its Growth and Development

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Authors' contributions

This work was carried out in collaboration between all authors. Authors SK and JRK designed the study, performed the statistical analysis and wrote the protocol. Author SK wrote the first draft of the manuscript. Authors SK, JRK and LL managed the analyses of the study. Author SK managed the literature searches. All authors read and approved the final manuscript.

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ABSTRACT

Creosote bush (*Larrea tridentata* [DC.] Cov.) is a perennial shrub which is a major dominant species in arid rangelands in southwestern Texas, U.S. Controlling creosote bush in desert rangelands is important because as it increases in density, perennial grass production is reduced. The purpose of this study was to investigate the association between morphological characteristics and understand how these characteristics interact with the environment to affect production of creosote bush. In this study, a range of morphological traits was investigated at several southwestern Texas sites, and growth ring and growth rate were o measured. Creosote bush plants with a wide range of ages occurred mostly in pure stands and sometimes in small groups in

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all study sites. Two groups were categorized based on the crown size: CB1 (mostly conical-shaped shrubs) and CB2 (mostly large hemispherical-shaped shrubs). The proportion of CB1 and CB2 at a site affected creosote bush production. Creosote bush productivity was highly associated with soil water availability. In wetter sites, more CB2 shrubs occurred than CB1, resulting in higher production. The results of this study can improve understanding of the most important factors that affect creosote bush production, which is critical for developing management strategies for desert rangelands.

Keywords: Creosote bush; Larrea tridentata; morphology; desert rangeland; production.

1. INTRODUCTION

With the rapidly increasing demand for food due to population growth, urbanization, and increasing incomes in developing countries, increasing effort is placed on production of livestock in arid rangelands not suited for cultivation [1,2]. Arid rangelands are found across much of the southwestern U.S. and typically have low biological productivity due to several limiting factors including rough topography, shallow soil, low rainfall, and severe temperature [3-6]. To overcome these limitations, drought-resistant herbaceous species have been recognized as desirable grasses for livestock in these rangelands [7]. However, production of herbaceous vegetation has been reduced over large areas by invasion of woody shrubs [8-10]. Among these shrubs, creosote bush (*Larrea tridentata* [DC.] Cov.) is a dominant species [11-13]. This species has a well-developed lateral root system, extending far beyond the plant canopy that allows it to outcompete neighboring plants [13,14]. Also, shrub invasion in grasslands leads to reduced soil nitrogen (N) available to grasses accompanied by increased soil erosion, runoff, and leaching [15-18]. While herbaceous grasses have decreased in density due to a combination of impacts including grazing [19,20], creosote bush has widely increased on rangelands since 1900, covering up to 330 million hectares in the semi-arid western states in the U.S. [11,21-23]. Therefore, control of creosote bush may aid in increasing the stand of desirable herbaceous grasses [7] and improved livestock productivity of rangelands of the southwestern U.S.

To control creosote bush in arid rangelands, it is important to investigate factors that determine its distribution and abundance. This will improve the understanding of how this species rapidly spreads and maintains its community in large rangeland areas. Creosote bush is a xerophytic, evergreen, perennial shrub usually occurring in open, species-poor communities, sometimes in pure stands. The growth of creosote bush is largely limited by water availability, with most growth occurring in pulses associated with infrequent and highly variable precipitation [24-27]. Besides water, its productivity is also influenced by nitrogen availability [26-28]. According to Fisher et al. [29], larger increases in vegetative growth of creosote bush were observed at high nitrogen fertilization in irrigated and non-irrigated plots. When given adequate water and nitrogen, creosote bush plants are larger due to repeated production of new tillers [30,31]. As new tillers grow at the periphery or center of the shrub, external tiller angle decreases, and the conical shape of shrub gradually becomes hemispherical [30,31]. Thus, the shrub size and shape reflect its growth rate and age [30,31]. For example, in comparison with conical shaped shrubs, large hemispherical shaped shrubs may live longer and have higher growth rates.

Since creosote bush habitats vary considerably in precipitation, soil nutrients, and topological characteristics, the shrub size and shape and its distribution pattern are expected to vary from place to place and from time to time. Previous studies have reported physiological drought resistant characteristics [27,29,32,33] and several stress responsive and stress-tolerant genes [34,35]. Also, there are morphological variations in creosote bush among different water and nitrogen treatments [24-28,36]. The growth rate of creosote bush varies among sites [37-39]. However, there have been relatively few studies investigating associations between those morphological characteristics (e.g., height, crown diameter and leaf area). How the characteristics interact with the environment (e.g. slope, elevation, and water run off index) affects distribution, abundance, and production of creosote bush. Such studies are also important for providing useful data to improve understanding of creosote bush growth and development. They can be used to develop growth parameters for evergreen shrub simulation in process-based models such as ALMANAC [40]. Examples of growth variables include leaf area per unit leaf dry mass, which plays an important role in the processes of shrub growth and photosynthesis [41].

This study was conducted on creosote bush naturally growing in several sites located in western Texas. The study was aimed at understanding the growth variability among creosote bush populations to determine relationships between a range of morphological traits and production as well as to determine environmental factors affecting its distribution and abundance. Based on these results, priority traits for consideration in both the development of management strategies for arid rangelands and the development of a process-based model to improve yield estimation can be identified.

