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CREOSOTE BUSH: LONG-LIVED CLONES IN THE MOJAVE DESERT[1]

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ABSTRACT

Creosote bush clones in the Mojave Desert develop by irregular radial growth, stem segmentation and the production of new stems at the outer edge of stem segments. The resulting circular clone encloses a central bare area as the central dead wood rots away. Old clones become elliptical and may exceed 20 m in length. Modern growth rates estimated from annual increments in stem wood of seedlings (0.73 mm/yr) and young clones (0.82 mm/yr) approximate those estimated for radiocarbon-dated wood samples (0.66 mm/yr). Assuming comparable growth rates through time, the extrapolated age of the largest known clone (average radius = 7.8 m) may approach 11,700 years. If growth rates have changed, that clone's age may be somewhat less.

CREOSOTE BUSH, *Larrea tridentata* (Sesse and Moc. ex DC) Cov., is a common, widespread, and often dominant plant over desert areas of the southwestern United States and northern Mexico. Numerous studies have been made into creosote bush ecology, distribution, reproduction, development, phenology, community structure, use by animals, etc. (see Mabry, Hunziker, and Difco, 1977 for summary).

Despite an extensive literature on creosote bush, its age and longevity have received scant attention. Large shrubs near Tucson, Arizona, were estimated at ages "well in excess of 100 years" on the basis that little change in size or bulk occurred during the course of a 30-year photographic record (Shreve and Hinckley, 1937). A population in southern Arizona, expanding after historically recent invasion, included plants approaching 65 years of age as estimated from counts of growth increments in stems (Chew and Chew, 1965).

Large clumps of several separate bushes or crowns were observed by Barbour (1969) who suggested that bushes may be aggregated as a result of asexual reproduction. The development of clones was briefly described (Vasek, Johnson, and Eslinger, 1975; Vasek and Barbour, 1977) as a process in which radial growth, the repeated production of new branches at the periphery of a crown, the death of old branches at the center of a crown, and eventual segmentation of a crown led to circular clumps of satellite bushes with dead stems or, eventually, a sterile or bare area in the center. With increased age the central bare area increases in size as the satellite bushes grow away from the center. The circular shape of a clone gradually becomes elliptical (Vasek and Barbour, 1977) owing to differential growth rates within the clone. The satellite members of clones were shown by isoenzyme analysis to be genetically the same within any one clone (Sternberg, 1976). Creosote bush clones were estimated to attain ages of several thousand years on the basis of growth rates derived from radiocarbon ages of two wood samples (Vasek et al., 1975; Sternberg, 1976).

However, two radiocarbon dates constitute a narrow base from which to project age estimates. Since creosote bush habitats vary considerably with regard to soils, slopes, exposures, elevations, precipitation, etc., its growth rate is expected to vary from place to place and from time to time. Consequently, a study was undertaken to determine growth rates in seedlings and clones on a variety of substrates in several localities. The objective of that study was to obtain growth rates from which the age of large clones could be estimated.

MATERIALS AND METHODS—Materials for analysis, either stems or wood fragments, were collected from several localities in the Mojave Desert of California as detailed in Table 1.

Two main methods were used to determine growth rates and to estimate ages of plants: counts of growth rings in stems, and radiocarbon dating of old wood samples. For purposes of this study, seedlings are defined as plants with a single main stem near ground level. Plants in which the stem undergoes segmentation into several (usually three) crowns are really young clones and not seedlings. Such

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TABLE 1. *Geographic location and elevation of creosote bush sampling areas, all in San Bernardino County (SB) or Los Angeles County (LA), California. In the reference description, letters refer to compass direction and numbers give approximate distance in km from the indicated reference town or place. Precipitation data came from the reference place except for Johnson Valley (data from 8 km east of study site) and Sheephole Pass (data from 6.5 km south of sampled location). Precipitation data extracted from published records of the US Environmental Data Service and the San Bernardino County Flood Control District*

No.	Locality	Elev.(m)	Reference	Elev.(m)	Ppt.(mm)
1	Black Butte	946	LA, 32 E Palmdale	717	225.3
2	Victorville	854	SB, 9.7 NNW Victorville	871	135.7
3	N. Lucerne Valley	976	SB, 19 NNE Lucerne Valley	919	108.2
4	S. Ord Fan	1,098	SB, 22.5 NE Lucerne Valley	919	108.2
5	Johnson Valley	921	SB, 3.2 N Old Woman Springs	852	91.8
6	Amboy	207	SB, 1.6 W Amboy	190	51.9
7	Sheephole Pass	732	SB, 32 S Amboy	372	53.9
8	Granite Pass	1,220	SB, 29 NNE Amboy	190	—
9	Cedar Canyon Fan	1,183	SB, 8 SSE Cima	1,282	—
10	Sacramento Mts.	793	SB, 26 W Needles	278	112.0

segmentation usually occurs well before a creosote bush reaches 90 or so years of age.

Stem growth increments—Growth rings were counted in seedlings and in stems of clone satellites. To count rings, seedlings in the field were measured, photographed and then excavated. In the laboratory, a 1–2-cm-(approx.) thick section was excised from the main, common stem below all the branches. The cut surface was then sanded, polished, wetted with water and observed under a dissecting microscope at magnifications of approximately 10× to 20×. Rings were counted along whatever radius gave the clearest count and that radius, usually the largest, was measured to the nearest 0.1 mm with the aid of a vernier caliper.

