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The Distribution and Phytosociology of Yucca elata in Southern New Mexico

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ABSTRACT: The ecological distribution and phytosociological characteristics, i.e., species correlations and associations and spatial patterning, of Yucca elata were examined on the New Mexico State University Jornada Ranch. Yucca elata has a similar geographical and edaphic distribution on the Jornada as in the Chihuahuan Desert as a whole. Yucca elata is significantly associated with Prosopis glandulosa and Xantho-cephalum sarothrae around a playa site on the Jornada Ranch. However, a general lack of significant correlations and associations between Y. elata and other species in desert scrub and grassland communities indicates the ubiquitous nature of this species. It reaches its best development in the desert grassland community and occurs in the more mesic areas of the desert scrub communities, possibly being a relic of past grassland vegetation in these areas. Individual canopies exhibit strong clumping due to vegetative propagation being the dominant form of reproduction. Cattle and fire disturbance appear to increase clumping in the species.

Introduction

Soaptree yucca (Yucca elata Engelm.) is one of the most characteristic plants of the Lower Sonoran Zone of the Chihuahuan Desert (Wooton and Standley, 1915). It is the dominant arborescent monocot of the northern Chihuahuan Desert, an area where the arborescent monocots reach their greatest development in the United States (Clements, 1920).

Yucca elata may be recognized by its well-developed trunklike stem, tall, ellipsoid panicle and capsular fruit (Webber, 1953). It varies from 1-9 m in height, with large individuals having 1-5 assurgent branches toward the top of the trunk (Correll and Johnston, 1970). Secondary growth occurs in the plant (Cheadle, 1937) and it is thought to be a long-lived perennial, possibly living 300 years or more (Little and Campbell, 1943). The plant produces new canopies of leaves mainly by vegetative means, either as stem branches or as basal sprouts (Webber, 1953).

Although numerous individual observations have been made, there is no synthesis of Yucca elata's ecological distribution; and, although information is available on its autecology (Campbell and Keller, 1932; Smith and Ludwig, 1976), there have been no quantitative studies on its synecology. The purpose of this study is to review the available information on the ecological distribution of Y. elata and to report on a study of its relationships with other species on the Jornada Range in southern New Mexico.

STUDY AREA

Location.—The study was conducted on the New Mexico State University Experimental Range (College Ranch) in Doña Ana Co., southern New Mexico (Fig. 1). Three sites were selected which were thought to be representative of the distribution of Yucca elata on the Jornada Range, and in the Chihauhuan Desert of southern New Mexico. The three sites were selected on a piedmont slope (watershed) at the base of Mt. Summerford at the northern end of the Doña Ana Mountains. The three sites will be called the Summerford, Bajada and Playa sites in subsequent discussions (Fig. 1). The Bajada and Playa sites are associated with the studies of the U.S./I.B.P. Desert Biome Program.

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² All nomenclature follows Correll and Johnston (1970).

Fig. 1.—Location of the Summerford, Bajada and Playa study sites on the New Mexico State University Jornada Ranch near Mt. Summerford in the Doña Ana Mountains in southern New Mexico. Each dot enclosed within the solid line indicates the position of a random transect sampled for the phytosociological analyses

Vegetation and soils.—The Jornada Range exemplifies the northern Chihuahuan Desert, with vegetation types of desert scrub and open yucca-grasslands (Buffington and Herbel, 1965). Around 1940, the Jornada Range was approximately 33% mesquite (Prosopis glandulosa var. torreyana), 30% black grama (Bouteloua eriopoda) grassland, and 11% tobosa (Hilaria mutica) grassland (Little and Campbell, 1943). In a subsequent study, Branscomb (1958) found that from 1915 to 1946 the black grama grassland decreased 12% and mesquite-dominated areas increased 20%.

The Summerford site is located at the base of Mt. Summerford (Fig. 1), and has more grass cover than shrub cover. It is dominated by needle grama (Bouteloua aristitoides) and 6-weeks grama (B. barbata). Yucca elata is the dominant perennial on the site, the only other well-established perennials being sotol (Dasylirion wheeleri) and mesquite. The Summerford site has a 10% slope with well-drained sandy loam soils (Gile et al., 1970). Based on species composition, it is characteristic of the desert grasslands (Whitfield and Beutner, 1938; Humphrey, 1958).

