EFFECTS OF RAINFALL AND TEMPERATURE ON THE DISTRIBUTION AND BEHAVIOR OF *LARREA TRIDENTATA* (CREOSOTE-BUSH) IN THE MOJAVE DESERT OF NEVADA[1]

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Abstract. The effects of rainfall and temperature on the distribution and certain behavioral characteristics of *Larrea tridentata* (Creosote-bush) at and near its northern limits in the northern Mojave desert of southern Nevada, were investigated at 39 sites with *Larrea* and 20 sites without *Larrea* in eight drainage basins at elevations of 915–1,770 m over a 2,600-km² area of the Nevada Test Site. Data used were (1) rainfall records for 9 yr (1963–71) for each site; (2) maximum and minimum air temperature records for each site, November 1962–February 1972; (3) percentage cover by all shrub species and by *Larrea*; (4) height and density data for *Larrea*; and (5) percentage of germinable seeds from 29 of the *Larrea* populations for three seasons (1963–65) in relation to the seasonal rainfall for each site.

Total percentage cover by all shrub species is highly correlated with mean annual rainfall, less well correlated with elevation. Percentage cover by *Larrea* follows two patterns of relationship with rainfall: (1) where mean rainfall is low to intermediate, the same pattern as total shrub cover in relation to rainfall, and (2) on sites of high mean rainfall, consistently low cover, a function of low density of *Larrea* on these sites. In general, in undisturbed communities, the taller the *Larrea* plants the fewer there are of them, but the relationship is not strictly linear. Using height as an index to plant volume, numbers of *Larrea* plants are highly correlated with total plant volume. Mean height is not strongly correlated with mean annual rainfall or temperature parameters, but is well correlated with the ratio of mean precipitation/mean temperature. Tall plants (>1 m) occur in low density and on sites with high rainfall (mean 160–183 mm).

The prevailing low minimum air temperatures and their extremes in the lowlands of enclosed drainage basins are inferred to be the primary cause of the absence of *Larrea* in three discrete vegetation zones (*Atriplex confertifolia*, *Lycium pallidum*, and *L. shockleyi*) in Frenchman Flat, and over most of the basin floor of Yucca Flat, where the communities are *Atriplex* and *Grayia-Lycium andersonii*. The year-round low minima in the lowlands of these basins result from nocturnal cold air drainage phenomena and formation of a cold air layer of variable depth. Average extreme minima on these sites were mostly below 0° F; the extreme minimum was –18° F in one of the *Atriplex* communities of Frenchman Flat.

Larrea occurs over the bajadas of Frenchman Flat on sites above the lower layers of cold air. In Yucca Flat, at its northern limits, it is restricted to certain upper bajada sites and notably one site on the basin floor. Average extreme minimum air temperatures on all *Larrea* sites were above 1° F; the absolute minimum was –8° F. Upper altitudinal limits of *Larrea* apparently are not determined by minimum temperatures since minima (including the extremes) in *Coleogyne* vegetation, which replaces *Larrea* altitudinally on the slopes, are well within the range of those recorded on *Larrea* sites.

There is no pattern of relationship between maximum temperatures and the distribution of *Larrea*, although the highest extreme maxima usually occur on non-*Larrea* sites in the lowlands of Frenchman Flat.

Mean annual rainfall on the *Larrea* sites ranged from 118 to 183 mm. Altitudinal and latitudinal limits of *Larrea* coincide with a maximum mean rainfall of 183 mm. Mean annual rainfall of 160–183 mm appears to be critical to the behavior of *Larrea*. Germination trials support the inference of a deleterious effect of high rainfall on *Larrea* populations through time: there were high correlation coefficients (negative or positive, depending on the year) between the rainfall of the effective rainfall season and the percentage of germinable seeds; highest mean germination percentages (20%–60%) occurred with 80–150 mm of seasonal rain, and either lower or higher seasonal rainfall resulted in lower percentages of germinable seeds (0%–20%).

Key words: Creosote-bush; desert; Larrea tridentata; *Mojave; Nevada; rainfall; temperature.*

INTRODUCTION

The distribution and behavior of *Larrea tridentata* (Ses. & Moç. ex DC.) Cov. (Creosote-bush), and their environmental controls in deserts of southwestern United States and Mexico, have long been of interest to desert ecologists. The shrub species is dominant over the Mojave, Sonoran, and Chihuahuan deserts, and reaches its northern limits, with a number of other shrub and herbaceous species, along an irregular boundary from the southwestern corner of
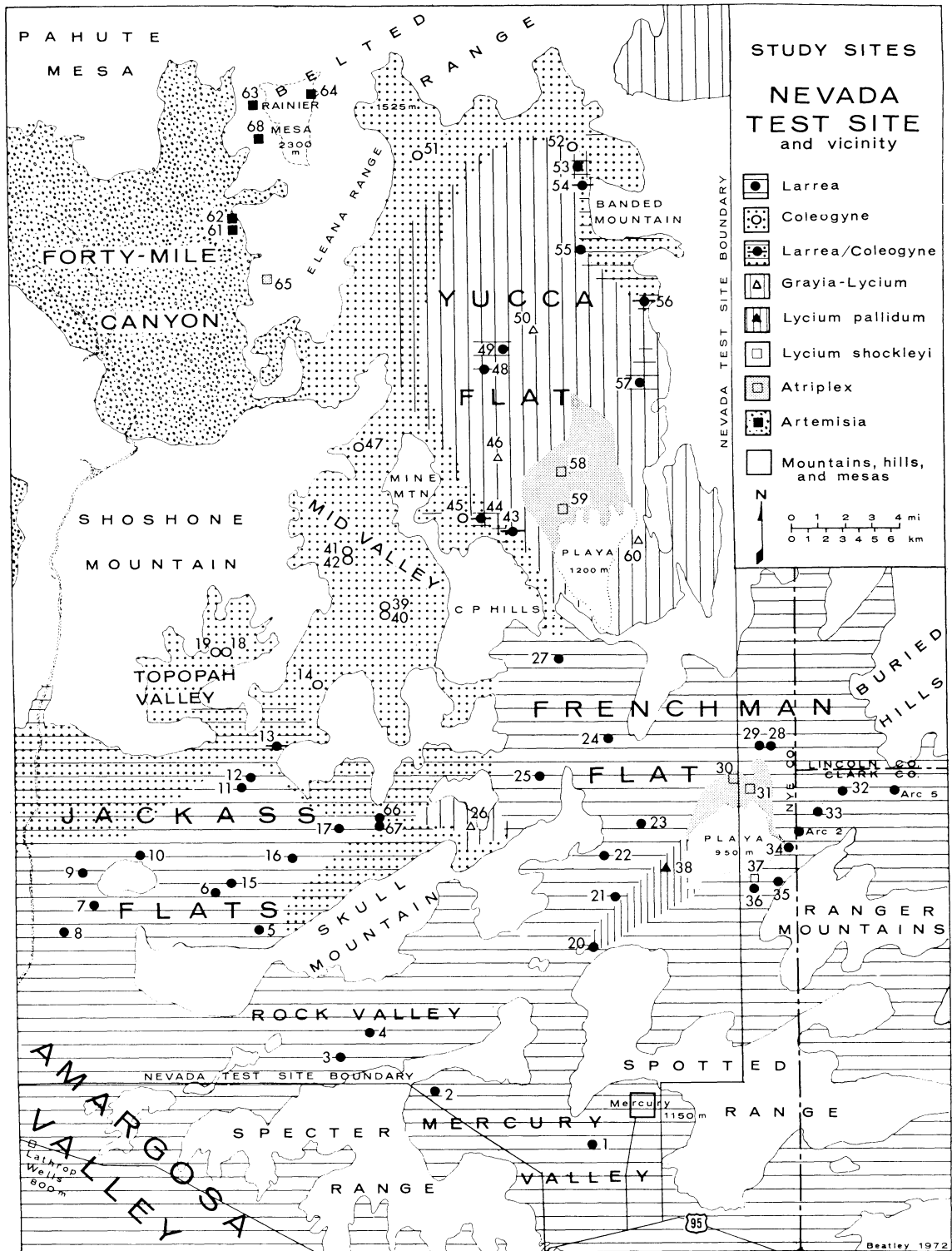
FIG. 1.   Location of study sites in relation to vegetation types and physiographic features, Nevada Test Site, central-southern Nevada.

Utah across southern Nevada, to southern Owens Valley in southeastern California. Its northern limits were geographically described first by Merriam (1893), who used the species to define the Lower Sonoran zone. The northern limits of *Larrea* were designated by Shreve (1942) and subsequently by most others to delimit the northern boundary of the Mojave desert, and most recently by Cronquist et al. (1972) to set the southern limits of the Intermountain Region in Nevada.

Shreve (1940), discussing the conditions limiting to *Larrea* at the margins of its range, claimed that no part of North America is too dry for *Larrea*, and that high temperatures are nowhere limiting. He noted that the species occurs in areas of Mexico with an average rainfall of around 20 in, and "the behavior of artificially watered plants shows that high rainfall would not be directly prejudicial to well established plants." Altitudinal limits of the species in southern Nevada were reported to be at an elevation of approximately 1,200 m (4,000 ft), with variations due to slope exposure. Of particular interest to the present study is the statement that "the northern edge of the range of *Larrea* is near the isoclimatic line for a maximum of six consecutive days of freezing temperature," but that "there is, however, no experimental evidence to confirm the apparent importance of this datum in limiting the range of *Larrea*." Pertinent also is his mention that "several botanists have noted the large number of dead plants found at all times along the northern edge of the range of *Larrea*, presumably indicating death from low temperatures . . . [and that] heavy snowfall is distinctly hostile to *Larrea*."

Objective of the present paper is a clarification of the roles of rainfall and temperature by way of an examination of (1) the behavior and distribution of *Larrea* in relation to 9 yr of rainfall and maximum-minimum air temperature data on 39 sites with *Larrea* and 20 sites without *Larrea* in the vegetation mosaic at or near the northern limits of the species in southeastern Nye and extreme northwestern Clark Counties, Nevada; and (2) supporting evidence for the rainfall relationships from 3 yr of seasonal rainfall and seed germination data for 29 of the *Larrea* populations.

DISTRIBUTION OF *LARREA* IN THE REGIONAL VEGETATION

The Nevada Test Site (Fig. 1) is a portion of the zone across southern Nevada straddling the northern boundary of the Mojave desert (as defined by Shreve 1942), the southern limits of the Great Basin desert, and the transition (hereafter referred to as Transition desert) between the two large desert regions. The area lies within the Basin and Range Province of Fenneman (1931) and encompasses all or part of

eight drainage basins, each circumscribed by mountains and hills.