A question arises as to whether a growth ring is equivalent to an annual increment. As a partial control, a 12-year-old shrub growing in the UCR Botanical Garden was excavated, sectioned, and found to have 12 stem growth increments (Fig. 2). It, therefore, produced one increment per year. The mild winter conditions of Riverside were sufficiently cold to cause a seasonal secession of growth. Even though this plant had been irrigated regularly and had not been subjected to drought, it already was showing signs of segmentation (Fig. 2). Whether a plant in nature produces one ring every year is not known for certain. However, the occurrence of partial rings, and of more "rings" on the larger side of an eccentric stem than on the smaller side suggests that partial ring suppression does occur and that suppression of entire rings may also be expected. Thus, if any error occurs, it would be that the stem is actually older than estimated from ring counts. Such errors would yield higher growth rates than actually had occurred since growth rate is the summation of radial increments divided by the number of increments (years) and expressed in mm/year.

Rings are usually somewhat obscure, but are easiest to count in young stems. In old stems, the heartwood becomes dark with metabolic waste products and the rings become more obscure. Thus, the chance for counting error increases with older stems. In actual practice stems were counted several times by the same investigator. If the counts differed by more than 10%, those stems were studied carefully and recounted. If counts were similar, i.e., within a 10% difference, the nearest whole number average was used. Therefore, ring counts are age estimates.

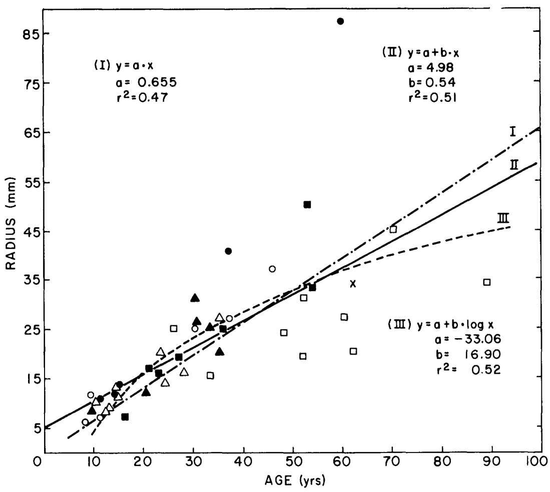


Fig. 1. Radial stem growth in creosote bush "seedlings." The several symbols correlate with the localities listed in Table 3 as follows: solid circles, Black Butte sandy; open circles, Black Butte rocky; solid squares, Victorville; X, S. Ord fan; open squares, Johnson Valley; solid triangles, Cedar Canyon fan; and open triangles, Sacramento Mts.