The Bajada site is a 25-ha alluvial fan between the base of Mt. Summerford and the Jornada plain. On this site, Yucca elata has an estimated density of 123 individuals per ha, with a large majority of them occurring in the numerous small arroyos (washes) dissecting the site (Whitford and Ludwig, 1973). The small arroyos have a 5% slope and a well-drained coarse sandy soil. Creosote bush (Larrea tridentata) is the most abundant shrub on the site (4800 ind ha-1) but is only a minor constituent of the small arroyos where Y. elata dominates. Other perennials common in the small arroyos are snakeweed (Xanthocephalum sarothrae), mariola (Parthenium incanum), tarbush (Flourensia cernua), banana yucca (Yucca baccata) and mesquite. The Bajada site, based on species composition and relative importance, is characteristic of the northern Chihuahaun Desert scrub formation (Gardner, 1951).

The Playa site is a 36-ha ephemeral lake area approximately 2 km N of the Bajada site. Yucca elata only occurs around the fringes (23 ha) of the playa bottom (13 ha), with an estimated average density of 152 ind ha⁻¹ of fringe (Whitford and Ludwig, 1973). The soil of the fringe is sandy loam to clay loam with an approximate slope of 2% (Gile et al., 1970). Mesquite has the highest ground cover of the shrubs on the fringe (24%), whereas Y. elata, although conspicuous, only has a ground cover of 0.5%. Snakeweed has the highest density of the perennial shrubs on the fringe (586 ind ha⁻¹), but only a 0.7% cover. The mormon-teas (Ephedra trifurca and E. torreyana) are also conspicuous shrubs with 417 and 154 ind ha⁻¹, respectively. Although common on the Bajada site, Y. baccata is absent from the Playa fringe. This plant association is restricted to playa fringes of the Chihuahuan Desert.

Climate.—The average annual precipitation (1851-1971) for Las Cruces is 211 mm, with 54% falling during July, August and September (Houghton, 1972). Precipitation on the Jornada Range is slightly higher than in Las Cruces, with about 226 mm per year (Herbel et al., 1970). Spring is the dryest season, with hot, desiccating winds common. Average annual evaporation (48-inch land pans of Weather Bureau Class A installations) on the Jornada Range is about 2400 mm (Gardner, 1951). Summers are hot, with an average daily maximum of 33.9 C and an average daily minimum of 16.8 C. Winters are mild, with an average daily maximum and minimum of 14.9 C and -2.9 C, respectively. The average frost-free season is 197 days, from 13 April to 28 October.

DISTRIBUTION

Yucca elata has a general distribution similar to that of the Chihuahuan Desert, occurring from western Texas to Arizona and from central New Mexico into northern Mexico (Engelmann, 1878; McKelvey, 1947; Kearney and Peebles, 1969),

but it also exhibits a secondary isolated range in southwestern Utah (Webber, 1953). It appears to reach its best development in southern New Mexico, where it grows abundantly on plains, rolling hills, playa fringes and rocky slopes. It grows where the soil is deep, since it has a long tuberous root (Cannon, 1911; Ludwig, 1977). Shreve (1939) reported it being most common in Chihuahua, Mexico, in the extensive dune areas in the northern part of the state, as it is in the dune formations of southwestern New Mexico (Harshberger, 1958). Johnston (1944) found Y. elata common in the open valleys and rolling plains of Chihuahua. He also reported it in the Mexican states of Coahuila, Zacatecas and Durango. In Coahuila, while restricted to the transition zone between desert and grassland, it extends more prominently into the grassland (Shreve, 1942).

Because it is an alkaline-tolerant plant (Small, 1946), Yucca elata grows well in the internal drainage basins characteristic of the Chihuahuan Desert. It also grows well on gypsum soils, and Waterfall (1946) observed it to be common on gypsum beds throughout western Texas, occurring in areas which other common related monocots, such as Y. baccata and Agave lecheguilla, could not tolerate. He thus concluded that Y. elata is a gypsophilous plant. Although Johnston (1941) observed it on gypsum soils in northern Mexico, he concluded it not to be a gypsophile, but simply gypsum-tolerant. Observations by Little and Campbell (1943) appear to support this, as they found Y. elata to be conspicuously absent from the extensive gypsum beds on the Jornada.

At the margins of its range, Webber (1953) found Yucca elata to hybridize freely with Y. glauca (central New Mexico and Arizona), with Y. angustissima (southern Utah) and with Y. constricta (western Texas). McKelvey (1947) felt that these were not hybrids, but separate species. However, Webber (1960) found greenhouse Y. elata-Y. glauca hybrids to have 84% and 86% seed germination in the F_1 and F_2 generations, respectively. Webber maintained that similar karyotypes in the different species of Yucca indicate parallel speciation, with the major barrier to interbreeding being spatial isolation. The Yuccas have possibly maintained this spatial isolation for some time, since the present distribution of Yuccas appears to be similar to that of 10,000 to 40,000 years ago, based on the findings of Laudermilk and Munz (1935, 1938) and Wells (1966).