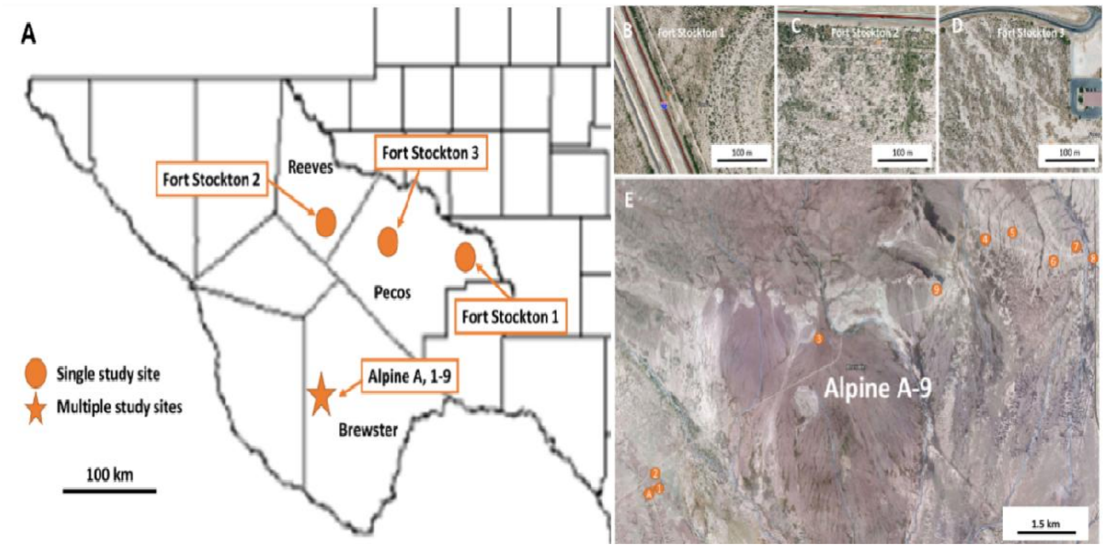

Fig. 1. Three counties conducted in this study (a) and all study sites detected from satellite images obtained from Web Soil Survey (available in http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx) (b-e). In image (a), a circle indicates that a single site was addressed, while a star indicates that multiple sites were addressed. In images (e), circles numbered as A to 9 show the study sites selected from Brewster county

Table 1. Elevation, soil type, hydrologic soil group, physical properties, carbonate availability, and water capacity of the upper 50 cm of soil at all study sites located in Reeves, Pecos, and Brewster counties in Texas, USA

Site ID	Elevation	Soil type	Percent soil particle (%)		
	m		Clay	Sand	Silt
Fort Stockton 1	726	Sanderson association, gently undulating	28	35.2	36.8
Fort Stockton 2	908	Reakor association, nearly level	26.8	30.3	42.8
Fort Stockton 3	928	Reakor association, nearly level	26.8	30.3	42.8
Alpine 1	1172	Quadria, Beewon and Musgrave soils	41.9	32.7	25.4
Alpine 2	1172	Quadria, Beewon and Musgrave soils	41.9	32.7	25.4
Alpine A	1172	Quadria, Beewon and Musgrave soils	41.9	32.7	25.4
Alpine 3	1208	Chilicotal very gravelly sandy loam	18.9	46.9	34.1
Alpine 4	1208	Crossen-Cienega complex	18.1	43.3	38.6
Alpine 5	1207	Crossen-Cienega complex	18.1	43.3	38.6
Alpine 6	1215	Mariscal-Rock outcrop complex	18.5	43	38.5
Alpine 7	1220	Mariscal-Rock outcrop complex	18.5	43	38.5
Alpine 8	1211	Crossen-Cienega complex	18.1	43.3	38.6
Alpine 9	1191	Gemelo and Straddlebug soils	15.8	62	22.2

The soil data was obtained from Soil Survey Staff, Natural Resources Conservation Service (SSURGO) (Available in http://websoilsurvey.nrcs.usda.gov/)

2. MATERIALS AND METHODS

2.1 Study Sites

This study was conducted at two sites in Pecos County (Fort Stockton 1 and 3), one site in Reeves County (Fort Stockton 2), and ten sites in Brewster County (Alpine A, 1-9), all in Texas (Fig. 1). Fort Stockton 1 was located in the highway right-of-way, 91 km west of Fort Stockton. Fort Stockton 2 was also located in the highway right-of-way, 61 km west of Fort Stockton. Fort Stockton 3 was inside Fort Stockton. Ten study sites (Alpine A, 1-9) were randomly selected within a 15 km wide distance on a large ranch 57 km south of Alpine. Alpine A was an airplane landing strip until 2005, so the creosote bush there has been established for only 12 years.