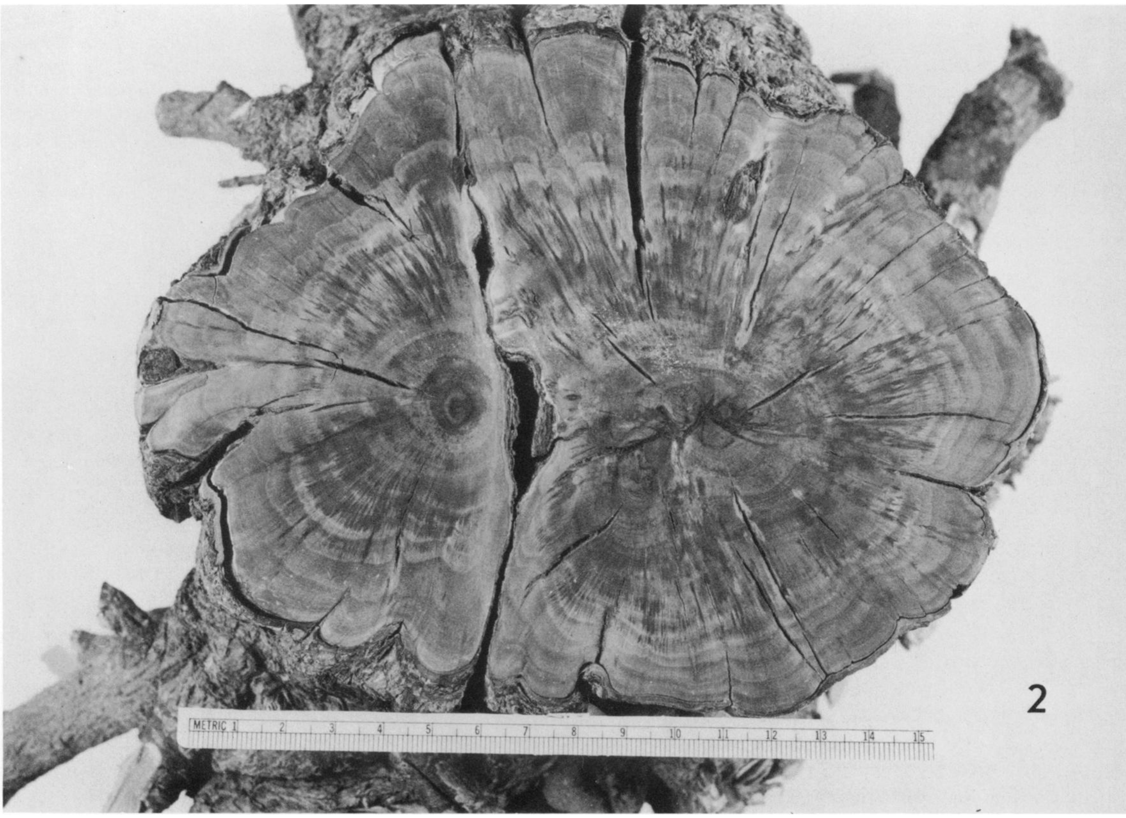


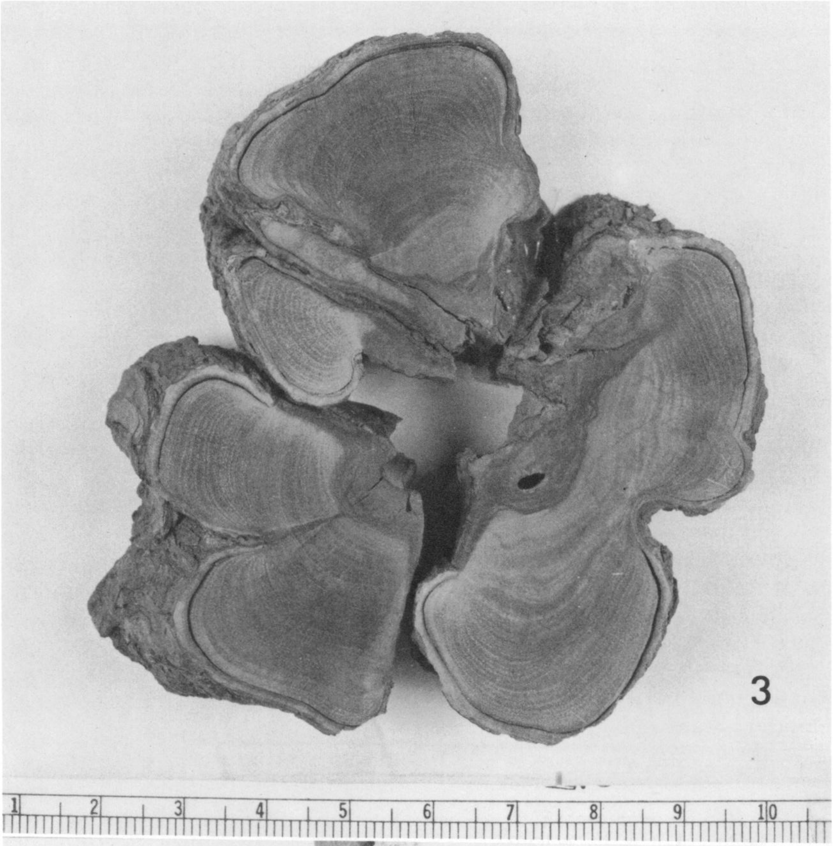
Fig. 2–4. Stem segmentation in creosote bush as seen in cross section. 2. A twelve-year-old plant grown from seed in the UCR Botanic Garden. 3. A native plant from Victorville. Note the hollow center, the compressed, dead wood with uncountable increments near the center, and necrotic areas between lobes of active growth. Counts varied from 29 to 39 increments along 5 different radial segments from 23 to 30 mm, yielding growth rates from 0.75 to 0.98 mm/yr and, by extrapolation to the center, age estimates of 42 to 56 years. A wood fragment 1 cm below the central hole of this section had a radiocarbon age of 235 ± 90 yrs. 4. A native plant from a sandy area at Black Butte with an estimated age of 60 yrs. Note the lobes of active growth and the wood splitting between lobes.

Wood of the Zygophyllaceae is described as diffuse porous (Metcalfe and Chalk, 1950). However, in *Larrea* I frequently observed a conspicuous concentration of vessels in a single row at the beginning of a growth increment. The remainder of that same increment, and also other entire increments, would have only a few scattered vessels.

Radiocarbon dating—Radiocarbon dates were determined for wood samples excavated from the interior of clones. First, areas with large or numerous clones were located in the Mojave Desert of San Bernardino County, California, with the aid of aerial photographs and general observations. Then clones in these areas were examined for evidence of old wood. Sometimes old stem crowns were apparent at the soil surface within the interior bare area of a clone; some clones accumulate a sand mound over the bare area and buried old wood was sometimes located by thrusting a pointed metal rod repeatedly into these sand mounds. Hundreds of clones showed no evidence of old wood and hence were not considered further.

Clones with evidence of old wood were photographed and measured. The central bare area was excavated in stages. The location of wood samples within a clone was recorded by a sketch, by distances measured to other samples and to living members of the clone, and by photographs. Excavated wood samples were tagged and taken to the laboratory where they were cleaned by scraping away soft, partially decayed outer layers. Hard inner portions weighing from 2 or 3 g up to about 40 g were coded and sent as blind samples to the UCR Radiocarbon Laboratory for analysis and dating.

