



Structure and function of C₃ and C₄ Chihuahuan Desert plant communities. Standing crop and leaf area index

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During the past 150 years, native C₃ shrubs have invaded and dominated extensive areas of former C₄ grasslands in deserts of the south-western United States. This vegetation shift has caused large changes in several aspects of the structure and function of these plant communities. To examine structural changes, we measured the standing crop of green herbaceous plants and live shrubs, leaf area index (LAI), and canopy cover and shrub density in grass and shrub plant communities that exist on sandy and clay soils in the Chihuahuan Desert. Standing crop ranged from 800 to 1800 kg ha⁻¹ for grass communities and from 2800 to 3500 kg ha⁻¹ for shrub communities. The LAI in grass communities was typically 0.1 to 0.2 and in shrub communities was 0.3 to 0.4. Averaged over the 2 years, the greatest LAI was in the shrub community on a clay soil that also had a herbaceous understory. Shrub canopy cover varied from 17% (*Flourensia cernua*, tarbush) to 33% (*Prosopis glandulosa*, honey mesquite). On sandy soils, this vegetation shift has resulted in a replacement of herbaceous vegetation with shrubs and a large reduction in species diversity, while on clay soils, due to greater soil fertility and soil water availability, there was only a slight decrease in herbaceous vegetation and little change in species diversity. This vegetation shift of desert grasslands has dramatically changed plant community structure.

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Introduction

During the past 150 years, there has been a shift in dominance of species in plant communities of deserts in the south-western United States. Native C₃ shrubs have invaded and subsequently dominated large areas of former C₄ desert grasslands. Possible causes of the vegetation shift include drought, grazing, wildfire suppression, and climate change (Grover & Musick, 1990; Mayeux *et al.*, 1991).

This vegetation shift has been particularly extensive and well-documented in the

northern Chichuahuan desert. Land surveys in the mid-19th century indicate that 58% of the Jornada Experimental Range (JER), located in the northern Chichuahuan Desert, was shrub free and that good grass cover was present on more than 90% of the area. By 1963, however, less than 25% of the Jornada had good grass cover and none was shrub free (Buffington & Herbel, 1965). York & Dick-Peddie (1969) examined early survey records and concluded that 75% of the vegetation in 31 townships in southern New Mexico consisted of open grasslands in 1858, but only 5% of the area was dominated by grasses in the 1960s. This trend has continued since the 1960s (Gibbens *et al.*, 1992).

This vegetation shift has increased the diversity and number of dominant plant communities in the Chihuahuan desert (Gibbens & Beck, 1987) and has increased the spatial variability of soil resources within these communities (Schlesinger *et al.*, 1990). This landscape fragmentation complicates land management, increases the difficulty of making vegetation measurements applicable to large areas, and affects ecosystem structure and function (West, 1993).

Although several studies quantify aspects of the vegetation in two of the JER shrub communities (honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa* and creosote-bush (*Larrea tridentata* (DC.) Cov.)), there are few studies for the three other important JER plant communities (black grama (*Bouteloua eriopoda* (Torr.) Torr.), tobosa (*Pleuraphis mutica* Buckley, syn. *Hilaria mutica* (Buckley) Benth.), and tarbush (*Flourensia cernua* DC.)) and essentially no studies examining all five communities simultaneously. Plant communities chosen for our study represent vegetation types that are increasing (shrubs) and decreasing (grasses) in spatial extent. Our objective was to quantify and compare standing crop and leaf area of grass and shrub communities and canopy cover and shrub density of shrub communities on the JER. These measurements will be interpreted in terms of measurements on ecosystem function, specifically energy balance measurements (Dugan *et al.*, 1996).

Study site

The research was conducted on the Jornada Experimental Range (JER), located about 40 km north of Las Cruces, NM, U.S.A. The 78,000 ha JER extends from the gently rolling plains of the closed Jornada Basin to the crest of the San Andres mountains on the east. Our study sites were located in the southern half of the JER (Fig. 1) on the plains at about 1320 m. The range of elevation between the five plant communities in this study was only 26 m.

The climate of the JER is typical of an arid region, with large diurnal and annual temperature ranges, low humidities, high radiation levels, high evaporative demands, and low and variable precipitation. Average maximum temperature is greatest in June (36°C) and least in January (13°C). Long-term (1915–1992) average annual precipitation is 241 mm, with 54% of this occurring from July through September (Table 1). Winter precipitation is usually widespread and is associated with frontal passages, while summer precipitation is associated with short-term, isolated thunderstorms. The growing season is primarily controlled by precipitation timing and amounts and is typically from July through September (Paulsen & Ares, 1962).

Soils in the Jornada Basin are mostly Haplargids and Paleorthids with a few Mollisols (Gile *et al.*, 1981). Soils were formed in alluvium from the surrounding mountains and overlie about 100 m of unconsolidated sediments laid down by the ancestral Rio Grande. Soils have little organic matter, little textural stratification of upper layers, and a caliche layer, the depth and thickness of which vary with site position and soil age.