2.2 Soil Data

For all study sites, elevation, soil type, and percent soil particle were obtained from Web Soil Survey (available in http://websoilsurvey.sc.egov.usda.gov/App/Web SoilSurvey.aspx) (Table 1). For Alpine A and 1-9 sites, wetness index (WI), stream power index (SPI), specific contributing area, ridge top flatness index (RTF), potential evapotranspiration (PET), and annual water deficit (AWD) varied widely among sites (Table 2). Soils of these sites were downloaded from Soil Survey Geographic Database (SSURGO) (available in http://websoilsurvey.nrcs.usda.gov/). The WI and SPI were calculated with ArcGIS (ArcGIS 10.2.2, EsriInc, CA, USA). The WI is defined as Ln (a/tanB), where a is the specific local upslope area draining through a certain point per unit isoline length and tanB is the local slope in radians, measuring water accumulation or soil saturation [42]. SPI is the measurement of soil erosion as a function of local slope and upstream drainage area [43,44]. The specific contributing area and RTF were calculated from 10 m DEM using TauDEM software (Terrain Analysis Using Digital Elevation Models 5.3, David Tarboton, Utah State University, UT, USA). The specific contributing area (SCA) is defined as the planar area upslope of a surface element that drains to the element [45]. RTF is defined as measurement of flat upper parts of the landscape [46]. PET and AWD were calculated by the jNewhall program (Java Newhall Simulation Model 1.6.1, USDA, USA) using temperature and precipitation data derived from PRISM (NACSE, Oregon, USA; available in http://www.prism.oregonstate.edu/). PET is defined as the amount of evaporation that could occur if sufficient soil moisture is available [47]. AWD is defined as the amount of water by which PET exceeds actual evapotranspiration [48].

2.3 Climate Data

Three weather stations which are closest to the study sites were selected for analyses (Fig. 2). For Fort Stockton 1 and 3, the weather station inside Fort Stockton was selected. For Fort Stockton 2, the weather station in Balmorhea was selected, while the weather station inside Alpine was selected for Alpine A and 1-9. Total May to September precipitation from 1990 to 2015 was obtained from National Oceanic and Atmospheric Administration (NOAA) (available in http://www.ncDC..noaa.gov/cdo-web/search) (Fig. 2).

Table 2. Soil and topographic characteristics of Alpine A and 1-9

Site ID	Wetness Index (WI)	Stream Power Index (SPI)	Specific Contributing Area (SCA)	Ridge top Flatness index (RTF)	Potential Evapotranspiration (mm) (PET)	Annual Water Deficit (mm) (AWD)
Alpine 1	10.954	-0.55	181.47	4.57	920	582
Alpine 2	9.691	0.05	130.64	4.44	920	577
Alpine A	11.971	1.77	961.16	4.54	920	582
Alpine 3	9.209	0.48	127.22	3.60	904	545
Alpine 4	9.122	1.82	237.55	1.48	903	546
Alpine 5	7.978	1.61	121.00	0.25	901	546
Alpine 6	6.168	1.62	49.03	0.34	899	558
Alpine 7	5.039	1.81	30.75	0.01	899	556
Alpine 8	9.867	1.82	345.62	1.40	900	543
Alpine 9	8.669	1.48	159.91	0.99	906	564

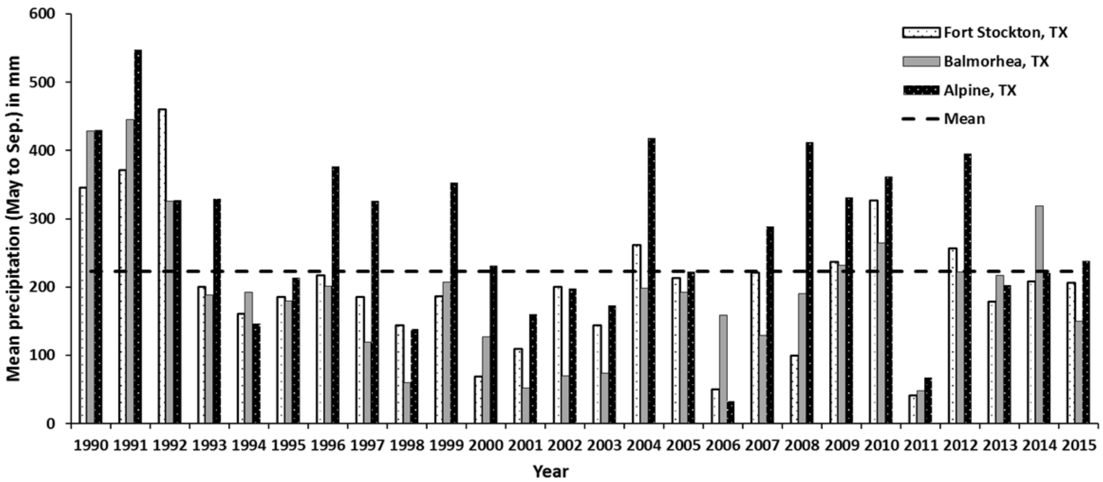

Fig. 2. Total precipitation (May – Sep) from 1990 to 2014 detected from three available weather stations close to study areas, located in Fort Stockton, Balmorhea, and Alpine, Texas, USA

The precipitation data is obtained from USA climate data (available in http://www.ncdc.noaa.gov/cdo-web/search)

2.4 Morphological Traits Collection

All measurements were performed from February to March in 2016. In Fort Stockton 1-3 and Alpine 1-3 locations, nine creosote bush of different sizes were randomly selected for measurements of plant weight, height, crown diameter, and crown diameter perpendicular to the maximum crown dimeter. Total fresh weights of each shrub and a subsample were weighed immediately following harvest. The subsample was dried in a forced-air 66°C oven until dry weight was stabilized. Shrub height was measured from the ground to the top of the highest leaf. Crown diameter was calculated by averaging the two perpendicular measured crown diameters. Crown size was calculated by multiplying two crown radii and pi (π). The shrub volume was calculated by assuming that the shrub was a cone. This consisted of multiplying the crown size by the shrub height and then dividing the outcome by 3. In all locations, shrub density and size distribution were estimated. In Fort Stockton 1-3, height, crown diameter and crown diameter perpendicular to the maximum crown dimeter were measured on all shrubs grown within a 15.24 m x 30.48 m. In Alpine 1-3, the same measurements were taken on all shrubs grown within a 15.24 m x 15.24 m area. In Alpine A and 4-9 sites, 15 shrubs were randomly selected to measure height, crown diameter, and crown diameter perpendicular to the maximum crown dimeter. For the shrub density measurement, number of shrubs was counted within a 15.24 m x 2 m area. The shrub yield was estimated using with total shrub dry weight and shrub density.