Radiocarbon dates are subject to several possible sources of error. One important source is the systematic anomalies in radiation values over time. This variation has been studied by Suess (1970), utilizing high precision



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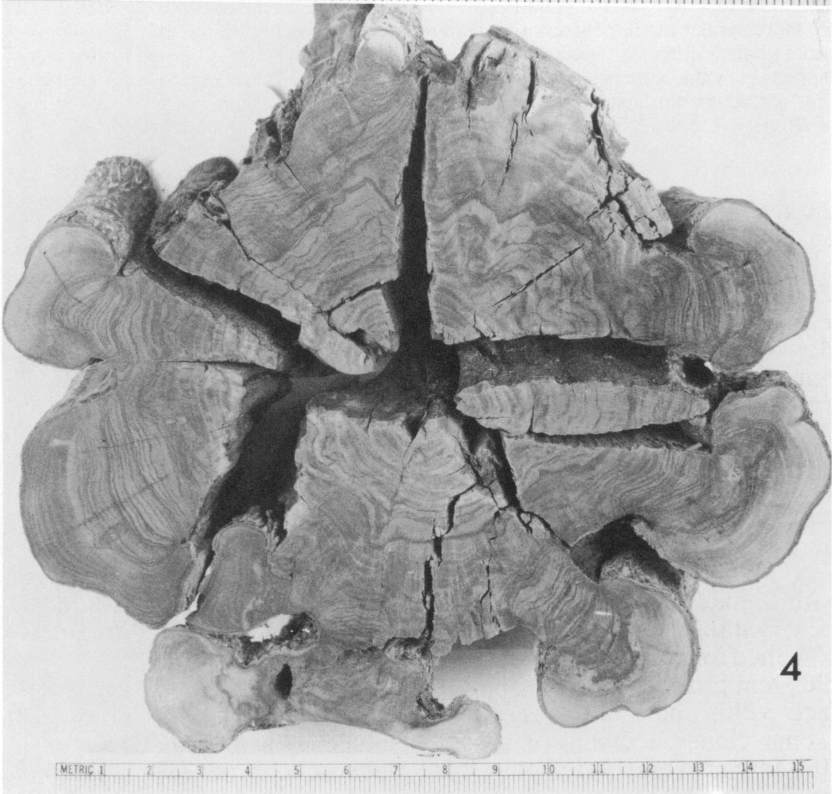

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radiocarbon determinations on dendrochronologically dated wood samples of bristlecone pine. These data allow radiocarbon values to be calibrated to calendar time periods back to 5200 B.C. A similar study, with similar conclusions and calibration, was made by Ralph, Michael, and Hann (1973).

The present study concerns material dating back about 700 years from the present. Two periods of time, from the present to about 190 years BP (before the present) and from about 220 to 330 BP, include anomalous episodes in which radiocarbon values have more than one calendar age equivalent. A narrow interval between 190 and 230 BP is available in principle, but counting errors of ± 100 years or so lend little confidence that a given date really falls within that interval. At 330 radiocarbon years BP, calendar values of about 400 BP and 520 BP may be read from the calibration curve (Suess, 1970). Beyond 330 BP, each radiocarbon value has a unique calendar age equivalent. However, the latter age is underestimated by about 100 years at 400 BP, and by about 50 years at 500 BP. The discrepancy decreases until virtual coincidence between radiocarbon years and calendar years occurs from about 600 to 700 BP. As a consequence, radiocarbon values less than 330 years must be used with great caution, if at all.

For this study, radiocarbon dates older than 330 BP were corrected according to the calibration curve of Suess (1970). Using the corrected age of wood samples, and the distance from that wood sample to other wood samples or to the nearest living clone member, a growth rate was calculated and expressed in mm/year. This growth rate is an average rate over the indicated period of time.

Two other sources of error are inaccuracies in determining distances and group age of dated wood samples. In the field, distances were measured from the center of a wood sample to the center of another wood sample or the center of a crown of a living clone member. Distances recorded to the nearest cm imply point-to-point precision. However, since both wood samples and living crowns are irregular in shape and vary in size up to several dm, the exact center cannot be determined with absolute confidence or precision. Furthermore, any given wood sample was produced over a series of years and therefore yields average data for an unknown period of time. Given these several sources of variation, the wood sample ages and the distances between "points" must be viewed as estimates.

RESULTS—*Growth pattern*—Creosote bush seedlings first develop one branch near ground level, then later develop several stem branches from a "stem crown." The initial central stem dies back leaving a hollow cone-shaped scaffold of branches. Later, stems arise at the periphery of the stem crown which continues to grow radially outward. However, that growth is not uniform, but occurs more rapidly in some arcs of the stem circumference than in others. Arcs of stems grow more rapidly below new branches whereas the stem sector between new branches grows more slowly or even stops growing. The stem, therefore, undergoes segmentation into several lobes or bulges of active growth separated by dead or inactive tissue (Fig. 2–4). Stem segmentation begins internally very early in seedling development and reaches a stage of several functionally separate ramets at about 40 to 90 years. For purposes of definition, isolation of ramets by dead stem tissue marks the end of the "seedling" stage and the beginning of a "young clonal" stage.