Plant communities

Vegetation on the JER is closely tied to soil type, with perennial plants dominating all communities, although annuals can be abundant in some years (e.g. Gutierrez & Whitford, 1987). We made measurements in five plant communities, each of which is dominated by and will be referred to in the current study by a perennial plant. (1) The C_4 black grama (*Bouteloua eriopoda* (Torr.) Torr) community is usually found on sandy soils in upland locations. Vegetation height is about 0.3 m and forbs are randomly dispersed throughout. The spatial extent of this community is decreasing at the expense of the next two communities. (2 and 3) The C_3 shrubs creosotebush (*Larrea tridentata* (DC.) Cov.) and honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) dominate extensive areas. The *L. tridentata* communities generally have formed on bajada slopes that have gravelly, shallower soils. Vegetation height is about 1 m. It is characterized by uniformly-spaced, evergreen shrubs underlain by bare soil. The *P. glandulosa* communities have developed on flatter areas with deeper soils. Coppice dunes, 0.5 to 1.5 m tall, have formed by sand accumulating in and around *P. glandulosa* plants, which protrude about 0.5 m above the dunes. The dunes are surrounded by large areas of bare soil. (4) The C_4 grass tobosa (*Pleuraphis mutica* Buckley) is found on sites with clay soils in low-lying areas that receive runoff water. Vegetation height is about 0.25 m. In these communities, fine-textured patches of grass are interspersed with areas of bare soil and forbs. This grass community is decreasing in spatial extent at the expense of the next community. (5) The C_3 shrub tarbush (*Flourensia cernua* DC.) has a mixture of evergreen shrubs (about 1 m tall),

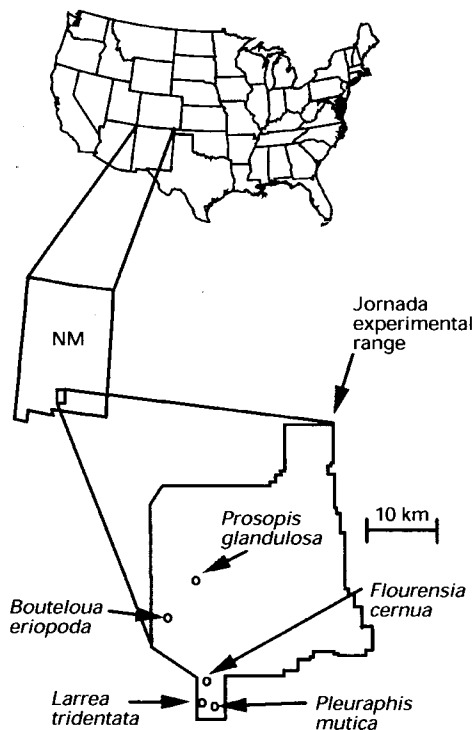


Figure 1. Location of *Bouteloua eriopoda*, *Larrea tridentata*, *Prosopis glandulosa*, *Pleuraphis mutica*, and *Flourensia cernua* communities on the Jornada Experimental Range, New Mexico (NM).

Table 1. Monthly precipitation (mm) during 1991 and 1992 in plant communities on sandy (Bouteloua eriopoda, Larrea tridentata, Prosopis glandulosa) and clay (Pleuraphis mutica and Flourensia cernua) soils

Community	Jan	Feb	Mar	Apr	May	June	Jul	Aug	Sep	Oct	Nov	Dec	Total
1991													
<i>B. eriopoda</i>	8	18	6	0	2	24	59	74	52	14	15	111	384
<i>L. tridentata</i>	16	10	23	0	1	3	103	82	38	8	13	89	387
<i>P. glandulosa</i>	7	15	4	0	1	50	47	79	51	13	12	106	386
<i>P. mutica</i>	13	22	6	0	1	10	91	78	51	8	15	80	376
<i>F. cernua</i>	11	19	9	0	2	23	113	100	54	10	14	76	428
Average	11	17	10	0	1	21	83	83	49	11	14	92	392
1992													
<i>B. eriopoda</i>	32	4	11	14	87	6	27	50	8	45	1	33	318
<i>L. tridentata</i>	40	5	20	15	48	16	45	60	8	24	1	34	317
<i>P. glandulosa</i>	32	4	12	13	82	4	37	45	18	36	1	30	314
<i>P. mutica</i>	25	4	12	21	71	6	34	80	11	22	1	32	318
<i>F. cernua</i>	28	4	9	10	79	2	38	75	18	26	1	32	322
Average	31	4	13	15	73	7	36	62	13	31	1	32	318
Long-term average	11	9	8	5	8	14	46	48	37	25	13	17	241

forbs (about 0.3 m), and grasses (about 0.2 to 0.4 m). Even with these three plant types prevalent, there is still a considerable amount of bare soil.

Measurements in each plant community were made within livestock enclosures that were > 15 ha. Plant nomenclature follows Ailred (1988, 1993).