2.5 Intercepted Light and Leaf Area Measurements

In Fort Stockton 1-3 and Alpine 1-2 sites, Photosynthetically Active Radiation (PAR) measurements were taken using an AccuPAR LP-80 Ceptometer (Decagon Devices, Pullman, WA, USA) to enable calculation of Fraction of PAR intercepted (FIPAR). Measurement of FIPAR was taken between 10:00 and 14:00. Three sets of readings were made under shrub canopy within an 80 cm x 80 cm sampled area. Care was taken to avoid shadows from neighboring rows. Measurements of PAR were also taken with an external sensor above the shrubs concurrently with each below-canopy measurement. The multiple above and below readings were averaged to estimate FIPAR. FIPAR was calculated as ratio of PAR below canopy to PAR above canopy subtracted from 1.0. A subsample was harvested within each sample area for the light measurement. This subsample was brought to the laboratory for LAI estimation. In the laboratory, the subsample was weighed and then separated into green leaves, dark brown live woody material, and grey dead woody material. The leaf area was measured with a LI-3100 Area Meter (LI-COR Biosciences, Lincoln, NE, USA). LAI was calculated as leaf area of subsample (cm^2) divided by ground area sampled (cm^2), and then multiplied by the ratio of total fresh weight (g) to subsample fresh weight (g). The light extinction coefficient (k) was calculated by modified Beer's law, as described by Meki et al. [49]. The value of k was calculated as the natural log of difference between 1 and FIPAR, and then divided by LAI. No light measurement was taken in Alpine A, 3-9 sites.

2.6 Growth Ring and Growth Rate Measurements

The largest stem diameter tiller which had no damage from insects and disease was collected from each shrub sample in all study sites. A total of 174 tillers, including 9 tillers for Fort Stockton 1-3 and Alpine 1-3, 15 tillers for Alpine 4-9, and 5 tillers for Alpine A, were used for measurements of radius of cross section of sampled tiller, growth ring count, and growth rate. To count rings, a 1 -2 cm-thick section was sliced from each tiller. The cut surface was then sanded and polished using sand paper of grit size 60-300 and observed under a dissecting microscope at 10x magnification. Rings were counted along the longest radius, and the length of this radius was measured with a ruler. The shrub growth rate was length of the radius divided by number of growth rings. Age of the sampled tiller was estimated using historical weather data. We determined the age by counting the rings, starting with the outermost ring (youngest ring). Missing rings or false rings were corrected and checked using pointer years (extremely wide or narrow rings). As the growth of creosote bush in a dry year can be negligible, we assumed that no rings formed during severe drought years.

2.7 Statistical Data Analysis

Statistical analyses were performed using Statistical Analysis Software version 9.3 (SAS Institute., NC, USA). Two crown size groups, including CB1 (crown size < mean, 9098 cm^2) and CB2 (crown size > mean, 9098 cm^2), with population means for each variable were compared using Welch's t-test due to unequal sample sizes [50,51]. The Spearman's rank-order correlation coefficients and their statistical significance (rho=0) were determined for the relationships among the following traits: shrub weight, height, shrub volume, LAI, growth ring number, and growth rate using data collected from Fort Stockton 1-3 and Alpine 1-3. To avoid any climate effects, data collected from Alpine A, 1-9 sites were only used for calculating the Spearman's rank-order correlation coefficients and their significance (rho=0) for the relationships among soil and topological characteristics and shrub production. The absolute value of correlation coefficient (r) represents a very strong correlation if above 0.8, a strong correlation if between 0.60-0.79, a moderate correlation if between 0.4 and 0.59, a weak correlation if between 0.20-0.39, and a very weak correlation if below 0.19 [52].

3. RESULTS

3.1 Soil and Climates

Study sites were each characterized as to elevation, soil type, and percent soil particles (Table 1). Fort Stockton 1 had lower elevation, different soil type, and percent soil particles from the other two Fort Stockton sites. In general, Alpine sites had higher elevation than Fort Stockton sites. Although Alpine sites were selected only within a small portion of a large ranch, sites differed in soil and topological characteristics (Tables 1 and 2). For example, Alpine 1 and 2 sites are close to each other and have the same soil characteristics. However, Alpine 1 had a negative SPI. This means that Alpine 1 had a lower potential for overland erosion during runoff events, resulting in higher value of WI. In addition, Alpine 7, which was located along the side of a hill, had the smallest RTF and Specific Contributing Area, resulting in the lowest WI.