Similar stem segmentation has been described in *Artemisia, Zygophyllum,* and *Peganum* (Ginzburg,1963). Each stem segment develops its own root system with main roots leading out away from the clone. Each stem segment continues growing radially along an outer peripheral arc. Uneven growth along that arc results in continued segmentation of daughter stem crowns. That pattern continues indefinitely, resulting in a "ring" of satellite stem crowns around first a dead stem crown at the clone origin and then later around a bare area after the early stem crowns rot away. Eventually the clone may have a large central bare area surrounded by clusters of satellite shrubs. In this growth pattern, radial stem incrementation is interpreted to be the same as radial spread over the ground. Only occasionally does some type of layering produce a substantial departure from the described pattern. As expected in clonal configurations, the groups of satellite shrubs in any one clone are genetically identical on the basis of isoenzyme analysis (Sternberg, 1976). Larger clones become elliptical rather than circular indicating differential radial growth rates within a clone. The long axis of an elliptical clone tends to be oriented perpendicular to the slope of drainage or to the direction of strong winds. However, the reasons for such orientation and for the observed development of ellipses are not clear. Growth along a peripheral arc sometimes occurs more rapidly around the end of the arc and doubles back toward the center of the clone leading to irregularities in the shape of the ellipse.

A mound of sandy soil accumulates around or within most clones, sometimes to a depth of about 0.5 m. Even when a sandy mound

TABLE 2. *Radial stem growth of creosote bush seedlings from several Mojave Desert localities. SD = standard deviation, r = correlation coefficient*

		Age (no. rings)		Radius (mm)			Growth rate (mm/yr)	
	n	mean	SD	mean	SD		mean	SD
Black Butte Sandy	5	27.40	20.96	33.36	33.15	0.99	1.08	0.24
Black Butte Rocky	6	24.00	15.86	18.72	13.07	1.00	0.76	0.07
Victorville	7	32.86	15.38	23.61	13.97	0.92	0.69	0.15
S. Ord Fan	1	62.00	—	34.00	—	—	0.55	—
Johnson Valley	9	54.67	18.86	26.76	9.11	0.61	0.52	0.19
Cedar Cyn Fan	6	26.17	9.87	20.38	8.91	0.81	0.76	0.14
Sacramento Mts.	9	19.22	8.61	14.33	5.99	0.89	0.77	0.16
Total	43	32.44	19.55	22.57	14.94	0.71	0.73	0.22

does not accumulate, the soil within a clone has a finer texture than that without. In the Sacramento Mountains for example, soil outside a clone had 21% sand and 57% gravel, including large rock fragments over ten cm long, whereas soil within the clone had 69% sand and only 24% gravel, the latter rather uniform with few fragments exceeding one cm. Evidently the physical process of the clone's radial growth through the soil correlates with a breakdown of rocks and large particles. Many clones attain diameters of several meters, and the largest clones known to me have long diameters of 20–22 m.

Age distribution—Size and age distribution in creosote bush populations varies extensively from one place to another. Average seedling ages vary from 19 to about 60 years in the areas sampled in the present study (Table 2). The oldest observed seedling was 89 years (Fig. 1). Mostly older seedlings were found in Johnson Valley, but old seedlings could scarcely be found in the Sacramento Mountains or on Cedar Canyon Fan despite a diligent search for pre-segmenting plants of all sizes.

Large clones occur mostly on stable land surfaces such as gentle alluvial fans or flats and benches not subject to severe or even moderate erosion. Large clones are not found on steep slopes subject to rapid run-off and soil erosion. Such slopes hold seedlings, small clones and clone fragments.

Modern growth rates—Seedling growth rates range, on average, from about 0.5–1.0 mm per year of radial stem incrementation (Table 2), depending on locality, with an overall average of 0.73 mm/year. Radial length is fairly well correlated with age (on the total sample r = 0.71 and most of the subsamples have even higher correlation coefficients).

The growth rate data for seedlings (Fig. 1) may be represented by any of three equations as determined by curve fitting. However, equation III ($y = a + b [\log x]$) is not likely since a y intercept of -33 is difficult to conceive in terms of a radial distance. Equation I passes through the origin and has a slope of 0.65, in good agreement with the calculated average of 0.73. Equation II has a y intercept of $+5$ and a slightly lower slope (0.54). Both equations explain just over half the variation in the y values. The lower slopes of both equations suggest that the average seedling growth rate may actually be less than the calculated average of 0.73 mm/year.

Recent growth rates in young clones (Table

TABLE 3. *Radial stem increments in segments of young clones (at early stages of segmentation). Notations as in Table 2, except Age is indicated as the number of increments (arcs rather than rings) countable*

			Age (no. incr.)		Radial length (mm)			Growth rate (mm/yr)	
	Id. No.	*n*	mean	SD	mean	SD	r	mean	SD
Black Butte Rocky	831-6	3	26.00	6.24	17.53	3.23	0.38	0.70	0.19
Victorville	615-7	5	72.60	15.66	67.80	11.45	0.44	0.96	0.22
	615-10	2	65.50	19.09	52.95	19.16	1.00	0.80	0.06
	615-6	5	33.60	4.22	27.42	3.22	0.60	0.82	0.09
S. Ord Fan	330-3	1	55.00	—	31.80	—	—	0.58	—
Johnson Valley	712-1	1	34.00	—	25.50	—	—	0.75	—
Cedar Canyon Fan	705-3	2	32.50	0.71	27.00	0.14	1.00	0.83	0.01
Total (pooled sample)		19	47.05	21.51	39.26	21.17	0.92	0.82	0.17