Methods

Herbaceous standing crop and leaf area

Herbaceous standing crop was estimated in each community between 5 and 17 September 1991 and 2 and 8 September 1992. This is near the time of peak standing crop. Twenty-five 1 m² quadrats were randomly placed within a 100 m × 60 m area in each enclosure. Grasses and forbs were clipped to a height of about 10 mm and separated by species into live and standing dead portions. For a randomly-selected subsample of three or more individual plants of each species occurring in the quadrats, the area (one-sided) of green leaves was measured using a Model LI-3000 photoelectric leaf area meter (Li-Cor Corporation, Lincoln, NE, U.S.A.). Samples were dried at 60°C to a constant weight. Specific leaf area (cm² g⁻¹) was calculated for all species in 1991 and the most common species in 1992. The 1991 specific leaf areas were used for infrequent species in 1992. (There was little difference in 1991 and 1992 specific leaf areas.) Total leaf area was calculated for each species using the specific leaf area and standing crop. Leaf area index (LAI) for a plant community was calculated by summing leaf areas for all species.

In the *P. glandulosa* community, quadrats for sampling were placed in interdune areas. Except where noted, references to standing crop in this paper refer to above-ground, living standing crop. Below-ground biomass was not measured.

To assist interpretation of energy balance measurements made in these plant communities (Dugas *et al.*, 1996), species were assigned (Appendix A) to either the C₃ or C₄ photosynthetic pathway (Syvertsen *et al.*, 1976; Kemp, 1983; Wentworth, 1983). Total LAI in each community was partitioned to plants of each pathway.

Shrub community characteristics

The point centered-quarter method (Cottam & Curtis, 1956) was used to estimate shrub density in *F. cernua* and *L. tridentata* communities. A 100 m baseline was established in each community and starting points > 5 m apart for five lines perpendicular to the base line were randomly drawn. Ten points, spaced 10 m apart, were sampled on each line. Distance, maximum and minimum canopy diameter, height, and number of stems were measured for the nearest shrub in each quarter at each point in September 1991.

Standing crop and leaf area of *F. cernua* and *L. tridentata* were estimated on 10 plants each selected at random from 100 m × 100 m plots. Stems on each plant were numbered and a randomly chosen stem was harvested from each plant. Leaves were separated from stems and the area of a subsample of fresh leaves was measured. New twigs were included for *F. cernua*. Specific leaf area was calculated from this subsample. Total shrub standing crop and leaf area were calculated from mean standing crop and leaf area per stem and mean number of stems per plant. Shrub and herbaceous LAIs were summed to calculate community LAI in shrub communities.

Using the baselines described above, five randomly chosen 60-m long transects were established. The percentage of soil surface covered by shrub canopy, bare soil, litter, or herbaceous basal area was recorded every 0.2 m along each line from 22 through 24

June 1991 in the *L. tridentata* community and on 6 and 7 August 1991 in the *F. cernua* community.

Different procedures were used to characterize *P. glandulosa* shrubs due to the coppice dunes in this community. In 1991, ten dunes were randomly selected from a 100 m × 100 m area. A rod was driven into the center of the dune to anchor the apex of a wedge-shaped frame with a base 1-m wide and sides subtending an angle of 18.4°. The frame was oriented in one of the cardinal directions randomly chosen for each dune. The frame included a proportional sample of the circular-shaped dunes. Shrub canopy radii within the frame were measured. If the radius of the dune exceeded the length of the frame, an area 1-m wide extending to the periphery of the dune was included. The average radius was used to calculate canopy area, assuming dune vegetation was circular. Plant material within the frame was harvested, separated into live stems, dead stems, and leaves, and dried and weighed. Area was measured of a sample of about 100 fresh leaves, including leaves of all sizes, and specific leaf area was calculated. Live standing crop and leaf area were calculated per square meter of shrub canopy. Canopy cover of *P. glandulosa* was determined by recording canopy interception along five, randomly chosen 200-m long line transects.

Although long-term (> 64 years) annual average precipitation differs by < 32 mm among the five plant communities, there can be considerable differences in precipitation for shorter periods. Thus, precipitation was measured in all communities using rain gauges located 0.4 to 1.8 km from the exclosures.

Results and discussion

Precipitation

Annual precipitation totals were greater than the long-term average for both years in all plant communities, but distributions differed markedly (Table 1). In 1991, precipitation totals were essentially equal to zero in April and May and were substantially greater than the average in June through September, especially in the *F. cernua* community. Precipitation was much greater than the average for December 1991 and January and May 1992 and about equal to the average in July through October 1992. Monthly and annual precipitation totals were less variable across plant communities in 1992.