Similar rainfall patterns were observed between the three weather stations close to the study sites (Fig. 2). Overall, more rainfall was received in Alpine between 1990 and 2015. Heavy rainfall occurred at all three stations from 1990 to 1992. The total annual rainfall was under 223 mm after 1992 in both the Fort Stockton and Balmorhea stations (Fig. 2). Several severe drought years were also observed from 2001 to 2011 at all three weather stations.

3.2 Morphological and Density Measurements

Shrubs were divided into two groups based on shrub crown size (cm^2): CB1 and CB2 (Fig. 3). CB1 consisted of shrubs with a crown size smaller than 9098 cm^2, while CB2 shrubs were larger than 9098 cm^2. With their larger crown sizes, CB2 shrubs had significantly larger mean values for dry weight per shrub, height, volume, and LAI (All P< 0.0001, Table 3). However, light extinction coefficient of CB2 was not significantly different from CB1 shrubs (P = 0.5636, Table 3). Shrub density and distribution patterns of CB1 and CB2 shrubs varied extensively from one study site to another (Fig. 4 and Table 4).

In general, shrub density increased as CB1 shrubs occurred more frequently within the area. For example, the highest shrub density was observed in Alpine 5, consisted of only CB1 shrubs, while the lowest shrub density, observed in Fort Stockton 1, consisted of 47% CB1 and 53% CB2. Greater densities of CB2 shrubs resulted in greater values of total canopy cover per area (Fig. 5). For example, Alpine 1 had the highest density of CB2 shrubs and the greatest canopy cover within the area (Fig. 5). Total yield of creosote bush was mainly due to total shrub density and proportion of CB2 shrubs within the area. The greatest yield was observed in Alpine 8, which has 3.47 Mg/ha yield potential. The lowest yield potential was observed in Alpine 4, where the shrub density was 1408 shrubs per hectare and only had CB1 shrubs (Table 4).

Table 3. Means of dry weight, height, volume, stem basal diameter, leaf area index, and light extinction coefficient of the two creosote bush (*Larrea tridentata* [DC.] Cov.) Crown size groups: CB1 (crown size < mean, 9098 cm^2) and CB2 (crown size > mean, 9098 cm^2). Welch's t-test comparison between the two crown size groups was performed for each variable at 0.05 probability level [50,51]

	CB1	CB2	Welch's test *P*-value
Dry weight (kg/shrub)	0.28	1.7	<0.0001
Shrub height (m)	0.72	1.2	<0.0001
Shrub volume (m^3)	0.12	0.71	<0.0001
Stem basal diameter (mm)	7.07	13.29	<0.0001
Leaf area index (LAI)	0.36	1.39	<0.0001
Light extinction coefficient (K)	-0.76	-0.66	0.5636

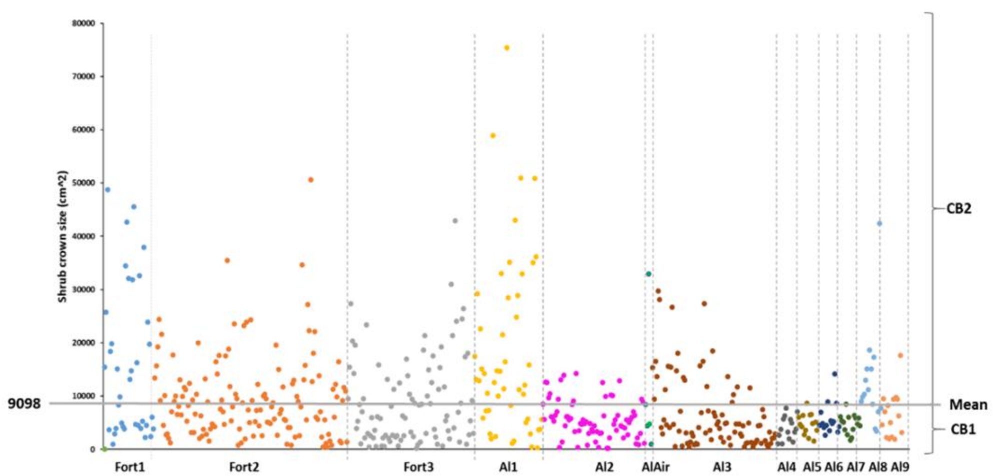

Fig. 3. Scatter plot of crown size of creosote bush (*Larrea tridentata* [DC.] Cov.)
Samples collected from all study sites including Fort Stockton (Fort) 1-3 and Alpine (Al) 1 – 9. Two groups were categorized based on the crown size: CB1 (crown size < mean, 9098 cm^2) and CB2 (crown size > mean, 9098 cm^2)

Fig. 4. Photographs of creosote bush (*Larrea tridentata* [DC.] Cov.) distribution in three study sites

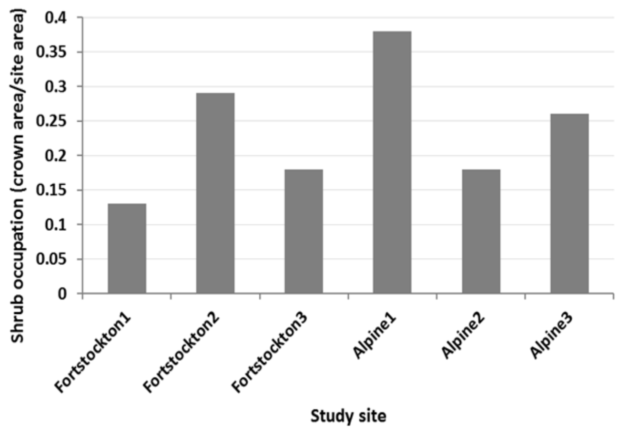

Fig. 5. Proportion of total creosote bush (*Larrea tridentata* [DC.] Cov.) canopy cover over each study site area