TABLE 4. *Analysis of stem growth increments in three regions of one clone (Victorville 915-1; d_1 = 80 cm, d_2 = 60 cm): I and II represent paired observations from portions of the same living stem crowns: I = stem increments produced in the distal portion during the recent 1 to 3 decades; II = stem increments in the proximal portion produced probably from 3 to 10 decades BP (in all cases, I and II are separated by damaged, decayed, dead or complex wood with uncountable increments); III = old dead wood from the clone interior probably prior to about 100 years ago (J1 was carbon dated at 200 ± 130 BP [= @ 260 yrs.] but J2 was dated as >100 BP). Satellite A was intact with a total radial length of 65.2 mm. By extrapolation from the growth rates in I and II, A would be about 95 years old. By further extrapolation the clone would be about 584 years old since A is 40 cm from the clone origin. On the other hand, since the clone has an average radius of 35 cm and an average growth rate of 0.52 mm/yr, it should be about 673 years old*

	Satellite	No. of increments	Radial length (mm)	Growth Rate (mm/yr)
I	A	10	6.4	0.64
	B1	11	5.3	0.49
	B2	12	7.1	0.59
	C	22	8.4	0.43
	D1	23	12.2	0.53
	D2	26	13.2	0.52
	H	14	5.7	0.41
	F	13	6.9	0.53
	Average			0.518 ± 0.076
II	A	14	10.2	0.73
	B1	36	15.5	0.43
	B2	10	6.9	0.69
	C	13	5.3	0.41
	D1	24	13.3	0.56
	D2	15	8.9	0.59
	H	31	13.3	0.43
	F	18	10.7	0.59
	Average			0.554 ± 0.122
III	J1	14	7.4	0.53
	J2	16	8.1	0.51
	K1	27	12.2	0.45
	K2	15	9.9	0.66
	L1	22	7.4	0.34
	L2	16	5.8	0.37
	Average			0.477 ± 0.177
	Grand average			0.520 ± 0.110

3), based on stem growth increments, mostly range slightly higher than those found in seedlings from the same areas (Table 2). However, the average rate in young clones (0.82 mm/yr) is not significantly different from the average rate in seedlings (0.73 mm/yr). On the total sample, radial length is well correlated with age in young clones (r = 0.92), even though some sub-samples have lower correlation coefficients (Table 3).

Historic growth rates—Another indication of the small range in growth rates through time is derived from analysis of stem increments in three different areas of one clone (Table 4). The regions are: I, the outer portion of living satellites with living branches and hence with wood increments produced during the last several decades; II, the inner portion of the same stem crowns as in I, and hence with wood increments produced prior to three decades ago; III, old dead stem crowns from the central area of the clone, and hence with wood increments produced prior to about 100 years ago. The growth rates in these three areas of one clone are respectively 0.52, 0.55 and 0.48 mm/yr on average (Table 4). Despite considerable variation between crowns within a clone, the average growth rate over the last century or so has varied remarkably little. Furthermore, these clonal growth rates are not strikingly different from seedling growth rates in the same area.

Ancient growth rates—Of 90 wood samples subjected to radiocarbon dating analysis, only 21 samples were older than 330 years BP and could be used as the basis for Table 5. Of the remaining 69 samples, 47 were less than 150 years old and 22 samples were aged between 150–330 years BP; the former are too young to be reliable and the latter fall within a period of possible anomalous interpretation.

Of the 21 usable samples, five were found at the center of clonal bare areas and were judged to be remains of the original first stem crown (Table 5A). Total age of these recent clones therefore is rather well established by the corrected age of the wood sample. The growth rates are easily calculated by taking the distance to the living satellites and dividing by the age (years) of the clone. The average growth rate over the last 5 to 7 centuries is 0.55 ± 0.23 mm/yr.

Nine samples were found near the periphery of clones in which the origin could not be determined (Table 5C). The growth rate of these clones averaged 0.82 ± 0.38 mm/yr over the last 4 to 7 centuries. Use of average growth rates is the only feasible approach to estimation of age inasmuch as most samples cannot be specifically identified with either the longest or the shortest "radius" of the clone.

Four samples were found in clone interiors at known distances from other dated samples or from the origin of a clone of known age (Table 5B). These samples yield growth rate estimates for time periods prior to about 400 BP, or in one case prior to about 100 BP. The average rate was 0.60 ± 0.18 mm/yr.

The last four samples were found near the

TABLE 5. *Clone age and growth based on radiocarbon age and position of old creosote bush wood samples: d = diameter in cm; cor. is corrected age; *H, a layer connected to J. (330-6), is assumed to be 100 years old; Loc. No. = locality numbers, as identified in Table 1; X = unknown; parentheses enclose (extrapolations); satellites (sats.) are the peripheral living portions of a clone. The average growth rate for all samples is 0.66 + 0.31 mm/yr*