The northern limits known for *Larrea* across southern Nye and western Lincoln Counties, Nevada, occur at upper altitudinal limits of 1,280 m (4,200 ft) to as high as 1,585 m (5,200 ft) on certain south exposures, and are recorded in detail in Beatley (1969a, 1971). On the Test Site, *Larrea* communities of the high Mojave desert are the prevailing shrub vegetation on the slopes (bajadas) of the drainage basins in the southern part, including most of the large basins of Jackass Flats and Frenchman Flat. In Yucca Flat to the immediate north, where communities belong to the Transition desert, *Larrea* is nearly restricted to the upper bajadas of certain areas in the southwestern and northeastern parts; here its occurrence is as local and more or less discontinuous populations near the bases of the surrounding mountains and foothills. In three areas of Yucca Flat, the populations extend down on to the low-gradient basin floor as peninsulas or islands. The species reaches elevations of around 1,350 m (4,500 ft) on both the north slope of Jackass Flats and in northeastern Yucca Flat at its extreme northern limits in the Test Site region. Nearly everywhere *Larrea* rises above the low (mostly less than 0.7 m) shrub matrix of other shrub species with which it is usually associated in discrete, irregular-shaped clumps.

On the north and east slopes of Jackass Flats, at around 1,200 m (4,000 ft) Transition communities in which *Coleogyne ramosissima* Torr. (Blackbrush) is the dominant species replace the *Larrea* communities, but *Larrea* and many of its Mojave desert associates of the lower elevations continue to be present over a broad ecotone of *Larrea/Coleogyne* between 1,200 to 1,350 m (4,000 to 4,500 ft). In Yucca Flat, *Larrea* occurs on the basin floor with Transitional *Grayia-Lycium* communities [*Grayia spinosa* (Hook.) Moq. (Hopsage) and *Lycium andersonii* Gray (Desert-Thorn)] and, as in Jackass Flats, with *Coleogyne* on the upper bajadas. In the Test Site region, *Coleogyne* communities, occurring mostly between 1,200 and 1,500 m (rarely to 1,800 m) (4,000 to 5,000 [to 6,000] ft) and on soils derived usually from predominantly calcareous parent materials, are replaced at around 1,500 m (5,000 ft) by the Great Basin desert *Artemisia* (Sagebrush) communities [*Artemisia tridentata* Nutt. and *A. arbuscula* Nutt. ssp. *nova* (A. Nels.) Ward]. At around 1,800 m (6,000 ft) Pinyon Pine (*Pinus monophylla* Torr. & Frem.) and Juniper [*Juniperus osteosperma* (Torr.) Little] enter the *Artemisia* communities; together they are the usual dominants of the *Artemisia*-Pinyon-Juniper of the mountains and mesas of the northern and western parts of the Test Site.

In the lowlands of Frenchman and Yucca Flats—both "closed" basins with respect to surface drainage

TABLE 1. Shrub and environmental data for 59 sites, 8 drainage basins, Nevada Test Site, Nye and Clark Counties, Nevada, 1962–72

Site no.	Vegetation type[a]	Elev. m	Mean ppt. 1963–71 mm	Mean, temp. extremes[b] Max. °C	Min. °C	Mean temps., all seasons 1963–71[c] Max. °C	Min. °C	Mean °C	Ppt./ temp. index[d]	Shrub cover[e] %	Larrea plants[e] Cover %	Nos.	Mean ht. m	Sum of hts. m
Mercury Valley														
1	Larrea (M)	1,027	140.7	43.4	−12.7	28.0	2.3	15.2	9.3	19.1	7.8	77	0.61	46.4
2	Larrea (T)	1,088	169.4	43.6	−15.2	28.5	0.4	14.5	11.7	27.4	4.6	29	1.11	32.0
Rock Valley														
3	Larrea (M/T)	1,038	176.3	45.9	−11.6	30.7	2.8	16.7	10.6	30.4	4.6	63	0.70	44.3
4	Larrea (M)	1,055	148.1	42.6	−13.6	28.1	1.2	14.7	10.1	22.7	2.5	26	0.55	14.3
Jackass Flats														
5	Larrea (M)	1,120	142.0	40.9	−11.0	27.2	4.5	15.9	8.9	9.6	2.3	32	0.67	21.3
6	Larrea (M)	1,064	140.7	43.2	−11.9	28.4	2.6	15.5	9.1	18.7	7.3	74	0.66	48.6
7	Larrea (M)	963	124.0	42.7	−14.3	28.0	1.1	14.5	8.6	22.1	4.6	73	0.65	47.0
8	Larrea (M)	938	120.1	43.8	−13.4	29.8	1.3	16.2	7.4	17.7	1.7	63	0.59	37.5
9	Larrea (M)[f]	989	132.3	42.6	−15.3	28.0	0.4	14.2	9.3	21.1	(0.2)	(13)	(0.52)	(6.8)
10	Larrea (M)	1,039	124.2	43.2	−14.4	28.9	2.0	15.4	8.1	19.1	5.0	57	0.79	45.2
11	Larrea (M)	1,189	141.5	42.6	−11.7	28.8	3.6	16.2	8.7	16.4	7.3	167	0.59	98.1
12	Larrea (M)	1,209	149.1	41.4	−11.7	27.7	3.1	15.4	9.7	18.9	9.9	158	0.58	92.0
13	Larrea/Coleogyne (T)	1,286	168.4	41.1	−12.8	26.6	2.1	14.5	11.6	26.0	1.8	29	0.91	26.5
14	Coleogyne (T)	1,448	192.5	38.2	−15.0	24.7	−0.1	12.3	15.7	42.5				
15	Larrea (M)	1,082	131.1	43.7	−10.8	29.5	3.6	16.5	7.9	13.5	10.9	92	0.87	79.8
16	Larrea (M)	1,158	144.0	42.4	−11.6	28.0	4.1	16.0	9.0	9.3	7.9	52	1.00	51.8
17	Larrea (M)	1,239	141.2	42.4	−12.1	28.1	3.4	15.8	8.9	23.1	9.1	65	0.92	59.8
66	Larrea (T)	1,320	165.1	41.3	−12.1	27.5	2.7	15.0	11.0	26.5	6.4	56	1.24	69.4
Topopah Valley														
18	Coleogyne (T)	1,487	228.1	41.6	−13.4	28.0	0.9	14.5	15.7	45.1				
Frenchman Flat														
20	Larrea (M)	994	136.4	43.5	−15.8	29.7	−0.2	14.7	9.3	20.6	8.3	70	0.91	63.9
21	Larrea (M)	977	128.3	43.4	−16.2	28.9	−0.2	14.4	8.9	10.0	7.7	98	0.74	72.5
22	Larrea (M)	997	126.7	43.5	−14.7	29.0	0.7	14.9	8.5	18.0	7.8	57	0.79	45.2
23	Larrea (M)	972	123.4	44.9	−16.6	30.1	−1.2	14.4	8.6	12.0	2.8	70	0.61	42.9
24	Larrea (M)	1,027	142.0	44.1	−14.1	29.0	1.9	15.5	9.2	19.4	11.4	131	0.66	85.7
25	Larrea (T)	1,103	160.0	43.9	−16.0	28.9	−0.2	14.4	11.1	13.8	2.6	25	1.27	31.2
26	Grayia-Lycium (T)	1,218	184.4	42.1	−15.1	28.1	0.2	14.2	13.0	21.7				
27	Larrea (M)	1,131	151.9	43.4	−12.8	28.6	2.6	15.6	9.7	16.8	9.5	116	0.78	90.1
28	Larrea (M)	986	120.7	42.0	−15.4	28.0	0.5	14.3	8.4	16.8	6.5	40	0.99	39.5
29	Larrea (M)[f]	986	121.7	42.2	−15.8	28.5	0.3	14.4	8.5	21.3	(1.8)	(9)	(0.43)	(3.9)
30	Atriplex canescens (GB)	943	126.0	45.3	−18.6	30.4	−3.3	13.5	9.3	5.4				
31	Atriplex confertifolia (GB)	940	131.1	45.4	−17.3	29.9	−2.9	13.5	9.7	8.6				
32	Larrea (M)	1,042	124.7	42.8	−14.2	28.5	1.6	15.0	8.3	18.0	2.0	33	0.69	22.7
33	Larrea (M)	994	121.7	43.4	−13.6	28.9	1.5	15.2	8.0	7.2	3.3	45	0.68	30.5
34	Larrea (M)	951	126.5	43.7	−16.8	29.4	−1.4	14.0	9.0	10.7	2.0	27	0.78	20.9
35	Larrea (M)[f]	1,006	140.2	43.3	−12.7	28.9	3.1	16.0	8.8	10.7	(0.3)	(4)	(0.31)	(1.2)
36	Larrea (M)	940	127.0	42.2	−15.6	28.3	−0.2	14.1	9.0	11.7	2.7	51	0.69	35.1
37	Lycium shockleyi (T)	939	129.8	44.5	−18.3	29.6	−3.1	13.3	9.8	11.9				
38	Lycium pallidum (T)	949	121.9	45.0	−18.4	29.9	−2.6	13.7	8.9	14.3				
Mid Valley														
39	Coleogyne (T)	1,376	197.6	41.3	−15.6	27.5	0.2	13.9	14.2	35.6				
41	Coleogyne (T)	1,449	243.6	41.6	−15.1	27.6	0.7	14.2	17.2	50.4				
Yucca Flat														
43	Larrea/Coleogyne (T)	1,276	182.3	41.5	−13.9	27.5	1.5	14.5	12.6	20.4	2.2	36	1.04	37.3
44	Larrea/Coleogyne (T)	1,259	182.9	41.2	−14.9	27.2	0.8	14.0	13.1	26.3	1.3	10	1.48	14.8
45	Coleogyne (T)	1,282	188.2	41.8	−15.4	27.8	0.3	14.0	13.4	37.5				
46	Grayia-Lycium (T)	1,227	176.0	43.1	−17.6	28.6	−1.9	13.3	13.2	31.3				
47	Coleogyne/Artemisia (T)	1,475	238.0	42.8	−16.3	27.5	0.0	13.8	17.2	37.7				
48	Larrea (T)[g]	1,280	163.3	40.6	−14.9	26.9	1.6	14.2	11.5	(4.1)	1.7	11	1.80	19.8
49	Larrea (T)	1,268	165.9	41.2	−15.8	27.4	0.4	13.9	11.9	17.4	2.2	18	1.36	24.4
50	Grayia-Lycium (T)	1,253	166.4	42.7	−18.7	27.8	−2.5	12.6	13.2	25.0				
51	Coleogyne (T)	1,509	229.4	44.9	−13.4	28.7	2.1	15.4	14.9	45.1				
54	Larrea/Coleogyne (T)[g]	1,344	174.0	42.1	−14.2	27.5	1.6	14.5	12.0	(17.7)	2.7	28	0.76	21.3
55	Larrea (T)[g]	1,341	159.5	40.9	−13.9	27.4	2.1	14.7	10.9	(9.8)	4.4	35	1.27	44.6
56	Larrea/Coleogyne (T)	1,317	164.6	41.7	−14.1	27.6	1.4	14.5	11.4	27.7	4.6	25	1.19	29.7
57	Larrea (T)	1,268	173.0	42.0	−15.9	27.9	0.5	14.2	12.2	27.0	4.6	37	1.03	38.0