Table 4. Total shrub density, occurrences (in proportion of total) and yields of the two creosote bush (*Larrea tridentata* [DC.] Cov.) crown size groups: CB1 (crown size < mean, 9098 cm^2) and CB2 (crown size > mean, 9098 cm^2)

Site ID	Plant density	Crown size distribution of total (%)		Yield Mg/ha		
	no./ha	CB1	CB2	CB1	CB2	Total
Fort Stockton 1	808	47.22	52.78	0.11	0.73	0.84
Fort Stockton 2	3116	56.83	43.17	0.50	2.31	2.81
Fort Stockton 3	2041	61.54	38.46	0.35	1.35	1.70
Alpine 1	2125	34.69	65.31	0.21	2.39	2.60
Alpine 2	3207	81.08	18.92	0.73	1.04	1.77
Air	-	80	20	-	-	-
Alpine 3	3902	74.44	25.56	0.81	1.72	2.53
Alpine 4	1408	100	0	0.39	0.00	0.39
Alpine 5	3359	100	0	0.94	0.00	0.94
Alpine 6	3143	93.33	6.67	0.82	0.36	1.18
Alpine 7	2060	100	0	0.58	0.00	0.58
Alpine 8	3034	40	60	0.34	3.13	3.47
Alpine 9	2601	67	33	0.49	1.48	1.97

-, Indicate that data is not available

3.3 Growth Ring and Growth Rate Measurements

A single creosote bush clone is comprised of tillers of various ages (Fig. 6). The tiller thickness was directly related to the growth ring numbers (shrub's age). More growth rings were observed in thickest tillers (oldest tillers), and fewer growth rings were observed in thinner tillers (younger tillers) (Fig. 6 b-d). Older tillers were positioned in the peripheral side within a clone, while younger tillers were usually in central regions of a clone (Fig. 6a). Gray-colored dead tillers were observed mostly in either central or peripheral regions of a clone (Fig. 6a).

The number of growth rings and the growth rate varied widely among sites (Table 5). Growth ring numbers varied from 3 to 18. The calculated year for initiating sampled tillers were estimated based on historical climate data with the assumption of no shrub growth rings formed during severe drought years. The calculated initiation years varied from 1987 to 2012. The oldest tiller was 18 years old and was initiated in 1987 at the Fort Stockton 1 site. Mean number of growth rings for CB2 was usually greater than CB1 shrubs. Due to severe damage from insects and disease in the thickest tillers within each clone, the sampled tiller was not the thickest tiller for some sampled shrubs. Thus, the ages of sampled tillers may not always reflect to shrub size. Growth rates also varied among sites. The highest growth rates were observed in Alpine 1 and Alpine 3 sites, while the lowest growth rates were observed in Fort Stockton 2 and Alpine 4.

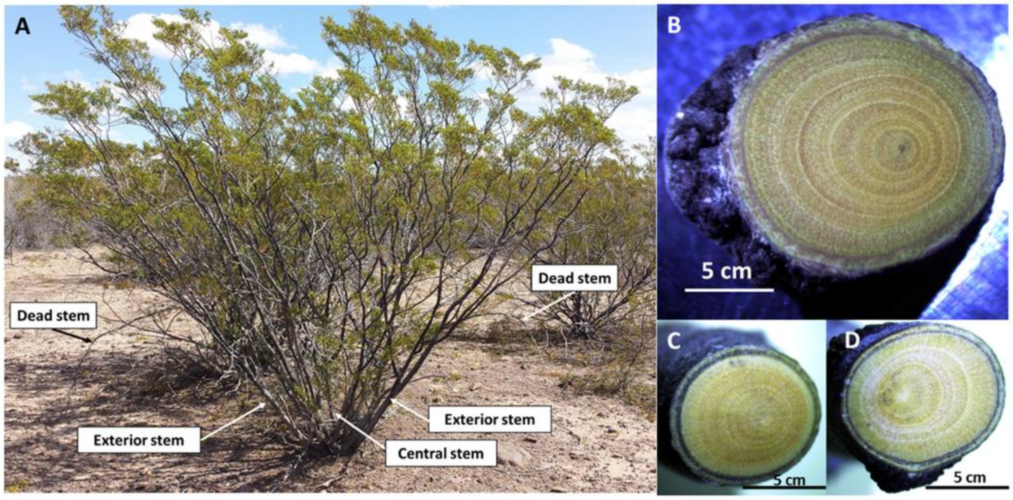

Fig. 6. Photographs of a creosote bush (*Larrea tridentata* [DC.] Cov.) (A) and its stem cross sections of an older stem (B) and younger stems (C and D)

Table 5. Means of each creosote bush (*Larrea tridentata* [DC.] Cov.) crown size groups: CB1 (crown size < 9098 cm^2) and CB2 (crown size > 9098 cm^2). Minimum and maximum values of number of growth rings, growth rate, and expected year of initiating stems that were used for counting age ring for shrub samples collected from all study sites