Plant communities on sandy soils

Bouteloua eriopoda

Species diversity was greatest in the *B. eriopoda* community (Appendix A). There were 34 species in the clipped samples in 1991 and 20 species in 1992. Perennial grasses contributed about 80% of total standing crop in both years (Table 2). Perennial grass standing crop was greatest in this community. Of the six perennial grasses represented in both years, *B. eriopoda* was dominant, contributing 63% of total perennial grass standing crop in 1991 and 76% in 1992. Mesa dropseed (*Sporobolus flexuosus* (Thurb.) Rydb.) was the second most abundant perennial grass in each year. Perennial grasses also were the principal component of standing dead, which was 752 kg ha⁻¹ in 1991 and 872 kg ha⁻¹ in 1992.

Annual grasses contributed < 2.5% of total standing crop in both years (Table 2), even though precipitation was above average in the spring of 1992. Principal annual grasses were six weeks threawn (*Aristida adscensionis* L.) and Mexican switchgrass (*Panicum hirticaule* Presl). Perennial forbs, primarily leatherweed (*Croton pottsii*

Table 2. Live herbaceous standing crop for different plant types and total live shrub standing crop (mean \pm 1 SE, kg ha⁻¹) in plant communities on sandy and clay soils in 1991 and 1992. The 1991 live shrub standing crop was used for the 1992 total standing crop in the *L. tridentata*, *P. glandulosa* and *F. cernua* communities

Plant type	Sandy soil						Clay soil						
	<i>B. eriopoda</i>		<i>L. tridentata</i>		<i>P. glandulosa</i>		<i>P. mutica</i>		<i>F. cernua</i>				
	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992			
Herbaceous													
Perennial grass	700±66	870±84	21±7	62±27	9±7	6±2	518±65	198±32	493±75	520±71			
Annual grass	20±8	1±1	59±11	5±2	0	0	14±13	0	0	0			
Perennial forb	90±26	114±31	14±6	84±24	19±11	77±43	5±2	10±5	64±18	41±8			
Annual forb	79±23	68±23	29±7	12±5	1±0.2	0	244±88	1585±227	1±0.2	2±0.2			
Total herbaceous	889±58	1054±86	123±13	163±40	29±13	83±43	781±105	1793±211	558±76	563±75			
Live shrub	0	0	2703±319	3402±418			0	0	2936±720				
			(330±39)*	(547±67)					(502±19)				
Total	889±58	1054±86	2826±324	2866±339	3432±422	3485±428	781±105	1793±211	3494±857	3499±858			

*Total green leaf biomass of shrubs.

(Klotzsch) Muell.-Arg), wrinkled globemallow (*Sphaeralcea subhastata* Coult.), and sicklepod (*Hoffmanseggia drepanocarpa* A. Gray), and annual forbs, primarily mouseear (*Tidestromia lanuginosa* (Nutt.) Standl.), faintcrown (*Aphanostephus ramosissimus* DC.), and sawtooth spurge (*Euphorbia serrula* Englem.), each made up about 10% of total standing crop in both years. There were very few shrubs in this enclosure because of past shrub control efforts.

Primarily due to the above-average precipitation (Table 1), herbaceous standing crop in the *B. eriopoda* community from this study (Table 2) was at the upper end of the values measured by Pieper & Herbel (1982) (500 to 1250 kg ha⁻¹), Paulsen & Ares (1962) (156 to 890 kg ha⁻¹), and Herbel *et al.* (1972) (173 to 1015 kg ha⁻¹). Standing crop of *B. eriopoda* itself in this study was within the range of values measured by Paulsen & Ares (1962) and Herbel *et al.* (1972). These latter two long-term studies highlight the large interannual variability of standing crop that occurs due to variation in amounts and timing of summer precipitation.

The *B. eriopoda* community LAI was least of all plant communities in both years (Fig. 2). The small LAI in this community was due in part to the small specific leaf areas of *B. eriopoda* (6 cm² g⁻¹) and *S. flexuosus* (10 cm² g⁻¹), which were the dominant components of the standing crop (Table 2). In this community, annual and perennial forbs with the C₃ photosynthetic pathway made up about 40% of total LAI (Table 3), even though they made up only 20% of total standing crop (Table 2). Specific leaf area of forbs was considerably greater than that of grasses. The contribution of plants with both pathways to total LAI was most evenly distributed in this community.

Larrea tridentata

Only about half as many species were sampled for standing crop in this community as opposed to those sampled in the *B. eriopoda* community (Appendix A). Herbaceous standing crop in this community was only about 5% of total standing crop and was

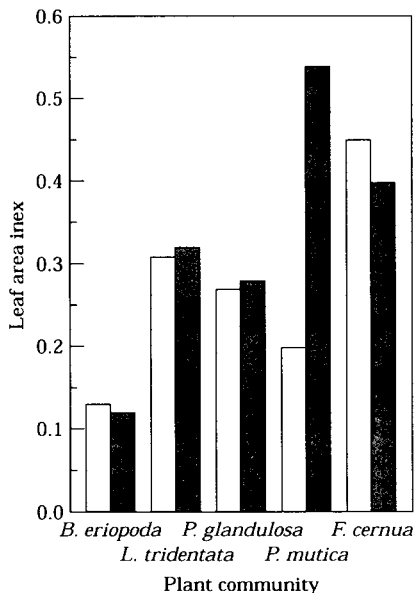


Figure 2. Leaf area index for *Bouteloua eriopoda*, *Larrea tridentata*, *Prosopis glandulosa*, *Pleuraphis mutica*, and *Flourensia cernua* communities in 1991 (□) and 1992 (■).