PHYTOSOCIOLOGY

Methods.—Species covariations (correlations) were examined from data obtained in line transects on the study area in 1970 (Fig. 1). A 2½ mile² area, indicated by the solid line in Figue 1, was delimited and divided into 0.1 mile segments to facilitate stratified random sampling. Within each of the segments, a random line was determined and along each line 10 randomly determined positions were located. If the random position fell on the rocky slopes of Mt. Summerford, it was excluded. At each random position two parallel 15-m (50 ft) N-S lines were oriented 3 m (10 ft) apart. Along the total 30-m (100 ft) line, intercept of plant species was recorded to determine percentage ground cover. The two lines also formed the boundaries of a rectangular 15 m by 3 m quadrat. Presence of any species in the quadrat not intercepted by the two lines was recorded and arbitrarily given a cover of 0.01%.

The data for the 18 most abundant perennial species in the transects sampled was first subjected to normal association analysis (Poole, 1974), which subdivided the data into two general groups, one representing desert scrub and the other desert grassland, and a specific small group representing the playa bottom, which was not included in further analyses. Each of the two groups of transect data, desert scrub and desert grassland, were then analyzed by principal components analysis, an ordination technique useful in studying the relationships of species in a

continuum (Poole, 1974). The species ordination scheme of Orloci (1966) was followed.

Data from belt transects sampled on the IBP Desert Biome Bajada and Playa sites (Whitford and Ludwig, 1973) were analyzed by a species association technique (Poole, 1974). The presence or absence of *Yucca elata* in relation to other common perennials was examined by constructing two by two contingency tables and testing for independence by chi-square analysis.

A nonrandom distribution of individual Yucca elata plants was examined on the three sites using a pattern analysis technique which tests for randomness based on distance measurements (Pielou, 1969). The test, developed by Hopkins and Skellam (1954), examines the distribution of distances from random points to the nearest plant and the distances from each plant to its nearest neighbor. Distance measurements were taken from the random plant to the nearest plant canopy not on the same aboveground caudex, and to the nearest plant canopy not connected by vegetative structures. This provided two types of spatial pattern analysis; of pattern due to basal sprout formation, and of pattern of Y. elata clumps. In addition to the three sites, an area which was burned in 1974 (located about 1 km E of the Playa site) was examined 1 year later. All of the perennials on this area were completely burned so a pattern analysis may reveal how Y. elata becomes reestablished following destruction. A nonburned grassland area adjacent to the burned area was also examined for comparison. On each of the five sites, 20 random points were used. The significance of any differences in distance distributions were tested with Hopkins' ratio test (Greig-Smith, 1964).

RESULTS AND DISCUSSION

Species covariations.—The correlation coefficients between Yucca elata and other perennial species in the desert scrub and grassland communities (Table 1), indicate the ubiquitous nature of this species since no significant correlations were found. For the desert grassland data, the largest positive correlation of Y. elata was with bush mully (Muhlenbergia porteri), a species not common in this community,

Table 1.—Correlation coefficients of Yucca elata with other perennial species occurring in transects for the Desert Grassland and Desert Scrub communities on the New Mexico State University Ranch

	Desert grassland	Desert scrub	
Species	community	community	
Shrubs:			
Larrea tridentata	*	-0.12	
Prosopis glandulosa	0.03	-0.06	
Flourensia cernua	-0.03	-0.01	
$oldsymbol{X}$ anthocephalum sarothrae	-0.03	-0.06	
Ephedra trifurca	0.01	-0.05	
E. torreyana	-0.05	-0.03	
Yucca baccata	*	-0.04	
Parthenium incanum	*	0.05	
Opuntia spp.	-0.04	-0.04	
Zinnia pumila	*	0.01	
Grasses:			
Aristida purpurea	0.15	-0.03	
Bouteloua eriopoda	-0.07	0.14	
Erioneuron pulchellum	-0.13	0.04	
Hilaria mutica	-0.04	-0.02	
Muhlenbergia porteri	0.24	0.01	
Scleropogon brevifolius	-0.08	0.02	
Sporobolus spp.	0.08	-0.01	

^{*} Not present in this community

but more often found with shrubs, such as Larrea and Flourensia (O'Laughlin, 1975). As expected, Y. elata has a negative correlation with Larrea, since it occurs on deeper soils and Larrea exhibited greatest cover on shallow soils.