<div align="center">TABLE 1 (continued)</div>

Site no.	Vegetation type[a]	Elev. m	Mean ppt. 1963–71 mm	Mean, temp. extremes[b]		Mean temps., all seasons, 1963–71[c]			Ppt./ temp. index[d]	Shrub cover[e] %	Larrea plants[e]			
				Max. °C	Min. °C	Max. °C	Min. °C	Mean °C			Cover %	Nos.	Mean ht. m	Sum of hts. m
58	Atriplex confertifolia (GB)	1,207	179.8	41.2	–18.7	27.7	–3.2	12.3	14.6	17.5				
59	Atriplex confertifolia (GB)	1,198	175.8	41.2	–19.3	27.5	–3.9	11.8	14.9	14.9				
60	Grayia-Lycium (T)	1,204	160.0	42.2	–19.3	28.2	–3.4	12.4	12.9	27.8				
Forty-Mile Canyon														
61	Artemisia arbuscula subsp. nova (GB)	1,756	206.0	39.6	–16.2	25.8	–1.1	12.4	16.6	37.3				
62	Artemisia tridentata (GB)	1,750	205.5	40.5	–19.1	27.0	–3.3	11.9	17.3	32.6				
65	Atriplex canescens (GB)	1,676	183.6	38.6	–18.7	24.9	–2.9	10.9	16.8	16.0				

[a] M = Mojave desert; T = Transition, between Mojave and Great Basin deserts; GB = Great Basin desert. Designations of desert to which each site is assigned in some cases have been changed from Beatley (1969b).
[b] Mean of extreme maximum temperatures recorded 9 summers (1963–71), and extreme minimum temperatures recorded 10 winters (1962–72).
[c] Mean of 307 readings.
[d] Mean precipitation divided by mean temperature, 1963–71 (9 yr).
[e] On study plots, 30.5 × 30.5 m (100 × 100 ft), total area 929 m² (10,000 ft²).
[f] Sites selected for paucity and extreme small size of Larrea plants, and therefore the Larrea parameters omitted from all calculations.
[g] All shrubs destroyed prior to 1963 from effects of blast or dust from nuclear detonations. The Larrea plants subsequently sprouted, but in other species there was differential recovery by sprouting. All or some of the Larrea parameters are accepted for this study, but not the % shrub cover.

—Atriplex confertifolia (Torr. & Frem.) Wats. (Shadscale) communities extend northward from the playa in discrete irregularly triangular-shaped areas. In Frenchman Flat, there is in addition a several-kilometer long zone extending southwest from the playa, in which the community dominants are Lycium pallidum Miers and Grayia, or in some areas Atriplex canescens (Pursh) Nutt. (Four-wing Saltbush); and in the southeastern corner of the basin, below the Ranger Mountains and adjacent to the south margin of the playa, there is a narrow zone (not delimited in Fig. 1) in which the southern Nevada endemic Lycium shockleyi Gray is the dominant shrub species. In all of these lowland communities Larrea and many of its associates are absent, and the transition to the adjacent Larrea communities is usually along exceedingly sharp vegetation boundaries. These boundaries are conspicuous landscape features in Frenchman Flat (Fig. 2). In the large Jackass Flats and Forty-Mile Canyon drainage basins, and the small basins of Mercury Valley, Rock Valley, Mid Valley, and Topopah Valley—all "open" basins—there are no sharp vegetation boundaries in the lowlands.

Three major problems, therefore, need to be solved with regard to the distribution of Larrea in the region of its northern limits: environmental controls of the local latitudinal and altitudinal limits, and those restricting its occurrence in the lowlands of enclosed drainage basins.

METHODS AND MATERIALS

Within the vegetation mosaic of the Nevada Test Site, sites representative of the major kinds of regional ecosystems and a permanent study plot sample of each were selectively chosen in 1962 for use in long-term studies with a number of objectives. Among the bases for site selection was the occurrence of Larrea communities in relation to physiographic and edaphic features, floristic variations, and elevation in the high Mojave desert of Jackass and Frenchman Flats, and in Yucca Flat the three major areas in which Larrea occurs as more or less discontinuous populations (Fig. 1). Sites in the other shrub types and major ecotones were also selected, some for their potential contrast and comparison with Larrea communities in the same part of the basin. In total, 39 of the sites were Larrea or Larrea/Coleogyne systems; three of these, selected because of the paucity of Larrea or its extreme size reduction in discrete but local areas, are excluded from treatments of the data for height, density, or percentage cover by Larrea. Other shrub types, distinguished at the level needed for the objectives of this paper, are Coleogyne, Grayia-Lycium, Atriplex, Lycium pallidum, Lycium shockleyi, and Artemisia. Of the nine disturbed sites of the network, data from three are used where the past disturbance does not influence the parameter under consideration. The total of 59 permanent study sites (and two additional sampling areas in Frenchman Flat) for which data are used are between 915 and 1,770 m (3,000 and 5,800 ft) elevation (Table 1).

Environmental measurements

Beginning in November 1962, and continuing into 1972 without break, records of the rainfall and maximum and minimum air temperatures were obtained (along with other measurements) on each of
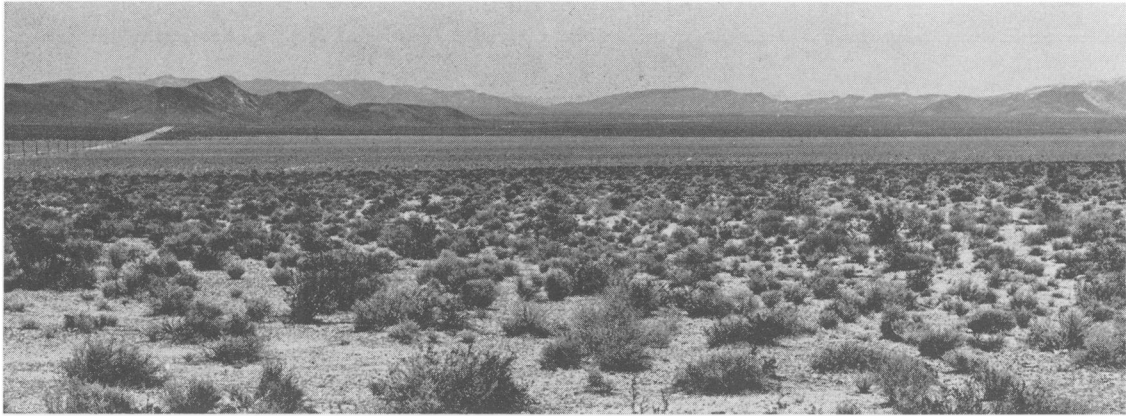
FIG. 2. Portion of the sharp north and south boundaries of *Larrea* vegetation along the east-west zone of *Lycium pallidum-Grayia* and *Atriplex canescens*, southwestern Frenchman Flat, Nevada Test Site, central-southern Nevada. Zone without *Larrea* is about 3 km wide (north to south), and extends eastward to the playa (right of photo). Photo June 1972.

the 59 sites. Readings were made weekly through most of 1966, and thereafter mostly biweekly, with intercalary rain gauge readings as needed. Instruments were read sequentially over the network from south to north during each 3-day reading period.

Rainfall.—Rain gauges were a 20-cm diameter polyethylene funnel feeding into a 2-liter (or 4-liter) bottle buried in the soil to the bottle neck (Fig. 3). Gauges were in the open between shrub-clumps. Measured milliliters of water were converted to millimeters (and inches) of rainfall.

Rainfall measurements are not directly comparable to U. S. Weather Bureau sampling data. Gauges used in this study were near the ground and only slightly subject to the wind-effects error of a standard recording gauge, whose receiving surface in this region is generally above the canopies of the matrix of the shrub vegetation. With the low-placed receiving surface, readings are consistently somewhat higher than from Weather Bureau gauges, especially under conditions of air turbulence accompanying high-intensity rainfalls.

Major control of rainfall patterns is the configuration of the topographic features, whose influences are expressed in general as increases in precipitation from lower to higher elevations. This relationship is everywhere subject to local modifications in the amount of rain water actually received at the earth's surface. The rainfall variations among the sites are predictable, once the patterns of variation are known.

Temperature.—Maximum and minimum air temperature measurements, recorded in degrees Fahrenheit, employed a partially exposed Taylor or Weksler Six thermometer, with the sensor at the 30-cm level, installed on the side of a narrow white wooden stake with a plywood shade offset to shade the thermometer bulb throughout the year (Fig. 3). Thermometers

faced north, and installations were on the northeast side and at the edge of a shrub-clump. Readings are not directly comparable to those obtained at 1.5 m (5 ft) inside U. S. Weather Bureau shelters.

The calculated mean maximum and minimum temperatures and the mean temperatures for the calendar years 1963–71 are based on a total of 307 maximum and minimum readings, with approximate equal distribution through the solar seasons. The means represent the average of the extreme temperatures registered during the time intervals between readings and hence are not comparable to mean values derived from daily temperature extremes.

The extreme and mean maximum and minimum air temperatures define the year-round maximum and minimum temperature relationships consistently expressed over the network of sites. Within the systems of measurement these parameters are reliable indices during all seasons to the relative daytime warmness and nocturnal coldness of air (and soils).

Plant measurements

Percentage cover by shrub species was calculated from 335 m of modified line interception data (11 lines, 30.5 m long, 2.5 cm wide) collected on the 30.5 by 30.5 m (100 by 100 ft) study plot of all sites in 1963.