Site ID	No. of growth rings				Growth rate	Expected
	Mean		Min.	Max.		
	CB1	CB2			mm/no.	Initiate stem
Fort Stockton 1	8	15	3	18	0.66	1987-2008
Fort Stockton 2	6	11	4.5	14	0.62	1996-2010
Fort Stockton 3	9	9	7	10.5	0.70	2002-2005
Alpine 1	7	11	6	13	0.85	1999-2007
Alpine 2	5	8	4	9	0.68	2003-2010
Air	5	-	3	5	0.88	2009-2012
Alpine 3	6	10	5	13	0.71	1994-2006
Alpine 4	6	-	4	8	0.62	2004-2010
Alpine 5	7	-	5	10	0.69	2000-2009
Alpine 6	6	8	4	8	0.77	2004-2010
Alpine 7	7	8	4	11	0.67	1999-2010
Alpine 8	9	8	5	13	0.77	1996-2009
Alpine 9	7	7	4	10	0.78	2000-2010

3.4 Correlation among the Traits

Shrub height, volume, LAI, and growth ring number were strongly correlated with shrub dry weight (all $r > 0.7$ and $P \leq 0.0001$, Table 6). Growth ring number was also strongly correlated with shrub height ($r = 0.78$) and volume ($r = 0.79$).

To avoid climate effects, only data obtained from Alpine sites were used to estimate correlation among yield, shrub density and the soil characteristics listed in Tables 1 and 2. Critical soil factors that moderately influenced creosote bush production was identified (Table 7). The density of CB1 was negatively correlated with yield ($r = -0.95$ and $P < 0.0001$). The yield was positively correlated with WI ($r=0.73$ and $P=0.02$). The density of CB1 was also dependent on WI ($r = -0.76$ and $P = 0.02$). There were some moderate and strong association features between soil and topological characteristics (Table 7). WI, SPI, RTF, and PET were either very strongly or strongly associated with elevation (all $r > 0.60$ and $P \leq 0.05$). WI was positively dependent on SCA, RTF, and PET (all $r > 0.53$ and $P \leq 0.05$). SPI was negatively correlated with PET and AWD (all $r < -0.78$ and $r > 0.53$) and the proportion of clay in soil ($r=-0.64$ and $P=0.07$), and was positively correlated with the proportion of silt (r=0.79 and *P*=0.01). RTF had positive correlation with PET (r=0.82 and *P*=0.01). PET and AWD had negative correlation with the proportion of silt in soil (all $r < -0.67$ and $P \leq 0.05$). The proportion of clay had negative correlation with the proportion of sand in soil ($r < -0.74$ and P=0.02).

Table 6. Phenotypic correlation coefficient among morphological and growth characteristics evaluated for creosote bush (*Larrea tridentata* [DC.] Cov.) collected from 6 study sites including Fort Stockton 1-3 and Alpine 1-3. PW: Plant weight; HT: Plant height; VL: Plant volume; LAI: Leaf area index; RC: Growth ring number; GR: Growth rate. The absolute value of correlation coefficient (r) represents a very strong correlation if above 0.8, a strong correlation if between 0.60-0.79, a moderate correlation if between 0.40 and 0.59, a weak correlation if between 0.20-0.39, and a very weak correlation if below 0.19 [52]

Traits	PW	HT	VL	LAI	RC
HT	0.82***				
VL	0.93***	0.88***			
LAI	0.83****	0.69***	0.79***		
RC	0.78***	0.78***	0.79***	0.69***	
GR	0.36*	0.38**	0.35**	0.25	0.15

*According to significance test of Spearman's correlation (rh0=0), ***significantly at P ≤ 0.0001, ** significantly at P ≤ 0.01, and * significantly at P ≤ 0.05*

4. DISCUSSION

Overall, creosote bush plants were randomly distributed in every study site; occurred mostly in isolated, nearly pure stands and sometimes in small groups; and represented a wide range of shrub ages 3 – 18 years. Each shrub had different ages of tillers, so the thickest tillers with the most growth rings were assumed to be close to the shrubs' actual age. However, the estimated ages of the oldest creosote bush in this study were relatively younger than creosote bush reported in previous studies [37,38,39,53]. Because most of the thickest tillers had damage from insects, disease, or drought, the bushes may be older than the measured values. The growth rate was estimated based on the number of growth rings and the tiller radius. Growth rates in the range of 0.62 to 0.88 mm of radius of dissected tiller per number of growth rings counted were observed. Similar growth rates have been observed in the Mojave Desert [39]. The sample tiller initiation year was also estimated. According to Orwig and Abrams [54], growth rings are indicators of annual climatic information shown as radial growth responses. These indicate the reaction of trees to past periodic droughts. In this study, either no formation of a growth ring or the presence of a very narrow radius between rings was observed during severe drought years. Thus, fewer rings than years of age were observed in most shrubs, which is common in many conditions [55,56].