Loc. No.	Clone Id. No.	Clone description	Dated wood samples Id.	(yrs. BP)	cor. age	Distance (cm) to origin	live sats.	Clone age	Growth rate (mm/yr)
5A. Growth rates based on wood samples found at the clone origin.									
2	615-2	Circle/w 3 sats.	B5	515 ± 80	530	0	50	530	0.94
4	330-6	Half ellipse	J	680 ± 100	680	0	30	680	0.44
							35		0.51
4	330-4	Fragment	K	650 ± 100	650	0	44	650	0.68
6	628-2	Half circle	A	400 ± 95	500	0	24	500	0.48
10	311-1	Circle d = 30	P	585 ± 150	585	0	15	585	0.26
5B. Growth rates based on wood samples from clone interiors; [a] from 800 BP to about 425 BP; [b] from 680 BP to about 100 BP; [c] from 650 to 470 BP; clone age determined in Tables 5A and 5D.									
3	204-3	Fragment	D	340 ± 100	425	23	X	(800)	0.62[a]
3	204-3	Fragment	E	365 ± 100	450	31	X	(800)	0.89[a]
4	330-6	Half ellipse	*H	>150	100	18	X	680	0.34[b]
4	330-4	Fragment	B	470 ± 100	505	8	X	650	0.55[c]
5C. Growth rates based on wood samples from near the clone periphery; the origin is not known.									
1	527-1	Fragment	1	730 ± 150	730	X	100	X	1.37
			1	640 ± 150	640	X	100	X	1.56
1	831-3	Fragment	B	350 ± 100	430	X	34	X	0.79
1	831-5	Fragment	F	615 ± 120	615	X	42	X	0.68
2	615-1	Fragment	S2	445 ± 85	515	X	30	X	0.58
3	204-6	Fragment	B	445 ± 100	525	X	26	X	0.50
3	204-6	Fragment	D	570 ± 100	570	X	30	X	0.53
7	628-4	Fragment	B	350 ± 100	430	X	24	X	0.56
8	705-13	Fragment	B	440 ± 100	515	X	43	X	0.83
5D. Growth rates based on wood samples taken near the clone periphery and extrapolated to the clone origin to estimate clone age.									
3	204-3	Fragment	A1	365 ± 100	450	18	23	(800)	0.51
4	330-1	Circle d = 100	L	375 ± 100	480	30	22	(655)	0.46
5	620-1	Ellipse d_1 = 1,100 d_2 = 800	G	540 ± 100	560	358	22	(9,170)	0.39
5	620-3	Ellipse d_1 = 175 d_2 = 95	K	695 ± 100	695	40.5	47	(1,290)	0.68

periphery of clones (Table 5D) in which the origin could be determined. The growth rates averaged 0.51 ± 0.12 mm/yr. The clone age can be estimated by extrapolation of the recent growth rate for that clone back to the clone origin. On this basis, several clones were age estimated at 655–1,290 years and one large clone estimated at 9,170 years (Table 5D).

The latter clone is not the largest in the area (Fig. 5). Sternberg (1976) studied a clone with a long diameter of about 22 m and an average radius of 7.8 m. He estimated its age to be over 5,000 years, based on one radiocarbon-determined growth rate from a sandy area at Black Butte, some 56 km away. We now have growth rates of 0.39 and 0.68 mm/yr for clones from the same area (Johnson Valley). Therefore, the rate used by Sternberg (1976) is far too high. Since we know an average radius for the large clone, application of the average growth rate would be reasonable, particularly since that average approximates one rate determined at the specific locality in question. However, this rate is probably still conservative since even lower rates were determined at that locality. In any event, applying the average rate of 0.66 mm/yr for all the samples (Table 5) to the large clone with an average radius of 7.8 m yields an age estimate of 11,700 years.

DISCUSSION—Rates have been determined for radial stem growth in creosote bushes for the most recent few decades, for the few decades just prior to a century ago, for the period