Absolute densities of *Larrea* were obtained from actual counts on the study plots in 1972. Height of the tallest branch of each plant, and whether or not the plant occurred with one or more other *Larrea* plants in a clump, were recorded. Where the plants occurred in clumps, a plant was considered a separate entity if its main stem at the soil surface was 30 cm or more distant from another main stem; such plants were apparently often members of a clone, but whether or not there were underground connections,
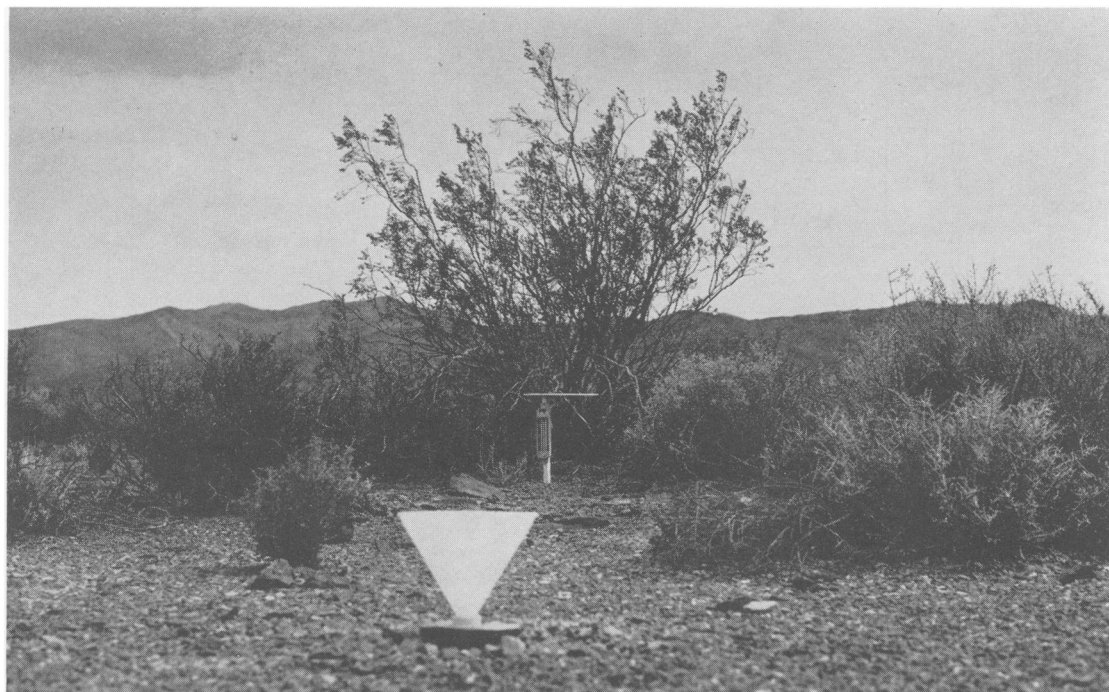
FIG. 3. *Larrea tridentata*, and thermometer and rain gauge installations, site 44, in a local area of *Larrea/Coleogyne* in southwestern Yucca Flat, Nevada Test Site, central-southern Nevada. Only 10 plants, averaging 1.5 m tall, occur on the 30.5- by 30.5-m study plot. Photo June 1972.

each was distinguishable above-ground as a distinct entity within the total clump structure.

Germination studies

Larrea sampling areas were established prior to 1962. Numbers of plants sampled varied with the population according to the sampling design of an ionizing-radiation effects study on reproductive characters in this species. Populations with larger samples (10 or more plants) were at time of selection either within or well outside of past or projected fallout patterns from nuclear tests. In 1962, on all of the permanent study sites where number of flowers on *Larrea* plants enabled sampling, usually three plants were selected as a population sample and included among the populations whose reproductive characters were to be compared.

In late May or early June of 1963, 1964, and 1965, the terminal 15–20 cm of three or more flower-bearing branches of each plant were covered with securely tied paper bags; the bags were removed and the contents combined in September of each year. The mature fruit collections were from the same plants all 3 yr, except for those with flowers in inadequate numbers to meet the sampling needs (in 1964 almost no plants in Jackass Flats had more than occasional flowers).

The fruit collections were kept outdoors until late November, then transported to Los Angeles, and kept at room temperature (controlled) while cleaned of debris and otherwise processed for the germination trials. Each fruit normally consists of five one-seeded indehiscent carpels, which separate at maturity; from the total carpels collected from each plant, 100 were randomly chosen and planted 1 cm deep in rows in wooden flats in a controlled-temperature room (growth chamber), using sterilized native Test Site sandy-loam soil (from site 20). The soil was thoroughly saturated with deionized water immediately before and after planting. Planting was done on January 28 and 29 of each of the years 1964–66.

Optimum conditions of temperature, moisture, light, and the germination medium were defined by prior exploratory studies. Growth chamber controls were set for 75° F (24° C) and a 12-hr light-dark cycle (cf. Barbour 1968). Soil in the flats was saturated with deionized water through a fine-spray nozzle once a day during the germination period. Seedlings were identified with toothpicks after emergence (mostly 5–10 days after planting). Percent germination was the total number of seedlings which emerged from the 100-carpel sample from each plant during a 23-day period.

In total, 29 *Larrea* populations were sampled during the three seasons (2 in Mercury Valley, 6 in Jackass Flats, 14 in Frenchman Flat, and 7 in Yucca Flat). Sources of field materials were 202 plants (6 in Mercury Valley, 33 in Jackass Flats, 104 in French-
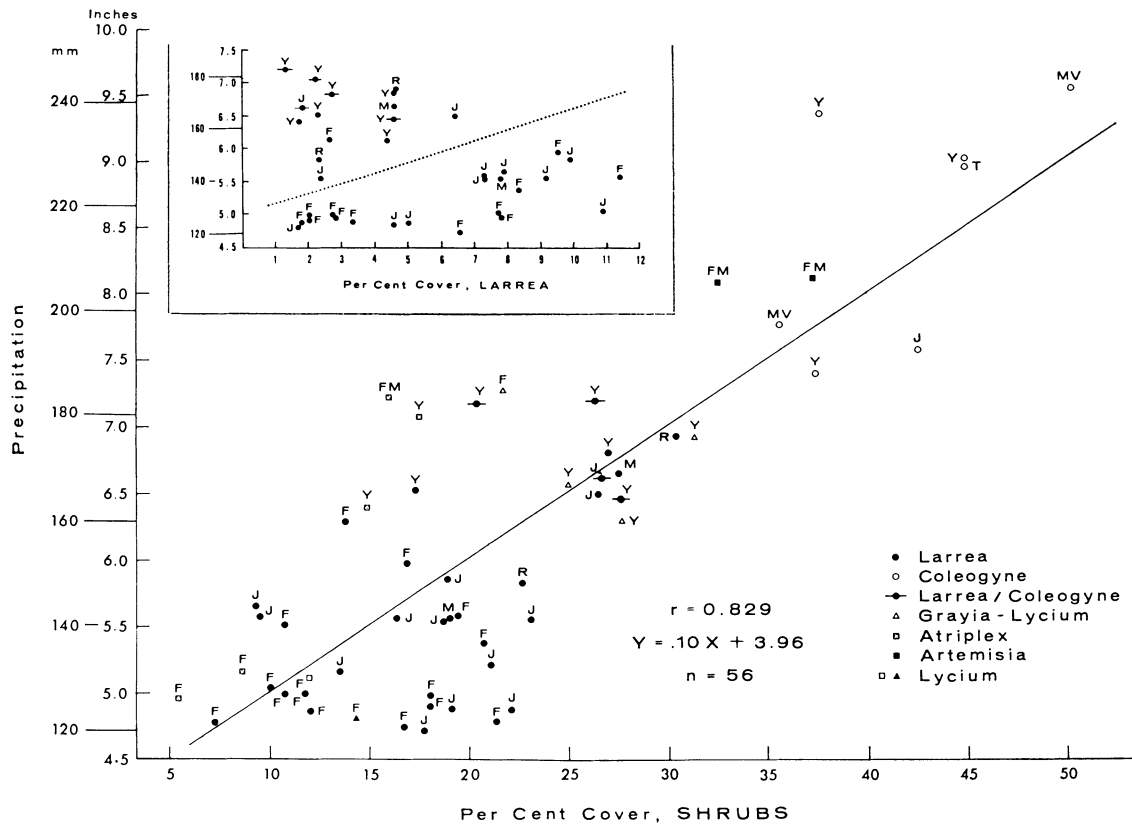
FIG. 4. Percentage cover by all shrub species in relation to mean precipitation on 56 sites, 1963–71, eight drainage basins, Nevada Test Site, central-southern Nevada. Upper left, percentage cover by *Larrea* and mean precipitation on 37 of the same sites. F = Frenchman Flat; FM = Forty-Mile Canyon; J = Jackass Flats; M = Mercury Valley; MV = Mid Valley; R = Rock Valley; T = Topopah Valley; Y = Yucca Flat.

man Flat, and 59 in Yucca Flat). Total number of plants from which the samples were obtained in the 3 yr was 468 (155 plants in 1963, 131 in 1964, and 182 in 1965).

RESULTS AND DISCUSSION

Site numbers, drainage basin, shrub type, desert to which each system is assigned, elevation, and the rainfall, temperature, and plant data are recorded in Table 1 for all sites used in the study; these include all of the network of 68 sites except the three *Artemisia*-Pinyon-Juniper and six of the disturbed sites.

Shrub cover

The relationship between percentage cover by all shrub species and mean annual rainfall, as defined by rainfall of the period 1963–1971, is shown in Fig. 4. With the method of measurement used, percentage cover is a direct function of number of plants and usually the distances between them, but to a lesser extent size of plants.

Increase in percentage shrub cover is highly correlated with increase in rainfall. Correlation between

shrub cover and elevation follows the same linear pattern of increase, as does also elevation and rainfall ($r = 0.850$), but the shrub cover-elevation relationship ($r = 0.689$) is less subject to prediction than that between shrub cover and rainfall ($r = 0.829$). Notable exceptions are the *Atriplex* communities, characterized by low shrub cover regardless of rainfall or elevation. Total shrub cover in the Mojave and Transition desert vegetation of this region is a highly reliable and useful index to the local rainfall regime. Where higher elevation rainfall regimes obtain locally on Mojave-Transition sites at the lower elevations (especially sites 2 and 3, Table 1), shrub cover values are correlated with the rainfall and not elevation.