Table 3. Percentage of total community leaf area index made up of species with C_3 and C_4 photosynthetic pathways in 1991 and 1992 for plant communities on sandy and clay soils

Community	C_3		C_4		Unknown pathway	
	1991	1992	1991	1992	1991	1992
Sandy soil						
<i>B. eriopoda</i>	33	44	57	52	10	4
<i>L. tridentata</i>	92	94	8	6	0	0
<i>P. glandulosa</i>	99	100	1	0	0	0
Clay soil						
<i>P. mutica</i>	9	1	91	99	0	0
<i>F. cernua</i>	78	80	22	20	0	0

about 15% of that in the *B. eriopoda* community (Table 2). A portion of this reduction of herbaceous standing crop may be due to root growth inhibition of nearby plants by *L. tridentata* (Mahall & Callaway, 1991). Due to differences in timing and amounts of precipitation, perennial grasses and forbs were more abundant in 1992, while annuals were more abundant in 1991. Only two perennial grasses were found, fluff grass (*Dasyochloa pulchella* (Kunth) Steud.) and bush muhly (*Muhlenbergia porteri* Scribn.). The only important annual grass was needle grama (*Bouteloua aristidoides* (Kunth) Griseb.). Annual forbs were principally *Eriogonum* spp. Perennial forbs were sand aster (*Leucelene ericoides* (Torr.) Greene), hairyseed bahia (*Bahia absinthifolia* Benth. var. *dealbata* (A. Gray) A. Gray), and rattlesnake weed (*Euphorbia albomarginata* Torr. & Gray).

Shrub standing crop of *L. tridentata* was two to three times greater than total herbaceous standing crop of the *B. eriopoda* community, but had the least shrub standing crop of all shrub communities (Table 2). Shrub leaves were a small fraction of this. Our *L. tridentata* standing crop measurements were similar to those of Whittaker & Neiring (1975), greater than the 1000 to 1500 kg ha⁻¹ estimated by Chew & Chew (1965) in Arizona, but were well within the range of estimates (848 to 8420 kg ha⁻¹) by Burk & Dick-Peddie (1973) on six sampling sites near Las Cruces, NM. The Burk & Dick-Peddie site with a density (3455 plants ha⁻¹) closest to our density (mean \pm 1 SE = 3331 \pm 439 plants ha⁻¹) had an estimated standing crop of 3263 kg ha⁻¹. *Larrea tridentata* age significantly affects standing crop (Chew & Chew, 1965), and, thus, comparisons are problematic unless community age structure is known.

Larrea tridentata stands are extremely variable in regard to size, density, and spatial distribution (Barbour, 1969). *Larrea tridentata* in this study averaged 1.13 m tall and 1.24 m in diameter. Our density is similar to the 3150 plants ha⁻¹ reported by Gibbens *et al.* (1987) for another *L. tridentata* community on the JER. Barbour (1969) reported *L. tridentata* densities for 13 sites in the Chihuahuan Desert ranging from 230 to 7460 plants ha⁻¹. Burk & Dick-Peddie (1973) found *L. tridentata* densities ranging from 2824 to 8420 plants ha⁻¹ on six sites near Las Cruces, NM.

Shrub canopy cover in the *L. tridentata* community (Table 4) was similar to the 30% cover measured by Tromble (1988a) and greater than that in the *F. cernua* community. The percentage of bare soil also was greater in this community than in other shrub communities (Table 4).

Larrea tridentata community LAI was intermediate to the LAI in *P. glandulosa* and *F. cernua* communities, and was about three times greater than the *B. eriopoda* LAI (Fig. 2). C_3 species made up > 90% of the LAI in both years (Table 3).

Table 4. Percentage (mean \pm 1 SE) of soil surface covered by shrub canopy, herbaceous plants, litter, and bare soil in *Larrea tridentata* and *Flourensia cernua* communities

Community	Shrub canopy	Herbaceous plants	Litter	Bare soil
<i>L. tridentata</i>	28 \pm 3	0	5 \pm 1	67 \pm 3
<i>F. cernua</i>	17 \pm 2	21 \pm 3	5 \pm 1	57 \pm 3

Prosopis glandulosa

The number of species sampled for standing crop was least in this community (Appendix A). The decrease in herbaceous standing crop caused by the vegetation shift from grasslands to shrub lands was most dramatic in the *P. glandulosa* community (Table 2). *Prosopis glandulosa* has been shown to reduce abundance and cover of herbaceous vegetation between *P. glandulosa* plants (Gibbens *et al.*, 1983). Herbaceous standing crop in the *P. glandulosa* community was less than 2% of total standing crop in both years and was only about 5% of *B. eriopoda* community standing crop. A few fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) plants also were growing in the dunes, but interdune areas had little vegetation. *Dasyochloa pulchella*, *Aristida adscensionis*, and *Sporobolus flexuosus* (Thurb.) Rydb. were the only grasses, and twin-leaf senna (*Cassia bahinioides* A Gray) and Russian thistle (*Salsola australis* R.Br.) were principal forbs.