Species ordination attempts to display the covariations of species along a continuum for each of the communities analyzed (Fig. 2). In the desert grassland, Yucca elata appears segregated from most of the other species, but does exhibit similar component loadings as Ephedra trifurca and Muhlenbergia porteri. Clements (1920) observed Y. elata to be associated with E. trifurca throughout the southwestern desert grasslands, and attributed this to similar water requirements and affinity of sandy soils. Yucca elata exhibits only minor covariation with Prosopis and Xanthocephalum, the two most characteristic range invaders of the southwestern grasslands.

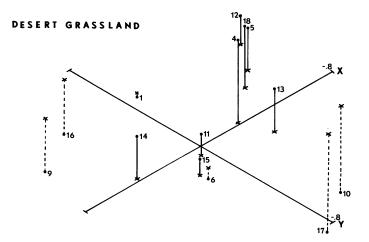
In the desert scrub, Yucca elata appears to covary most closely with the grasses. This is probably due to the moderate to low cover of these species in the desert scrub transects, with Y. elata only abundant in the more mesic areas of desert scrub, which also tend to have higher grass cover. Balding (1971) found Y. elata to occur in more mesic areas of an arroyo system than Larrea, Flourensia and Parthenium; thus Y. elata is segregated from the lower arroyo shrubs, which tend to group together. The ordination also shows Y. baccata to covary most closely with Larrea, Prosopis and Opuntia. Due to its fibrous root system (Webber, 1953), this covariation could be due to Y. baccata's tendency to occur in shallower soils than Y. elata.

Species associations.—On the alluvial fan of the Bajada site, the only significant positive association of Yucca elata based on presence or absence is with Opuntia (Table 2); however, it negatively covaries with Opuntia based on cover data (Table 1). A chi-square value cannot be given for Y. elata's association with Larrea, since Larrea occurs in every transect sampled on the Bajada site. Lack of association with other arroyo shrubs such as Flourensia and Parthenium may be due to the arroyo gradient previously discussed.

On the Playa site, Yucca elata was significantly positively associated with both Prosopis and Xanthocephalum (Table 2). The playa bottom is surrounded by a belt of dense Prosopis thickets, mixed with a band of Y. elata and Xanthocephalum. Observations on playas in other areas of southern New Mexico indicate this association is characteristic.

The general lack of significant correlations and associations of Yucca elata with other species is probably due to the past and present successional changes in the area. The Jornada was historically a desert grassland with the only large perennial being Y. elata (Wizlezenus, 1848; Clements, 1916). However, grass cover has since diminished, with Larrea, Flourensia, Prosopis and Xanthocephalum greatly increased (Whitfield and Anderson, 1938; Branscomb, 1958; York and Dick-Peddie, 1969). Gardner (1951) suggested that as the grassland was reduced Y. elata persisted in areas where shrubs invaded, so that it now occurs on slopes dominated by Larrea, in the extensive mesquite dune areas of the Chihuahuan, and on the fringes of ephemeral lakes, as well as remaining the dominant nongraminoid perennial of the desert grasslands of the northern Chihuahuan Desert.

Spatial pattern.—Although Yucca elata invests large amounts of energy into seed production (Smith and Ludwig, 1976), and seed germination can be very high in controlled experiments (Arnott, 1962; McCleary and Wagner, 1973), the establishment of new individuals from seed appears to be very low in the Chihuahuan Desert (Wooton, 1918; Campbell and Keller, 1932; Webber, 1953). Webber only observed 29 Y. elata seedlings in 4 years of field observations on the Jornada. He attributed this to present arid conditions, since other Yucca species in more humid areas have high seedling establishment, perhaps due to better forage conditions to



DESERT SCRUB

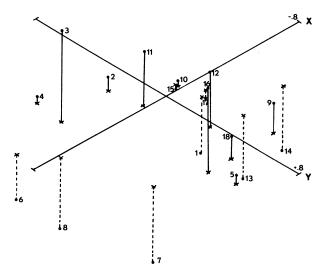


Fig. 2.—Ordination of Yucca elata with other shrubs and with perennial grasses in the Desert Grassland and Desert Scrub communities on the New Mexico State University Ranch. Species:

Shrubs

- Yucca elata
 Y. baccata
- 3. Larrea tridentata
- 4. Prosopis glandulosa
- 5. Xanthocephalum sarothrae
- 6. Flourensia cernua
- Parthenium incanum
 Zinnia pumila
- 9. Ephedra trifurca
- 10. E. torreyana
- 11. Opuntia spp.

