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RIPARIAN VEGETATION OF THE LOWER RIO GRANDE

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ABSTRACT—The riparian vegetation of the lower reach of the Rio Grande was studied at 7 locations using 3 line intercepts at each location. There were no trees at the mouth of the river and the vegetation was similar to that found along the Laguna Madre shore of barrier islands. Mesquite (*Prosopis glandulosa*) was the dominant tree near the coast and in the western section of the river near Falcon Dam. Sugar hackberry (*Celtis laevigata*) was the dominant tree species at all other sites except at Santa Ana National Wildlife Refuge, where cedar elm (*Ulmus crassifolia*) and anacua (*Ehretia anacua*) were the dominant trees. Granjeno (*Celtis pallida*) was a dominant shrub throughout the riparian corridor. The dominant trees and shrubs appeared to be replacing themselves. Species similarity in the tree, shrub, and ground layers was greater among transects at a given site than between sites. The introduced Guinea grass (*Panicum maximum*) and buffel grass (*Pennisetum ciliare*) were the dominant species in the ground cover, displacing native species.

RESUMEN—La vegetación riparia de la sección baja del Río Bravo fue estudiada en siete localidades utilizando tres líneas de intercepción en cada localidad. No hay árboles en la desembocadura del río y la vegetación es semejante a la de la orilla de las islas barrera de la Laguna Madre. Mesquite (*Prosopis glandulosa*) es el árbol dominante cerca de la costa y en la sección occidental del río cerca de la Presa Falcón. El palo blanco (*Celtis laevigata*) es la especie de árbol dominante en todos los demás sitios excepto en el Refugio Silvestre Nacional de Santa Ana donde el olmo (*Ulmus crassifolia*) y la anacua (*Ehretia anacua*) son los árboles dominantes. Granjeno (*Celtis pallida*) es el arbusto dominante en todo el corredor ripario. Parece que los árboles y arbustos dominantes se están reemplazando. La semejanza de especies entre árboles, arbustos y cobertura de tierra es más alta entre transectos en un sitio que entre sitios. Las hierbas exóticas, *Panicum maximum* y *Pennisetum ciliare*, son las especies dominantes de la superficie terrestre, desplazando a las especies nativas.

The Rio Grande is legendary for its role in the history of the southwestern USA and Mexico, and it is the second longest river system in the USA. The river extends 3,040 km from its source in the San Juan Mountains of Colorado to the mouth at the Gulf of Mexico (Gilpin, 1949). Surprisingly, the riparian vegetation of the Rio Grande in Texas is poorly known. Only 2 studies, Butterwick and Strong (1976) and Vora (1990), contain quantitative data, and each of these studies examined a limited area (immediately below Falcon Dam and Santa Ana National Wildlife Refuge, respectively). Other workers (Clover, 1937; Davis, 1942; Diamond et al., 1987; Jahrsdoerfer and Leslie, 1988; Lonard et al., 1991; McLendon, 1991) provided subjective characterizations or classifications of the riparian vegetation. These workers differed on the number and composition of communities comprising the riparian vegetation of the Rio Grande in southern Texas. Diamond et al. (1987) emphasized that published quantitative data on plant communities of the South Texas Plains and lower Rio Grande Valley were especially lacking. They also pointed out that data on Texas riparian forests outside the Piney Woods were generally lacking.

The lack of information on composition and structure of riparian communities is especially important in southern Texas because of the deforestation occurring in the Rio Grande floodplain by clearing for dam construction and agricultural and flood control purposes. Since 1900, 99% of the riparian vegetation adjacent to the Rio Grande has been removed (Jahrsdoerfer and Leslie, 1988). Riparian vegetation in southern Texas provides critical habitat for many animal species, including some that are classified as threatened or endangered. Indeed, the lower reach of the Rio Grande has been identified by the United States Fish and Wildlife Service and the Texas Parks and Wildlife Department as an area where wildlife habitat is rapidly vanishing and in dire need of protection. To preserve existing forest remnants and to establish a wildlife corridor along the Rio Grande, the United States of America and Texas governments are purchasing land. It will be difficult for wildlife managers to reestablish vegetation in the "Rio Grande Wildlife Corridor" if they do not know the composition of existing natural remnant riparian forests. Consequently, we studied the riparian vegetation in the lower reach of the Rio Grande (the 240-km segment from the mouth of the river in Cameron County to near Falcon Dam, Starr County, Texas) to provide a quantitative description of its floristic composition and structure, determine if native communities are maintaining themselves, and elucidate patterns of variation.