Total herbaceous standing crop was least in this community, but *P. glandulosa* standing crop was the greatest shrub standing crop (Table 2). Because *P. glandulosa* canopy cover was 33% and interdune vegetation was sparse, this community was similar to the *L. tridentata* community (Table 4) in having a large percentage of soil that was bare.

Prosopis glandulosa community LAI was < 0.3 (Fig. 2), the least of the three shrub communities (Fig. 1) and less than the LAI shown by Sharifi *et al.* (1982) for a site in California. Although *P. glandulosa* had the greatest shrub leaf standing crop (Table 2), it had the smallest specific leaf area, 49 cm² g⁻¹, as compared to 88 cm² g⁻¹ for *L. tridentata* and 62 cm² g⁻¹ for *F. cernua*. C₃ species made up essentially all the LAI in both years (Table 3).

Plant communities on clay soils

Pleuraphis mutica

Species diversity varied widely in this community for the 2 years. There were 24 species in 1991 (Appendix A), but only 8 in 1992. Standing crop of perennial grasses, predominately made up of *P. mutica* with minor amounts of burrograss (*Scleropogon brevifolius* Phil.), was less in 1992 than in 1991 and was less than that in the *B. eriopoda* community (Table 2). Reduced perennial grass standing crop and species diversity in 1992 were probably due to increased competition for soil water caused by a dense *Salsola australis* stand present in 1992. Large numbers of *S. australis* germinated in the spring of 1992 likely due to the above average precipitation from December 1991 through May 1992 (Table 1).

Aristida adscensionis and minor amounts of three other annual grasses were present in 1991, but were completely absent in 1992. Perennial forbs, primarily *Sphaeralcea subhastata*, *Hoffmanseggia drepanocarpa*, and talinum (*Talinum angustissimum* (A. Gray) Woot. & Standl.), had small standing crop values in both years (Table 2). Although

nine annual forbs were represented in 1991 (Appendix A), only *S. australis* and scarlet creeper (*Ipomoea cristulata* Hallier f.) had large standing crops. Annual forb standing crop was more than six times greater in 1992 than in 1991 (Table 2) due to the superabundance of *S. australis*, the only annual forb present in 1992. Standing dead was large in both years (1335 kg ha⁻¹ in 1991 and 1164 kg ha⁻¹ in 1992).

Perennial grasses made up 66% of total standing crop in 1991 but only 11% in 1992. Perennial grass standing crop was in the middle to bottom end of perennial grass yields (103 to 1488 kg ha⁻¹) measured by clipping studies in the same enclosure between 1981 and 1988 (R.P. Gibbens, unpublished data). Although precipitation in the *P. mutica* community was above average for 1991 and 1992, we suspect that its standing crop was low because concurrent phenological studies suggest precipitation distribution within these 2 years was not conducive to high growth rates (R.P. Gibbens, unpublished data).

The *P. mutica* community LAI was much greater in 1992 than in 1991 (Fig. 2) due to *Salsola australis*. The *P. mutica* community LAI exceeded *B. eriopoda* community LAI in both years, but especially in 1992. Specific leaf area of *P. mutica* (22 cm² g⁻¹) and *Sporobolus brevifolius* (17 cm² g⁻¹) was greater than that of *B. eriopoda* community perennial grasses. The contribution of C₄ species to the LAI was much greater in the *P. mutica* community as compared to the *B. eriopoda* community (Table 3), being 91% in 1991 and 99% in 1992.

Flourensia cernua

Unlike the two shrub communities on sandy soils, there was no large reduction of herbaceous standing crop in the *F. cernua* community due to presence of shrubs (Table 2) and there was almost an equal number of species in the two communities on clay soil (Appendix A). In this community, perennial grass standing crop was about equal to that in the *P. mutica* community. Herbaceous standing crop was about ten times greater in this community than in two shrub communities on sandy soils likely due to the increased soil water-holding capacity, soil water contents (Dugas *et al.*, 1996), and soil fertility at this site with a clay soil.

Perennial grass standing crop, primarily made up of *P. mutica* and *S. brevifolius*, and total herbaceous standing crop were nearly the same in the 2 years (Table 2). Annual grasses and forbs and perennial forbs (desert holly (*Perezia nana* A. Gray), *Hoffman seggia drepanocarpa*, and *Sphaeralcea subhastata*) made up about 10% of herbaceous standing crop in both years. Herbaceous standing dead was 275 kg ha⁻¹ in 1991 and 672 kg ha⁻¹ in 1992. Total community live standing crop was about 3500 kg ha⁻¹ in both years (Table 2), the largest in the five plant communities.