When the percentage cover by *Larrea* alone, however, is considered in relation to rainfall (Fig. 4, upper left), there is a dichotomy in the relationship: (1) Those sites following the relationship for total shrub cover, which are nearly all of the sites with less than an average 160 mm (6.29 in) of rainfall; and (2) the sites in Yucca Flat, Rock Valley, Mercury Valley, and the higher-elevation sites in Jackass and Frenchman Flats near drainage divides, with rainfall mostly in excess of 160 mm (6.29 in), in
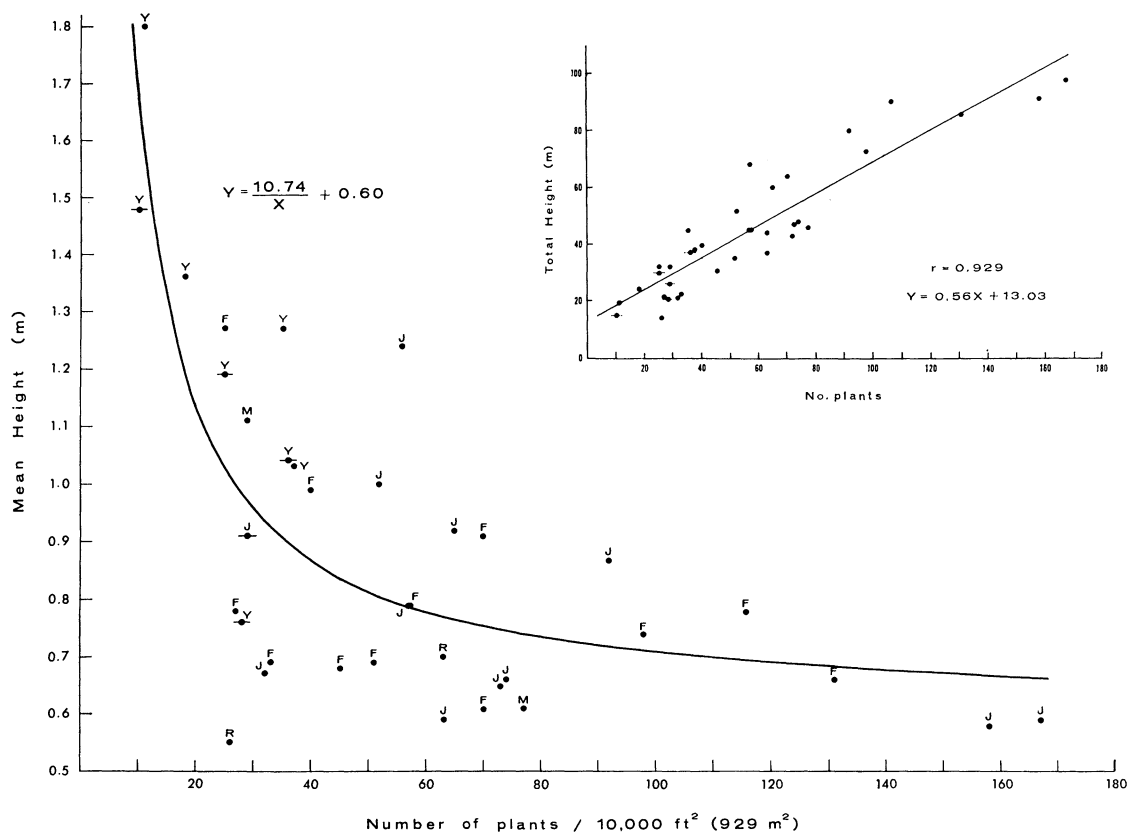
FIG. 5. Mean height of *Larrea* plants, and total height (upper right), in relation to number of plants (density), 36 sites, five drainage basins (legend, Fig. 4), Nevada Test Site, central-southern Nevada. Black dot, *Larrea* site; dot with line, *Larrea/Coleogyne* site.

which the total cover by *Larrea* is at the lower end of the range for percentage cover by this species. The latter results from the lesser numbers of plants on sites with higher rainfall, as discussed later.

Height and density of Larrea

A relationship between height and numbers (density) of *Larrea* is evident from casual observation of *Larrea* vegetation. In general, in undisturbed communities the taller (and otherwise larger) the *Larrea* plants, the fewer there are of them. The height-number relationship (Fig. 5) may be described by the equation $Y = a + b/X$, where X is the number of plants per unit area (density), Y is the mean height of the plants on each site, a is the intercept value, and b is the regression coefficient.

Apparent from the data of Fig. 5 are the low densities and greater mean height of *Larrea* in the populations of Yucca Flat, where the species is at its northern limits, and extremely low average heights where numbers of plants are at the maximum (lower north slope of Jackass Flats). The possibility that total above-ground volume (using height as an index to size and hence volume) might be nearly equal on

all sites, with numbers and total heights approaching some constant value, was explored through the relationship shown in Fig. 5 (upper right), where the sum of the heights is plotted against the number of plants on each site. Such a volume/number constant apparently does not exist: increased size of plants does not offset reduction in numbers, and in fact low-to-high numbers of plants are highly correlated ($r = 0.929$) with corresponding low-to-high total plant height.

Mean height is not strongly correlated with mean rainfall of this 9-yr period of measurement. The pattern of relationship is linear, but the correlation coefficient (0.577) suggests that other variables play important roles also in the average height of plants on a given site and at any point in time. Nevertheless, populations with the consistently tallest plants always occur in the areas of highest rainfall, and those with mostly tall plants (average height >1 m) do not occur where precipitation was less than an average of 160 mm (6.29 in) in the period of the record. The 1-m tall population on site 16, with only 144 mm (5.67 in) mean rainfall, and the extreme height of *Larrea* on site 48 (where the tallest plant [2.8 m] of

all sites occurs) are both inferred to reflect greater moisture availability to *Larrea* with the paucity of other shrub species present on these sites (as indicated in Table 1). The tall and otherwise large plants that characterize the high-rainfall area of Yucca Flat (Fig. 3) appear to be entirely comparable to the *Larrea* plants of road shoulders and depressions, and frequently along drainage courses, whose often conspicuous large size is inferred to be the result of increased soil moisture from pavement run-off or other local distributions of surface water following rains; such conditions are equivalent to increases in rainfall.

Mean height is even less well correlated with temperature parameters. Highest correlations are with maxima temperatures: Mean of the extreme maximums for the nine summers, $r = -0.518$; mean of the 307 maxima temperature readings, $r = -0.495$; and an even lower correlation with the mean of all maximums and minimums of the 9-yr period ($r = -0.451$). However, when the mean precipitation and mean temperature are combined in a precipitation/temperature (P/T) ratio for each site (Fig. 6), the coefficient of correlation with mean height increases to 0.727 (omitting site 4, on which the low height of *Larrea* is apparently under the primary control of edaphic variables not under consideration). The groupings in both Figs. 4 and 6 consist of the same sites, and are in both cases related to rainfall above and below 160 mm (6.29 in).

Numbers of *Larrea* plants (density) in relation to average rainfall of the 9-yr period also follow essentially the same dichotomy in pattern as percentage cover and rainfall (Fig. 4, upper left), since the absolute densities and percentage cover derived from line interception data are generally well correlated ($r = 0.751$). Above 160 mm (6.29 in) of rainfall, the populations of *Larrea* nearly always have low densities. Overall, however, density is poorly correlated with mean annual rainfall ($r = 0.321$), and highest correlation with the temperature parameters is with the mean of the extreme maximum temperatures ($r = 0.546$). With the precipitation/temperature ratio the correlation is intermediate ($r = 0.463$). Rainfall and the temperature parameters, alone or in combination, cannot be clearly cited from the data as direct controls of density variations, although both rainfall and temperature appear unquestionably to be involved in the maintenance of numbers of plants in *Larrea* populations. The Cabazon, California, site of Woodell et al. (1969) is another example of this high rainfall-low density relationship.

When rainfall and temperature are considered together in the P/T ratio for each site (Table 1), in relation to height and density (mean height times numbers of plants), the two groups of sites remain distinctly separated. For those with low to moderate
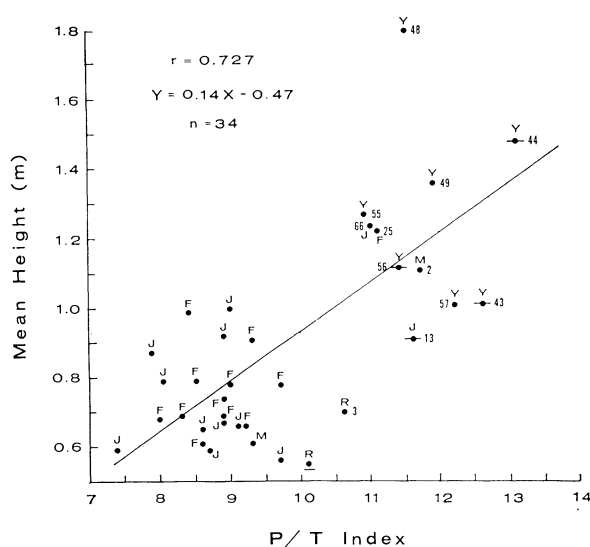

FIG. 6. Mean height of *Larrea* plants, in relation to mean precipitation/mean air temperature (P/T index) as recorded 1963–71, 34 sites, five drainage basins (legend, Fig. 4), Nevada Test Site, central-southern Nevada. Black dot, *Larrea* site; dot with line, *Larrea/Coleogyne* site.

rainfall (and P/T ratios less than 10), the correlation coefficient is 0.401; for the high rainfall sites, whose P/T ratios are from 10.6 to 13.0, $r = -0.551$. The pattern of relationship in both groupings is linear; the positive correlation in the one group, and the negative correlation in the other, and the clear separation of the groups, are a confirmatory summation of the relationships: there is an average rainfall of around 160 mm (6.29 in) which is critical to the behavior of *Larrea*; below this critical value, size and numbers of plants generally increase with increases in rainfall, and above this value increases in rainfall continue to result in increases in size but a concomitant decrease in numbers of plants. The principal role of temperature is probably through its influence on increases or decreases in evaporation processes in the systems and hence precipitation effectiveness, as reflected in the P/T ratio.

Distribution in relation to temperature

In Fig. 7, all of the 59 sites are plotted according to the average of the extreme minimum air temperatures for the 10 winters of the record and the mean rainfall for 9 yr. Sites with *Larrea*, and sites without *Larrea*, are clearly separable when these two environmental parameters are used in combination.