Table 7. Correlation coefficients among yield, density, and occurrences of creosote bush (*Larrea tridentata* [DC.] Cov.) crown size group of CB1 (crown size < 9098.29 cm^2), and soil and topographic characteristics evaluated from Alpine 1-9. WI: Wetness index; SPI: Stream power index; SCA: Specific contributing area; RTF: Ridge top flatness index; PET: Potential evapotranspiration; and AWD: Annual water deficit. The absolute value of correlation coefficient (r) represents a very strong correlation if above 0.8, a strong correlation if between 0.60-0.79, a moderate correlation if between 0.40 and 0.59, a weak correlation if between 0.20-0.39, and a very weak correlation if below 0.19 [52]

Traits	Yield	Total density	CB1 %	Elevation	WI	SPI	SCA	RTF	PET	AWD	Clay	Sand
Density	0.32											
CB1	-0.95***	-0.08										
Elevation	-0.31	-0.17	0.43									
WI	0.73*	0.07	-0.76*	-0.60*								
SPI	-0.4	-0.4	0.46	0.76*	-0.39							
SCA	0.47	-0.3	-0.56	-0.39	0.78*	0.11						
RTF	0.52	0.07	-0.61	-0.67*	0.88**	-0.58	0.6					
PET	0.38	0.1	-0.51	-0.94**	0.68*	-0.78*	0.45	0.82*				
AWD	0	-0.23	-0.22	-0.58	0.08	-0.66*	-0.13	0.3	0.53			
Clay	0.21	0.22	-0.21	-0.26	0.37	-0.64	-0.21	0.57	0.36	0.43		
Sand	0.06	0.17	0	0.16	-0.18	0.29	0.16	-0.27	-0.1	-0.58	-0.74*	
Silt	-0.37	-0.07	0.52	0.57	-0.21	0.79*	0.06	-0.42	-0.67*	-0.74*	-0.37	0.11

*According to significance test of Spearman's correlation (rh0=0), ***significantly at P ≤ 0.0001, ** significantly at P ≤ 0.01, and * significantly at P ≤ 0.05*

Based on correlation analysis, shrub age was positively correlated with shrub height and volume. In this study, the two groups CB1 and CB2 were categorized based on shrub crown size. CB1 shrubs were mostly conical-shaped shrubs, while CB2 shrubs were large hemispherical-shaped shrubs. CB2 shrubs had significantly larger values in height, volume, and leaf area index (LAI) than CB1 shrubs, resulting in 6 times greater dry weight than CB1. Although canopy light extinction coefficient (k) of CB2 was not significantly different from CB1 shrubs, the higher growth rate in CB2 appeared to be related to lower k values than CB1. The k value is a parameter that describes the efficiency of light interception for the canopy of the shrub and is influenced mainly by the leaf angle [57]. A low k indicates that more radiation can reach the bottom of the canopy, while a high k indicates that less radiation can pass through the canopy. The gradually increased number of new tiller may lead to decreased external tiller angles, resulting in smaller k values in CB2 shrubs. According to Smith and Hamel [58], the CB2 shrubs with smaller k values may have more even light distribution within their canopies and less light saturation for photosynthesis of individual leaves. Since CB2 shrub weight was much greater than CB1 shrubs, the total yield (Mg/ha) of creosote bush in each site was highly affected by the proportion of CB1 and CB2 within the area. For example, in Alpine 4 and 5 sites, only CB1 shrubs were present. Biomass production was lower than 1.0 Mg/ha at both sites. In contrast, in Alpine 1 and 8, CB2 shrubs occurred more frequently than CB1 shrubs, which resulted in higher yield production. Calculated yields were 2.59 Mg/ha in Alpine 1 and 3.47 Mg/ha in Alpine 8.

The proportion of CB1 and CB2 shrubs varied across study sites with different climate, soil and topological characteristics. According to association analysis, the proportion of CB1 was negatively associated with WI, leading to a positive association between the proportion of CB2 and WI. The WI was strongly associated with Specific Contributing Area (SCA), referring to area per unit contour length (SCA= TCA / w), and TCA (Total Contributing Area) is a contributing area, also known as basin area, upslope area, or flow accumulation, of interest [59]. The concept of SCA is critical for hydrologic application since it can be interpreted as an equivalent water flow path length [59,60]. With a given high WI, shrub growth rates increased, resulting in increased production of new tillers within a clone. With increased new tiller production within a clone, conical-shaped shrubs rapidly became large hemispherical-shaped shrubs. This is why CB2 shrubs were more frequently found in wet areas than dry regions. Similar results have been observed in several studies which reported that creosote growth is highly dependent upon soil water availability [24-27].

Although the proportion of CB1 and CB2 shrubs was not significantly affected by RTF, the proportion of CB1 was strongly associated with land slope (r=-0.61 and P=0.08). In this study, there were fewer and smaller creosote bushes along the hillsides. This may be related to the positive correlation between WI and RTF, which means that water availability becomes more limited in slope areas. Due to high water limitation, creosote bush may become either less dominant or drop out completely on some of the steepest slopes. This is why creosote bush is dominant only on gentle slopes, valley floors, sandy flats, and in arroyos [61-63].

5. CONCLUSION

Each study site has different proportions of CB1 and CB2 shrubs (grouped based on shrub crop size). CB1 shrubs included mostly younger conical shaped shrubs, while CB2 shrubs included older, larger, hemispherical shaped shrubs. The proportion of CB1 and CB2 was an important factor for creosote bush production. Creosote bush production was also mostly influenced by soil water availability because CB2 shrubs occurred more frequently in wet soils. This study identified some important factors that affect creosote bush production in rangelands in southwestern Texas. These findings will help to improve creosote bush control strategies and will be useful for developing modeling tools to predict yields of these evergreen shrubs in rangelands.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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