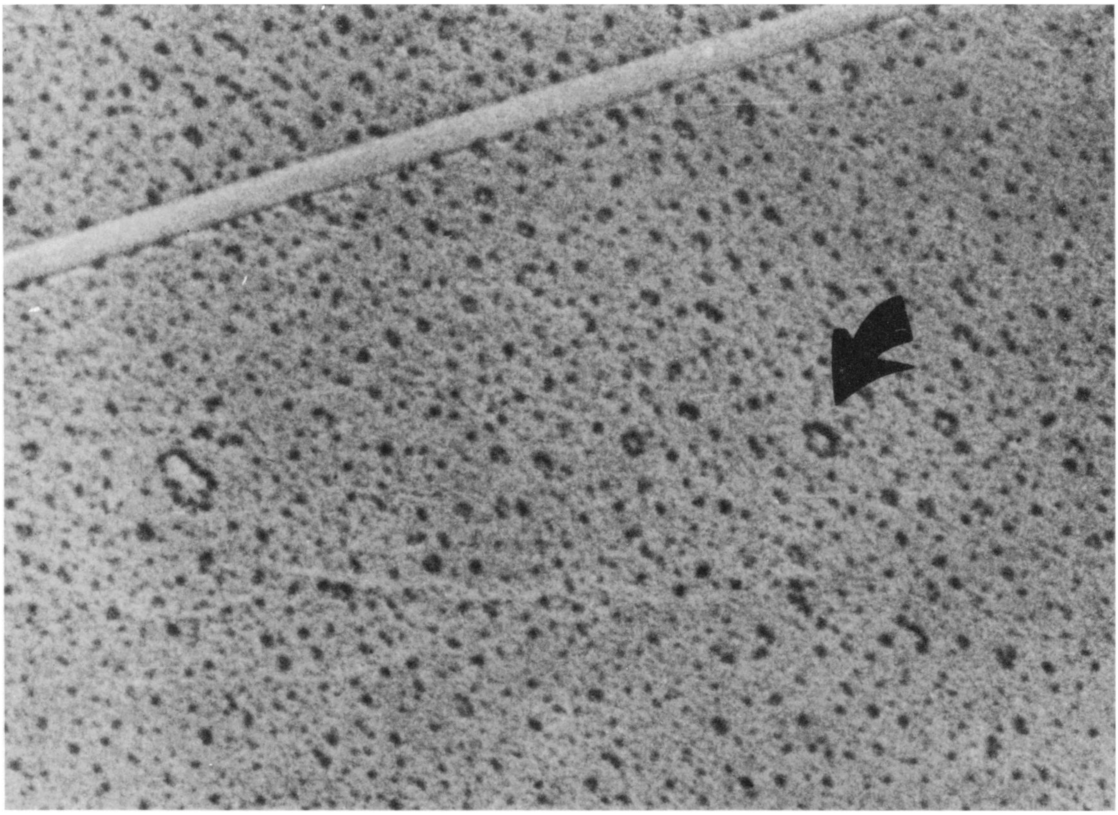

Fig. 5. Creosote rings in Johnson Valley. Aerial view recorded in infrared color film at a scale of 1:20,000, flown under special contract December 26, 1972, for the Dry Lands Research Institute, UCR. The road is 10 to 10.5 m wide. Clone 620-1 of this study is indicated by an arrow and the largest clone we know is about 180 m to the west (left).

from about 1–2 centuries ago, and for the period from about 4–7 centuries ago. Despite all the variation within one clone at the same time, and despite the fact that the position of a sample relative to the long or short axis of a clone is usually not known, the average growth rates for all these time periods fall within a quite narrow range. This general agreement lends confidence to the interpretation that growth rates may reasonably be extrapolated back through time in order to estimate ages of clones. However, extensive extrapolation, to nearly 12,000 years, may or may not be justified. Such extrapolation implicitly assumes that no major changes in growing conditions have occurred during that period.

What was the climate like during those 12,000 years? Several studies document vegetational changes and suggest warming climatic trends in the southwestern desert areas during the Holocene (= post Pleistocene), although the details of timing vary considerably (Martin and Mehringer, 1965; Flint, 1971; Axelrod, 1966; Porter and Denton, 1967; Antevs, 1948, 1955; Martin, 1963; La Marche, 1973).

Perhaps the most useful study is that of King (1976) who dated material from several pack rat middens in the Lucerne Valley region of the Mojave Desert. All the middens studied by King are surrounded by creosote bush desert scrub vegetation. All these middens are also located within 32 km of the large creosote clones in the Johnson Valley area (Sternberg, 1976, and this paper) and one is within 8 km. The Johnson Valley clones are at 921 m elevation, whereas the rat middens are at 972, 1,006, 1,097 and 1,219 m elevation. Midden records indicate a pinyon and juniper woodland at 1,219 m some 11,850 years ago and Utah juniper woodlands at the lower elevations at 12,100 years BP, 11,100 years BP, 8,300 years BP and 7,800 years BP. Then desert scrub vegetation with *Larrea, Ephedra* and *Ambrosia* is recorded at 5,880 years BP, 5,800 years BP, 4,300 years BP, 3,750 years BP and 3,690 years BP. That vegetational shift doubtless followed a climatic shift and corresponds to the start of the altithermal period (Antevs, 1948, 1955) and to the period of high summer temperatures reported in the White Mountains by La Marche (1973). The hypsithermal (Flint, 1971) seems to have started earlier, i.e., about 9,000 years BP.

In all probability the climatic shift in the Mojave Desert occurred some time prior to the vegetational shift. Since junipers (and creosote bushes) are long-lived plants, they probably could survive for extended periods of time after conditions suitable for reproduction and establishment have ceased to exist. Whether such a lag could extend to several millenia, as suggested by the creosote bush age estimates in this paper, is problematical and perhaps doubtful. However, the time problem may be more apparent than real since the ancient creosote rings occur at lower elevations than do any of the rat middens. Therefore, populations of creosote bushes could have established on flats and in valleys while junipers persisted on the nearby hills or at slightly higher elevations. At present, Utah junipers occur less than 12 km away and only about 400 m higher in elevation on the San Bernardino Mountains.

But what effect does climatic change have on creosote bush growth? Growth rates probably would be more rapid during warm, wet periods (the latter hypsithermal) and slower during cool periods (neoglacial maxima) since creosote bushes seem to be limited by cold more than by wet conditions (see Beatley, 1974).

On balance the climatic history suggests that the early post pluvial would probably be the most suitable for establishment of creosote bush populations since the climate was similar to that of the present. The oldest reliable record of *Larrea* in North America, from Yuma County, Arizona (elev. 162 m), was dated at 10,850 ± 500 BP (Wells and Hunziker, 1976; Van Devender, 1973). The large clones in Johnson Valley should have started at some more recent time. Assuming that the average clonal growth rate of 0.66 mm/yr prevailed only during the last 7,000 years, and was double that rate prior to 7,000 BP, the age of the largest clone in Johnson Valley might reasonably be revised to about 9,400 years. Even granting considerable error in extrapolation of creosote clone ages, the largest clones are certainly among the oldest living things known and may have persisted continuously since the first seedlings established in the Mojave Desert at the close of the Wisconsin glaciation.

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