Flourensia cernua density was 3583 ± 683 plants ha⁻¹. Plant height averaged 1.13 m and diameter averaged 1.24 m. Shrubs covered 17% of the ground area (Table 4). Our *F. cernua* cover measurement is close to the 15% measured by Tromble (1988b) at the JER, but is greater than the 10% measured by O'Laughlin (1975) for a *F. cernua* community elsewhere in the Jornada Basin. Mauchamp *et al.* (1993) reported cover values ranging from 13 to 35% in the southern Chihuahuan Desert. Although shrubs and herbaceous plants were relatively abundant, 57% of the ground surface was bare (Table 4).

Flourensia cernua community LAI was slightly larger in 1991 than in 1992 and was the greatest of the three shrub communities (Fig. 2), likely related to greater precipitation amounts (Table 1) and soil. The LAI differences between years seem to be in contradiction to herbaceous standing crop (Table 2). However, *Perezia nana* was more than twice as abundant in 1991 than in 1992 and this greatly influenced the LAI. C₃ species made up about 80% of the LAI in both years (Table 3).

Conclusions

The vegetation shift in desert grasslands from communities dominated by C_4 perennial grasses to ones dominated by C_3 perennial shrubs has resulted in a dramatic change in plant community structure. There has been about a threefold increase in above-ground, live standing crop and a twofold increase in leaf area. In all shrub communities, a substantial fraction of standing crop is contained in more permanent structural plant parts. On sandy soils, grasslands once dominated by *Bouteloua eriopoda* are now dominated by *Larrea tridentata* or *Prosopis glandulosa*. Plant communities on clay soils that were dominated by the grass *Pleuraphis mutica* have seen a large increase in the shrub *Flourensia cernua*.

There is, however, a substantial difference in the vegetation of plant communities on sandy vs. clay soils. On sandy soils, herbaceous plants have been almost completely eliminated, resulting in a community made up almost exclusively of C_3 perennial shrubs associated with 'resource islands' (Schlesinger *et al.*, 1990) and a large decrease in species diversity. However, on clay soils, increases in the abundance of *F. cernua* have been associated with only a slight decreases in herbaceous vegetation standing crop and species diversity.

This dramatic difference between plant communities on clay and sandy soils is a result of greater availability of resources on clay soils. Clay soils are at lower elevations and thus receive runoff water from the upland areas with sandy or gravelly soils. Also, clay soils are deeper, more fertile, and have a higher soil water-holding capacity than sandy soils.

Our standing crop and leaf area measurements were made in 2 years with similar, and above-average precipitation amounts. Thus there was little difference in standing crop for these 2 years, except in the *P. mutica* community due to the flush of *S. australis* in the second year. Precipitation variations can, however, cause large changes in standing crop and leaf area in both shrub and grass communities in this ecosystem (Paulsen & Ares, 1962; Herbel *et al.*, 1972).

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Appendix A. Species sampled for standing crop in each plant community (Boer = *Bouteloua eriopoda*; Latr = *Larrea tridentata*; Prgl = *Prosopis glandulosa*; Plmu = *Pleuraphis mutica*; and Flce = *Flourensia cernua*). Photosynthetic pathway is shown. 'x' denotes presence in a community

Species	Photosynthetic pathway	Community				
		Boer	Latr	Prgl	Plmu	Flce
Perennial grasses						
<i>Aristida divaricata</i> Willd. var. <i>havardii</i> (Vasey) Trent	C ₄	x			x	
<i>Aristida purpurea</i> var. <i>longiseta</i> (Steud) Vasey	C ₄	x		x		
<i>Bothriochloa laguroides</i> (DC.) Herter subsp. <i>torreyana</i> (Steud.) Allred & Gould	C ₄				x	
<i>Bouteloua curtispindula</i> (Michx.) Torr.	C ₄					x
<i>Bouteloua eriopoda</i> (Torr.) Torr.	C ₄	x				
<i>Dasyochloa pulchella</i> (Kunth.) Steud. [<i>Erioneuron pulchellum</i> (Kunth) Tareoka]	C ₄	x	x	x		
<i>Enneapogon desvauxii</i> Beauv.	C ₄	x			x	
<i>Muhlenbergia arenacea</i> (Buckl.) A.S. Hitchc.	C ₄					x
<i>Muhlenbergia porteri</i> Scribn.	C ₄		x			x
<i>Panicum obtusum</i> Kunth	C ₄					x
<i>Pleuraphis mutica</i> Buckley [<i>Hilaria mutica</i> (Buckley) Benth.]	C ₄				x	x
<i>Scleropogon brevifolius</i> Phil.	C ₄				x	x
<i>Sporobolus contractus</i> Hitchc.	C ₄	x				
<i>Sporobolus flexuosus</i> (Thrub.) Rydb.	C ₄	x		x		
Annual grasses						
<i>Aristida adscensionis</i> L.	C ₄	x	x	x	x	
<i>Bouteloua aristoides</i> (Kunth) Griseb.	C ₄	x	x			
<i>Bouteloua barbata</i> Lag. var. <i>barbata</i>	C ₄	x	x	x	x	
<i>Erogrostis cilianensis</i> (All.) Vign. ex Janchen	C ₄				x	
<i>Munora squarrosa</i> (Nutt.) Torr.	Unknown	x				
<i>Panicum hirticaule</i> Presl	C ₄	x			x	
Perennial Forbs						
<i>Allionia incarnata</i> L.	C ₄	x				
<i>Ammocodon chenopodioides</i> (A. Gray) Standl.	C ₃					x
<i>Astragalus mollissimus</i> Torr.	C ₃					x
<i>Bahia absinthifolia</i> Benth. var. <i>dealbata</i> (A. Gray) A. Gray	C ₃		x			x
<i>Cassia bauhinioides</i> A. Gray	C ₃	x		x		
<i>Croton pottsii</i> (Klotzsch) Muell.-Arg	C ₃	x				
<i>Desmanthus cooleyi</i> (Eaton) Trel.	Unknown	x				