Minimum temperature relationships.—Extreme minimum temperatures have been held to be the probable control of the northern limits of *Larrea* (Shreve 1940, Cottam 1937). Although the parameter used in Fig. 7 is the extreme minimum air temperature, and *Larrea* communities of the network
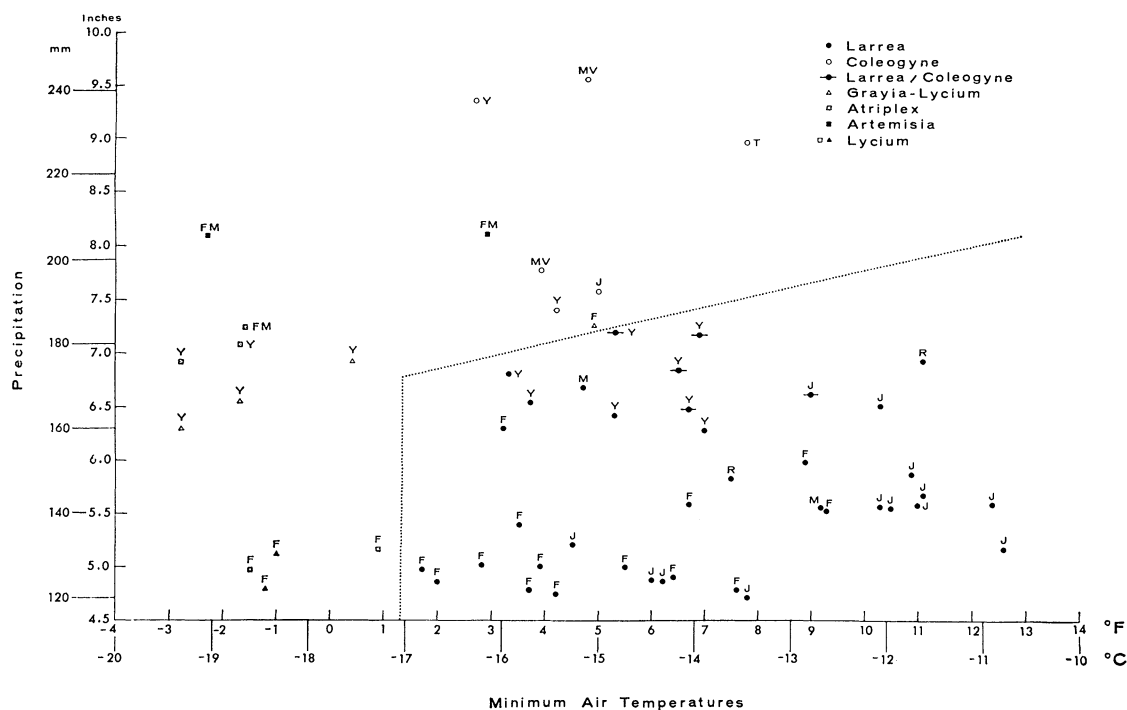
FIG. 7. Mean annual extreme minimum temperature, 1962–72 (10 winters), in relation to mean precipitation, 1963–71 (9 yr), 59 sites, eight drainage basins (legend, Fig. 4), Nevada Test Site, central-southern Nevada.

are restricted to sites with average extreme minimums above 1° F (−17° C), the pattern of mean minimum air temperatures among the sites is also here expressed. On all but three of the *Larrea* sites (Table 1), the year-round mean minima for the 9-yr record are below the 38.3° F (3.5° C) January isotherm cited by Garcia et al. (1960) as coinciding with the northern limits of *Larrea*.

The *Larrea* sites of Fig. 7 are all below the 183-mm (7.20-in) rainfall line and above 1° F (−17° C) extreme minimum temperatures (i.e., below and to the right of the dotted line); these are also above the year-round mean minima of 28.5° F (−2° C) (Table 1). Two groupings of the non-*Larrea* sites are apparent:

1) Those sites with rainfall above 183 mm (7.20 in) and in which the minimum temperatures fall well within the range of sites with *Larrea*. Nearly all of these are in *Coleogyne* vegetation of the middle elevations. There is no suggestion from these data that minimum air temperatures might be limiting to *Larrea* on the upper bajadas in this region, since *Larrea* is replaced altitudinally by *Coleogyne* communities where the minimum air temperature parameters are without exception within the same range as those with *Larrea*. Some of the *Larrea* communities occur in environments having, in fact, consistently lower minimums than occur in any of the *Coleogyne* sites of the network.

2) Those sites on which the mean extreme winter minimum is below 1° F (−17° C), and the mean minimum is below 28.5° F (−2° C), regardless of whether the rainfall mean is high, low, or intermediate. The nine Frenchman Flat sites with mean extreme minima of less than 4° F (−15.6° C) and year-round mean minima of less than 32° F (0° C), are under the influence of a layer of cold air which apparently nightly covers the lowlands of Frenchman Flat, and lower portions of which appear to define the areas of the *Atriplex*, *Lycium pallidum*, and *L. shockleyi* communities whose locations are shown in Fig. 1. Cool air moving during the nighttime hours out of the mountain canyons and down the bajadas toward the lowest point in the basin (the playa), is a year-round phenomenon. Temperature contrasts at night along highways crossing into and out of the sharply defined non-*Larrea* zones of Frenchman Flat (Figs. 1 and 2) are well known to local observers.

A similar situation obtains in the enclosed, symmetrical, elliptic-shaped drainage basin of Yucca Flat. Here the basin floor, in contrast with the steeper bajadas of the irregular- but more nearly circular-shaped Frenchman basin, is long and low-gradient [20 m/km (100 ft/mile)] from the playa northward to the base of the Belted Range. In the *Atriplex* and *Grayia-Lycium* communities of the basin floor, the mean extreme minima are mostly below 0° F (−18° C), and the *Larrea* communities

of the bajadas above the cold air layer, and even the local islands of *Larrea* vegetation on the basin floor (sites 48 and 49) have minima contrastingly well above the apparently critical mean extreme minimum of 1° F (−17° C) and year-round mean minimum of 28.5° F (−2° C). Here, as in Frenchman Flat, cold air accumulations are a nightly event, most intensively expressed when surface soils are dry, and on clear, calm nights of autumn and early winter. Year-round minima in the lowlands of both basins, i.e., near the playas at 950 m (3,100 ft) in Frenchman Flat and 1,200 m (3,900 ft) in Yucca Flat, are often below those on Rainier Mesa (Fig. 1) 1,070 to 1,370 m (3,500 to 4,500 ft) higher than the playas to the south.

That cold air drainage phenomena, including a cold air layer over the lowlands of Frenchman and Yucca Flats, were the probable causes of the conspicuous phenological gradients from the lowlands to the upper bajadas during the spring growing season, and of the distribution of *Larrea* in Yucca Flat, were discussed by Beatley (1959). Lower minimums below the level of *Larrea* along a vegetation transect in southwestern Yucca Flat were subsequently documented in the winter and spring of 1961 by Wells and Shields (1964).

The absolute minima recorded during the 10-yr period were −8° F (−22.2° C) for *Larrea* communities (sites 34 and 36 near Frenchman playa); −7° F (−21.7° C) in *Coleogyne* (site 41 in Mid Valley); −14° F (−25.6° C) in *Grayia-Lycium* (site 50, Yucca Flat); −11° F (−23.9° C) in *Lycium pallidum* and *Lycium shockleyi* (sites 38 and 37, Frenchman Flat); −18° F (−27.8° C) in *Atriplex* (site 30, Frenchman Flat), the all-time low minimum temperature for all sites of the network; and −10° F (−23.3° C) in *Artemisia* (site 62, Forty-Mile Canyon drainage). Lowest winter temperature recorded in *Artemisia*-Pinyon-Juniper at 2,290 m (7,500 ft) on Rainier Mesa was −12° F (−24.4° C), and the mean extreme minimum of −1.7° F (−18.7° C) is higher than the −2.8° F (−19.3° C) average for the two sites nearest Yucca playa (sites 59 and 60) at 1,100 m (3,600 ft) lower elevation; readings below 0° F (−17.8° C) are in fact much less frequent in the record for site 64 on Rainier Mesa than on most sites of the lowlands of Frenchman and Yucca Flats.

The extreme minimum temperatures of late autumn and winter in the lowlands of these basins occur one or more times in the record for most years of the period of measurement. Each year these are within the range recorded by the U. S. Weather Bureau during periods considered to be extremely cold for southwestern United States. The extensive damage to desert species, resulting from the low temperatures of one such period, was described by Turnage and Hinckley (1938); it occurred in late January 1937

over much of western United States, and in many areas the all-time extreme low minimum temperatures of the Weather Bureau record were set at this time. In St. George, Utah, where sub-zero °F (below −17.8° C) temperatures had been recorded only a few times in the 49-yr record to that date, from January 21 through 27, 1937, minima were from −1° to −11° F (−19.4° to −23.9° C), and for these 8 consecutive days the maxima were from 17° to 31° F (−8.3° to −0.6° C); it was therefore an 8-day period in which air temperatures in the shelter did not rise above freezing.

The actual day and night temperatures to which *Larrea* plants were exposed in the St. George area, and elsewhere near the northern margin of the species' range, are of course not known, but the degree and duration of the subfreezing temperatures were sufficiently intense to cause widespread killing of the aboveground parts of *Larrea* in the St. George area (Cottam 1937). However, new shoots already 10–50 cm tall by the following summer were reported by Fosberg (1938), along with the observation that none of the *Larrea* plants had in fact died.

No temperature records for this extreme cold period are available for the Test Site region, but it is inferable from what is known of temperature regimes over the Test Site that minimum temperatures greatly exceeding any recorded in the Weather Bureau shelter at St. George must have occurred at this time in the Frenchman and Yucca Flat lowlands. These perhaps approached the −50° F (−45.6° C) recorded by the Weather Bureau in Elko County, Nevada (see Climatological Data for Nevada), particularly if the ground was snow-covered, as was reported to be the case in many parts of Nevada and Utah during this January. It seems a well-justified inference that *Larrea*, and probably many of its Mojave desert associates, have long been excluded from the lowlands of Frenchman and Yucca Flats, and from their topographic counterparts elsewhere in the southwestern deserts, by the minima below 0° F (−17.8° C) which must have characterized the winter climates of such lowlands for many centuries. Extension of the extreme minima downward during occasional periods of regional extreme cold should effectively eliminate any beginnings of encroachment of *Larrea* into these climates.