- Grasses 12. Aristida purpurea 13. Bouteloua eriopoda
- 14. Erioneuron pulchellum
- 15. Hilaria mutica
- 16. Muhlenbergia porteri
- 17. Scleropogon brevifolius
- 18. Sporobolus spp.

reduce rodent damage. Yucca elata seedlings are extremely slow in top growth and they retain their grasslike juvenile leaves for a full year. Herbivory by small mam-

mals, particularly lagomorphs and woodrats, can be especially damaging.

The results for spatial patterning in Yucca elata plant canopies indicate a significant clumping in all the sites (Table 3). Solitary plants were rarely encountered in the sampling, and distance to nearest neighbor was usually less than a meter. Kershaw (1963) indicates that vegetative spread and heavy seeds are the two most likely factors causing pronounced clumping in plants. Since the seeds of Y. elata are flat, light and winged (Arnott, 1962), it seems probable that clumping in Y. elata is due to vegetative propagation. Webber (1953) observed Y. elata produced new individual plants in the vicinity of the parent plant from branched rhizomes. Excavations of basal sprouts from parent plants in this study support this. Although all the sites exhibited significant clumping of individuals, the Playa and Grassland sites exhibited the greatest degree of clumping. These sites have the highest cattle density, and thus support our previous hypothesis that cattle disturbance increases clumping in Y. elata (Smith and Ludwig, 1976).

Although clumping is clearly evident for all the sites, the clumps themselves are differently patterned on the study sites (Table 3). On the sloping Summerford and Bajada sites Yucca elata clumps are randomly distributed, although some contagion of clumps is indicated. Visual analysis of the sites confirms this, as Y. elata is mainly confined to the arroyos, which have coarser-textured, deeper soils. On the level Playa and Grassland sites, Y. elata clumps show a significant regular distribu-

TABLE 2.—Chi-square indices of association for Yucca elata with other perennial species occurring in belt transects on the Playa and Bajada sites on the New Mexico State University Ranch

Species	Playa	Bajada
Larrea tridentata	3.13	&
Prosopis glandulosa	5.55 *	0.14
Xantĥocephalum sarothrae	5.94 *	-0.33
Flourensia cernua	&	0.20
Ephedra trifurca	0.05	&
E. torreyana	0.07	&
Yucca baccata	&	0.09
Opuntia spp.	&	11.6*
Parthenium incanum	&	0.90
Zinnia pumila	&	1.31
Muhlenbergia porteri	&	0.01

Table 3.—Spatial pattern analysis based on distance measurements for Yucca elata on five Jornada sites

	Mean point to plant	Mean plant to plant	Mean plant to clump		nt plant	
	dist. (P)	dist. (I)	$\mathrm{P}^2/\mathrm{I}^{rac{\mathbf{a}}{2}}$	dist. (C)	P^2/C^2	
Site	in m	in m	ratio	in m	ratio	
Summerford	5.64	2.50	3.75***	6.51	1.08	
Bajada	8.70	1.545	11.94***	8.265	1.38	
Playa fringe	3.26	0.49	46.1***	5.015	0.48**	
Grassland	4.52	0.59	36.58***	7.57	0.35**	
Burned grassland	3.98	0.60	7.60***	5.90	0.45**	

A ratio greater than one indicates clumping, less than one indicates regular pattern, and not significantly different from one indicates random patterning
 *** Significantly different from one at P_{.001}; ** at P_{.01}

^{*} Significant at $P_{.05}$ at 1 df & Not present on this site or present in every quadrat so that chi squire is indeterminant

tion. Thus, Y. elata clumps may distribute in a regular fashion given a uniform, utilizable habitat.

Results from the burned site indicate that destruction of Yucca elata plants greatly accelerates basal sprouting. Out of 20 plants examined, 18 had produced at least one new basal sprout, and an average of 3.9 basal sprouts were found. One large stump produced eight new sprouts, while two others each produced seven. Not a single seedling was observed on the site. The Y. elata clumps exhibited a significant regular distribution on the Burned Grassland site.

Thus, clumping of Yucca elata individuals occurs after disturbance, such as fire or cattle, or following flowering and completion of fruit formation (Smith and Ludwig, 1976). The inflorescence stalk is a terminal structure so that a new apical meristem must be produced by either a new growth center at the base of the stalk or at the base of the plant caudex—sometimes both. At least initially, basal sprouts are dependent on the parent plant, thus differing from stem branches only with respect to origin. Spatial pattern of Y. elata clumps appears to be a function of habitat availability.

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