Appendix A. (Continued)

Species	Photosynthetic pathway	Community				
		Boer	Latr	Prgl	Plmu	Flce
Perennial Forbs <i>continued</i>						
<i>Euphorbia albomarginata</i> Torr. & A. Gray	C ₄		x			x
<i>Gaillardia pinnatifida</i> Torr.	Unknown	x				
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	C ₃	x	x	x		x
<i>Hoffmanseggia drepanocarpa</i> A. Gray	C ₃	x		x	x	x
<i>Iva dealbata</i> A. Gray	C ₃				x	
<i>Leuceleone ericoides</i> (Torr.) Greene	C ₃		x			
<i>Melampodium leucanthum</i> Torr. & A. Gray	C ₃		x			
<i>Mirabilis linearis</i> (Pursh) Heimerl.	Unknown					x
<i>Opuntia phaeacantha</i> Engelm.	CAM				x	
<i>Perezia nana</i> A. Gray	C ₃		x		x	x
<i>Psilostrophe tagetina</i> (Nutt.) Rydb.	Unknown	x				
<i>Solanum elaeagnifolium</i> Cav.	C ₃	x				x
<i>Sphaeralcea subhastata</i> Coult.	C ₃	x			x	x
<i>Talinum angustissimum</i> (A. Gray) Woot. & Standl.	C ₃				x	x
<i>Tetradlea coulteri</i> A. Gray	Unknown	x				x
<i>Zinnia acerosa</i> (DC.) A. Gray	C ₃		x			
Annual forbs						
<i>Amaranthus blitoides</i> Wats.	C ₄				x	
<i>Aphanostephus ramosissimus</i> DC.	C ₃	x				
<i>Astragalus nuttallianus</i> DC.	C ₃					x
<i>Baileya multiradiata</i> Harv. & H.A. Gray	C ₃	x				
<i>Boerhaavia spicata</i> Choisy	C ₄	x				
<i>Chenopodium incanum</i> (Wats.) Heller	C ₃	x	x			
<i>Dithyrea wislizenii</i> Englem.	C ₃	x				
<i>Eriogonum abertianum</i> Torr.	C ₃		x			x
<i>Eriogonum rotundifolium</i> Benth.	C ₃		x			
<i>Eriogonum trichopes</i> Torr.	C ₃		x			
<i>Euphorbia parryi</i> Englem.	C ₄	x			x	
<i>Euphorbia serrula</i> Englem.	C ₄	x	x		x	x
<i>Glandularia bipinnatifida</i> (Nutt.) Nutt. [<i>Verbena wrightii</i> A. Gray]	C ₃				x	x
<i>Gutierrezia sphaerocephala</i> A. Gray	C ₃	x				
<i>Ipomoea cristulata</i> Hallier f.	C ₃				x	
<i>Kallstroemia parviflora</i> Nort.	C ₄	x			x	
<i>Linum australe</i> Heller	C ₃	x				
<i>Mollugo cerviana</i> (L.) Ser.	C ₃	x				
<i>Pectis papposa</i> Harv. & A. Gray	C ₄	x	x			
<i>Portulaca mundula</i> I.M. Johnst.	C ₄	x				

Appendix A. (Continued)

Species	Photosynthetic pathway	Community				
		Boer	Latr	Prgl	Plmu	FIce
Annual forbs						
<i>Portulaca oleracea</i> L.	C ₄	x			x	
<i>Salsola australis</i> R. Brown [<i>S. kali</i> L.]	C ₃	x		x	x	
<i>Sanvitalia abertii</i> A. Gray	Unknown				x	
<i>Tidestromia lanuginosa</i> (Nutt.) Standl.	C ₄	x				
Shrubs						
<i>Flourensia cernua</i> DC.	C ₃		x			x
<i>Larrea tridentata</i> (DC.) Cov.	C ₃		x			
<i>Prosopis glandulosa</i> Torr. var. <i>glandulosa</i>	C ₃			x		