Maximum temperature relationships.—Average extreme maximum air temperature for nine summers, on all sites, is plotted against the mean rainfall for 9 yr in Fig. 8. The maxima are on the whole higher in Frenchman Flat and Jackass Flats than in Yucca Flat at 1,525 to 3,050 m (500 to 1,000 ft) higher elevation. There is no discernible pattern of relationship between maximum temperatures and occurrence of *Larrea* in any of the basins. As with the minimum temperatures, *Coleogyne* sites span the range of mean
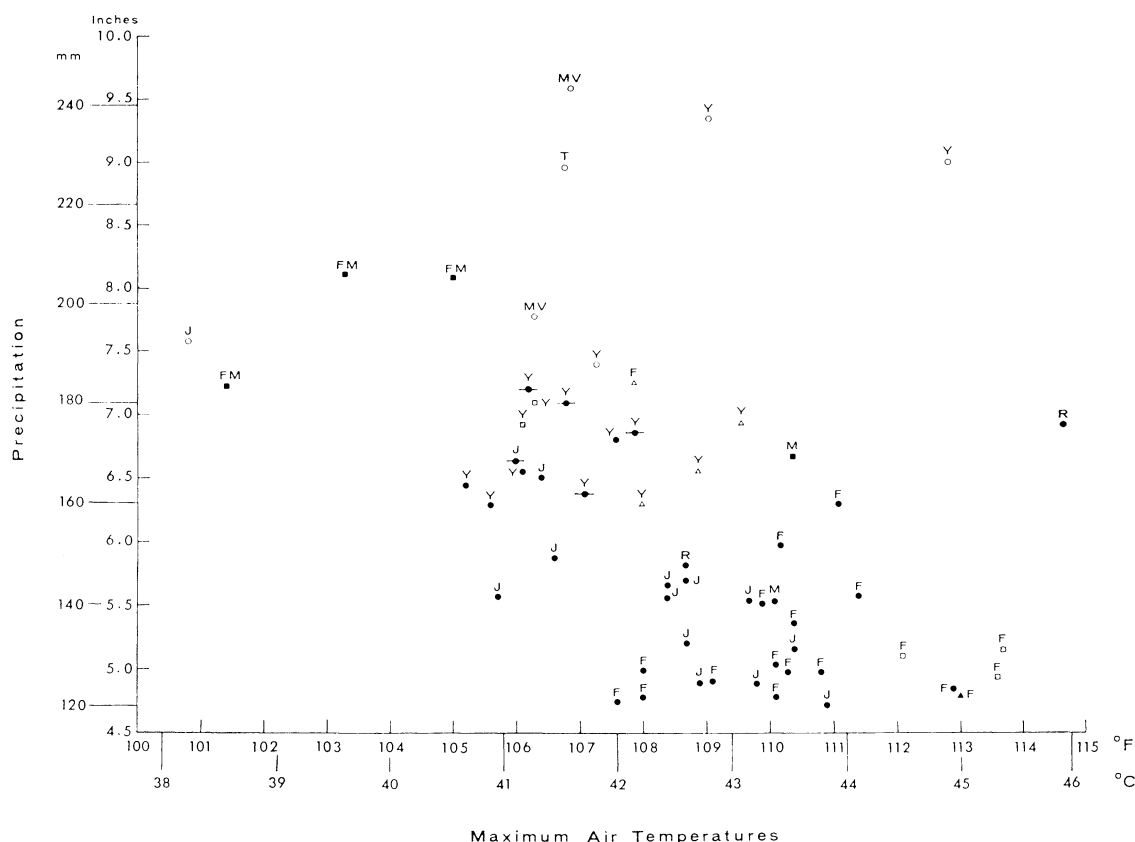
FIG. 8. Mean annual extreme maximum temperature, 1963–71 (9 summers), in relation to mean precipitation, 1963–71 (9 yr), 59 sites (legend, Fig. 7), eight drainage basins (legend, Fig. 4), Nevada Test Site, central-southern Nevada.

maximum temperatures [both the extremes (Fig. 8) and year-round maxima (Table 1)], although topographically *Coleogyne* occurs above the *Larrea* communities and is identified with the middle elevations of the region.

Frenchman Flat sites with mean extreme maxima above 112° F (44° C) (extreme right in Fig. 8) are nearly all the same sites characterized by mean low minima and are within a few kilometers of the playa (Fig. 1). Daytime air temperatures are often sensibly higher on these sites at all seasons. The consistent high maxima in the lowlands of Frenchman Flat are perhaps an anomaly to the usual daytime temperature patterns on the floors of closed basins. The patterns of daytime air flow and the pronounced heating in the lowlands are evidently influenced by the circular shape and mountain irregularities of the Frenchman Flat drainage basin (Fig. 1). In the symmetrical, elliptic-shaped Yucca Flat basin, with a low-gradient basin floor, the highest maxima are often on sites well above or distant from the lowlands near the playa.

Highest maximum temperature recorded in the nine summers of the record was 121° F (49.4° C) in

Atriplex vegetation (site 30, north side of Frenchman playa, on which the all-time extreme minimum temperature also was recorded), and also twice on site 3 on the south slope of Rock Valley, which by all criteria in combination is probably the warmest site of the network. Maxima of 117°–120° F (47°–49° C) occur in the record of site 3 and all of the *Atriplex* and *Lycium* sites near Frenchman playa, and also in *Coleogyne* (site 51) on the upper bajada of northwestern Yucca Flat. Of the sites of the network with extremely high summer temperatures in the record, *Larrea* is present only on site 3.

Rainfall relationships

Larrea communities of one kind or another occupy sites with mean rainfall from the lowest recorded [120 mm (4.72 in)] to 183 mm (7.20 in) (Table 1), and are absent from all sites with mean rainfall in excess of 183 mm (7.20 in). The Transition desert vegetation of Yucca Flat, where the species is at its northern and upper altitudinal limits in the region, is under the apparent major control of the rainfall regimes, and locally as these regimes are influenced by topographic features. The region is subject to
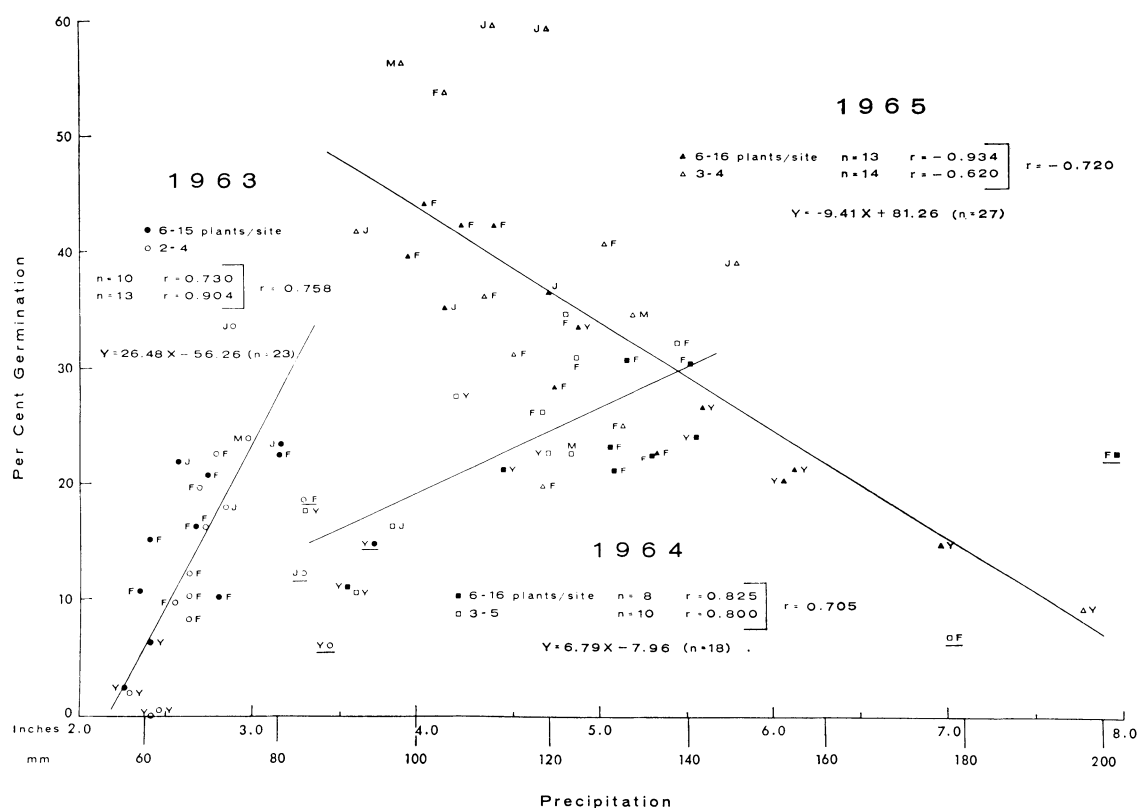
FIG. 9. Seasonal precipitation (discussed in text) in relation to mean percent germination/site of seeds collected from the same *Larrea* plants in 1963, 1964, and 1965 on sites in four drainage basins (legend, Fig. 4), Nevada Test Site, central-southern Nevada. The underscored 1963 and 1964 populations have rainfalls placing them in the 1964 and 1965 germination/rainfall patterns, respectively, and are omitted from the calculations. If included in the 1964 and 1965 calculations, *r* value for 1964 (n = 22) increases to 0.769, and to −0.734 for 1965 (n = 29).

winter snowfall, but snows are rarely in amounts that would be destructive to shrub vegetation; snow accumulation and persistence occur especially in the northern half of Yucca Flat, but are usually of short duration in the more southerly basins.

On sites 44 and 45, about a kilometer apart on the upper bajada, soils and topographic position are essentially the same, and both lie in the path of storms dissipating as they move eastward from Shoshone Mountain (Fig. 1). The more westerly site 45, with a slightly higher predictability for rains incoming from the west, is *Coleogyne* without *Larrea*, and site 44, a short distance farther east, is *Coleogyne* with *Larrea*. Site 43, also *Coleogyne* with *Larrea* (and *Atriplex*) and with somewhat different soils and topographic position, often receives rain incoming from the east and diminishing as the storms move west across sites 44 and 45 (Fig. 1). In addition to an average slightly lower rainfall on sites 43 and 44, these two *Larrea* sites are apparently somewhat warmer than the *Coleogyne* site 45, with their higher minima offsetting their slightly lower maxima and resulting in a slightly reduced precipitation effective-

ness and hence exaggeration of the small rainfall differences among the three sites; these relationships are reflected in the P/T ratios (Table 1). Precipitation effectiveness, as influenced by higher temperatures, is inferred to account also for at least some of the altitudinal extensions of *Larrea* on southern exposures in southern Nevada, and perhaps its occurrence in southern California at the high rainfalls cited by Woodell et al. (1969) and Garcia et al. (1960).

Coleogyne vegetation is everywhere in the region identified with high rainfall, whether on bajadas or valley floors [as in Topopah Valley and Mid Valley, with an annual average 200 mm (8 in) or more]; the broad ecotones of *Larrea/Coleogyne*, as on the north and east slopes of Jackass Flats (Fig. 1), are the areas within a rainfall gradient upslope which receive between 160 and 180 mm (6–7 in) on the average. *Artemisia* communities are also characterized by average rainfall in excess of 200 mm (8 in); at the high elevation of Rainier Mesa where *Artemisia* occurs with Pinyon and Juniper, the mean rainfall as recorded during the 9 yr was nearly 300 mm (11.8 in).

Seed germinability.—Results of the *Larrea* germination trials for 1963, 1964, and 1965 are shown in Fig. 9 in relation to the rainfall of what is here defined as the "biologically effective season" for each of the years: 1962–63 season, beginning with late September rains in 1962, and continuing through early June 1963; 1963–64 season, beginning with late September rains in 1963, and continuing through August 1964; and 1964–65, beginning with light rains in November 1964 and continuing through August 1965.

Fruits used were those maturing and abscising during the summer months, and summer rainfall, as well as the rains of the growing season preceding late spring flowering, usually contributes to the maturation success of the fruits. In the season 1962–63, with the lowest rainfall of the nine-season record, summer rains were ineffective in altering seed maturation success, which was apparently already determined by the low rainfall of the autumn-through-spring season—inclusion of summer rains reduces the 1963 correlation coefficient from 0.758 to 0.216. If summer rainfall (mid-June through August) is excluded from the biological seasons of 1963–64 and 1964–65, *r* values decrease respectively to 0.659 and –0.449. Influence of summer rainfall (with a predictability of around 25% of the annual total in this region) in itself is of interest in a region with an autumn-winter-spring biological season for most plant species. This aspect of the reproductive behavior of *Larrea*, i.e., the requirement of summer rains for successful reproduction, is probably associated with the species throughout its range, in much of which summer rainfall constitutes the major part of the annual total (Shreve 1942).

In the 1964–65 season, the heavy rains of March and April 1965, which appeared to trigger most biological activity this season and which resulted in profuse vegetative growth and flowering of shrub species throughout the region (Beatley 1969*b*, *c*), were much less well correlated with the percent germination of *Larrea* seeds ($r = -0.538$) than rainfall of the season November through August ($r = -0.720$).

Mean percent germination/site was 14.1% in the 1963 samples, 22.8% in 1964, and 35.2% in 1965. Highest percent germination for samples from any one plant was 89% in 1964 from a plant on site 55.

From the 3 yr of data plotted in Fig. 9, it is evident that the current seasonal rainfall plays a dominant role in the success of reproduction in *Larrea* each year, and that if the rainfall is known for what is here termed the effective season, there is a good basis for prediction of the percent of germinable seeds which will be produced in a given population of *Larrea*. In general, if there are 50–80 mm (2–3 in) of rain or more than 150 mm (6 in) during this season, germinability of seeds is usually less than 20%; if the rainfall is 80–150 mm (3–6 in)—the range most predictable for the Mojave desert of this region—germinability is mostly 20% to 60%. Percent germinability of seeds was not correlatable with any of the maximum or minimum temperature parameters for any of the seasons or combinations of seasons within the 3 yr; among these parameters was the extreme minimum winter temperature, the lowest of which occurred during the 2nd wk of January 1963, when extreme minima on the *Larrea* sites ranged from –7° to 8° F (–21.6° to –13.3° C) and the period was one of the three coldest of the 10-winter record.

Larrea populations of areas with mean rainfall in excess of 150 mm (6 in)—those at the northern limits of the species' range in Yucca Flat, and certain other sites—in the drier years are just as capable of producing a high percentage of germinable seeds as those populations which in most seasons receive only 80–130 mm (3–5 in) of rain. The relationship between seed germinability and rainfall is a remarkably close one, considering the very long sequence of physiological processes which must occur in the *Larrea* plants between the time of water absorption by the roots beginning in the autumn, and the ultimate formation of viable seed embryos the following summer. So close is the relationship that seed samples from only three plants per population appear adequate for determining the percent germinability of seeds from a given site. The relationship supports the inference that the portions of the root system in the upper soil layers are in *Larrea*, as in most other desert plants, those most active in absorption of water.

Two field observations made in the course of the materials collections additionally indict high rainfall as detrimental to the processes of reproduction in this species. In years of higher rainfall—of the magnitude usually resulting in highly successful herbaceous plant populations in the spring—or along drainage courses, where input of water is somewhat greater, a high proportion of flowers often are diseased. Externally the maturing buds appear normal, but within the flower the pistil and stamens are imperfectly developed and the tissues darkened; commonly fewer than half of the 10 stamens have functional anthers. Proportion of diseased flowers varies with position on the branch, and from plant to plant on a given site.

Numbers of flowers and fruits are highly variable among plants, sites, and seasons. Flowering success in *Larrea* populations is conspicuously greatest in areas with moderate rainfall, and flowering and fruiting may even be spectacular in these areas in seasons of near failure of herbaceous species. In the Yucca Flat populations, with usually relatively high rainfall, flowers are commonly sparse in relation to

size of plants, but in drier years these same plants may flower and fruit in profusion. A high correlation between increased January–September precipitation and reduced fruit production was noted by Valentine and Gerard (1968) in their *Larrea* studies in the Chihuahuan desert (New Mexico) over a 6-yr period.

Effects of high rainfall.—From the relationships between high rainfall within the regional pattern and the distribution of *Larrea* (Fig. 7), and between seasonal high rainfall and seed germinability (Fig. 9), the conclusion seems inevitable that the northern boundary and upper altitudinal limits of this species in southern Nevada are determined primarily by rainfall in excess of a critical amount, and by the rainfall regimes over probably a very long time. The critical mean rainfall indicated by the particular 9-yr period and the method of measurement of this study is 183 mm (7.20 in); this would not be directly comparable to the lesser rainfall amounts recorded by the U. S. Weather Bureau, and is subject to increase or decrease with the long-term records required to establish the range of absolute critical rainfall values in relation to fluctuations of other environmental variables of influence (especially air and soil temperatures) to the local behavior of *Larrea* populations. Since rainfall delivered to the earth's surface is not the same on any two sites, and may differ within even short distances, its measurement must be on the site of interest; rainfall data collected at some distance are at the least imprecise and perhaps misleading or irrelevant to the amounts of water actually received.

In this region rainfall distribution during the 9-yr period was around 25% from early June to mid-September (summer); 25% from mid-September through early December (autumn); 35%–40% from mid-December until late March (winter); and 10%–15% from late March to early June (spring). If the winter season is extended to include the latter half of November and the first week of December—the period with greatest predictability of heavy rains—winter rainfall constitutes 50%–55% of the annual total on most sites. The seasons as here defined are based on the phenological calendar for the plant species of the study sites and elsewhere in the region, as recorded during the decade of plant and environmental measurements. Seasonality of rainfall is under the control of regional atmospheric variables (polar and tropical maritime air masses), and although the amount of water delivered is variable from site to site, the seasonal percentage among the Mojave, Transition, and Great Basin sites is essentially the same.

Larrea is identified elsewhere with annual rainfalls greatly exceeding the maximum of 183 mm (7.20 in) of this study. In the comprehensive treatment by Garcia et al. (1960) of rainfall and temperature data from stations throughout the range of *Larrea*, the annual rainfall reaches 548.5 mm (21.6 in) at Cer-

ritos, San Luis Potosi, Mexico; less than 50 mm (2 in) of this is winter rain (8.6% of total). Particularly relevant is the fact that in this compilation, using the rainfall records from 185 stations widely distributed in southwestern United States and Mexico, wherever the mean rainfall is reported to be over 181.1 mm (7.13 in)—which includes nearly all of their stations in the eastern Sonoran and Chihuahuan deserts—the percent of rainfall delivered in the winter is less (usually much less) than 35%; where 35% to over 50% is referred to as winter rain—in the western Sonoran and Mojave deserts—the maximum total annual rainfall is 181.1 mm (7.13 in) (Bakersfield, California, with 54.6% of the total designated as winter rainfall). This maximum is in extraordinarily close agreement with the 182.9-mm (7.20-in) maximum value for *Larrea* communities in the microclimates of the Test Site. It seems probable that the rainfall parameter critical to the distribution and behavior of *Larrea* near its northern limits in southern Nevada is not the average annual total but that of the late autumn–winter season, i.e., mid-November until late March.

On the sites with an annual average 160–183 mm (6.29–7.20 in) of rainfall, the *Larrea* plants in nearly all populations are conspicuously tall, usually averaging more than a meter high, and are correspondingly large in diameter. These characteristics, as previously discussed, appear directly attributable to the higher rainfall (and lower temperatures) on these sites. The corresponding reduction in density, however, is more difficult to explain. In view of the low percentage of germinable seed produced probably in most years by these populations, the low densities of established populations seem most likely to be the result of failure of the reproductive processes through time to maintain the populations at higher densities. There is no evidence to suggest that "competition" with other shrub species plays any significant role in maintaining these low densities of *Larrea*.

At least some germinable seeds are produced in years of higher rainfall, and in drier years percentage of viable seeds equals that of the lower rainfall areas elsewhere. That germination and establishment of seedlings may be highly successful at the very northern limits of the species is evident from data for site 54 in northeastern Yucca Flat: Of the 28 *Larrea* plants present on the study plot in 1972, 8 were of seedling origin since 1964 (mean height, 28 cm). The site is one on which the above-ground parts of all shrubs were killed by dust effects from the Sedan thermonuclear detonation in 1962 (Beatley 1965), and the 20 (of the original 21) *Larrea* plants that subsequently sprouted averaged 0.96 m tall in 1972 and were scarcely distinguishable from the nearby plants of the same population beyond the

limits of dust deposition. That the heavy dust deposits on the original soil surface of the site, or the failure of most other shrub species to have recovered by sprouting, or the original low density of *Larrea*, in themselves, were major factors in successful establishment of seedlings is denied by the successful establishment during the same time interval of 16 seedlings (mean height in 1972, 25 cm) on the plot of an undisturbed site with exceptionally high *Larrea* density (site 24 in Frenchman Flat, with the third highest density of the network).

The relationship between high rainfall and distribution of *Larrea* is in apparent contradiction to the size and apparent vigor of plants in areas of high rainfall or its equivalent in available soil moisture. It was pointed out many years ago by Spalding (1904), Shreve (1940), and others in the early physiological work on this species that artificially watered established seedlings grow at sometimes greatly accelerated rates in continuously moist soils. Extremely high winter rainfall in southern Nevada in itself is not detrimental to established plants, which are usually growing under conditions of excellent internal drainage of the soils. This is inferred from the failure of the Test Site plants to exhibit any death or apparent damage to the branches following a 3-mo period from January into early April 1969, when rainfall on the *Larrea* sites was 150–270 mm (6.0–10.6 in) [to 380 mm (15 in) elsewhere below 1,770 m (5,800 ft)]. *Larrea* at the margin of its range in Yucca Flat is not characterized by high incidence of dead branches, as reported by Shreve (1940); dead branches occur less frequently here than on a number of sites in Jackass and Frenchman Flats.

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