METHODS AND MATERIALS—*Study Area*—The Rio Grande in southernmost Texas forms the international boundary between Mexico and the United States of America. The present Rio Grande floodplain is about 1.0 km wide in northwestern Starr County where the river leaves the Falcon Dam impoundment. The floodplain broadens as the river passes Starr County and enters Hidalgo County. The current floodplain is 4.0 to 6.0 km wide in much of Hidalgo County and it broadens into a 50-km wide delta fronting the Gulf of Mexico near the mouth of the river in Cameron County. The delta includes old cut-off meanders of the river (resacas) that are fringed by natural levees (Clover, 1937; Lonard et al., 1991).

In Starr County, the soils belong to the Rio Grande-Reynosa association, which are characterized as nearly level to gently sloping, deep loamy soils of the floodplain (Thompson et al., 1972). In Hidalgo County, the soils of the present Rio Grande floodplain belong to the Rio Grande–Matamoros association, which are characterized as deep, moderately and slowly permeable silt loam or silty clay soils (Jacobs, 1981). In Cameron County, the soils of the Rio Grande floodplain belong to the Laredo-Olmito association and the Rio Grande–Matamoros association. The Laredo-Olmito association is characterized as nearly level to gently sloping, well-drained and moderately well-drained silty clay loams and silty clays (Williams et al., 1977). This association follows the pattern of old resacas on a low terrace of the Rio Grande. Laredo soils occupy the higher, well-drained areas adjacent to the resacas, and the Olmito soils occupy the level or slightly concave areas away from but parallel to the resacas (Williams et al., 1977). The Rio Grande–Matamoros association occupies a narrow band less than 3.2 km wide adjacent to the Rio Grande and consists of nearly level to gently sloping, well-drained and moderately well-drained silt loams and silty clays.

In Cameron and Hidalgo counties our surveys were located on Rio Grande–Matamoros soils and in Starr County on Rio Grande–Reynosa association soils. Except for a low rise known as the Mission Ridge, all of the area was subject to flooding in the past (Clover, 1937), but dams (Falcon and Anzalduas) and drainage projects have eliminated the cyclic flooding of the river. Flooding still occurs, but it results from rainfall and poor drainage rather than from the Rio Grande.

Southeasterly winds from the Gulf of Mexico prevail throughout the year except in December, when a northwest wind is common. The onshore winds do not produce a truly marine climate, and the area is classified as semiarid (Thornthwaite, 1948). Average annual rainfall ranges from 66 cm at the mouth of the river to 43 cm at Falcon Dam in Starr County. The peak of precipitation is in September and October. Summer temperatures are high during the daytime and range from 36°C (or higher) in the western extreme of the area to about 34°C near the mouth of the river. Winter temperatures are mild. Average monthly minimum temperatures are above 8°C in the western reach of the river and above 10.5°C at the mouth of the river. The mean length of the frost-free period is 305 days in the western extreme of the area and 330 days near the mouth of the river. Frequently, an entire winter will pass without a freezing temperature.

Field Methods—Riparian vegetation was studied at 7 locations along the Rio Grande between the mouth of the river and Falcon Dam (Fig. 1). The Anzalduas site is owned by the Lower Rio Grande Valley National Wildlife Refuge (NWR). Three parallel transects (at least 10 m apart) were established at each site. Transects began at the river's edge and extended at a right angle up the river's bank and across the first terrace to the second terrace of the river or until there were no more trees, whichever occurred first. Transect lengths were the same at a given site, but because of differences in the width of the riparian corridor at the sites, transect lengths varied among sites. Transects at sites 1, 2, and 6 were each 30 m long. Transects at site 7 were each 40 m long, and transects at sites 3, 4, and 5 were each 50 m in length. We used the line intercept method of vegetation analysis (Canfield, 1941). Transects were subdivided into 10-m intervals and readings were taken along the total length of each interval. Each species intercepted by the line was rated individually

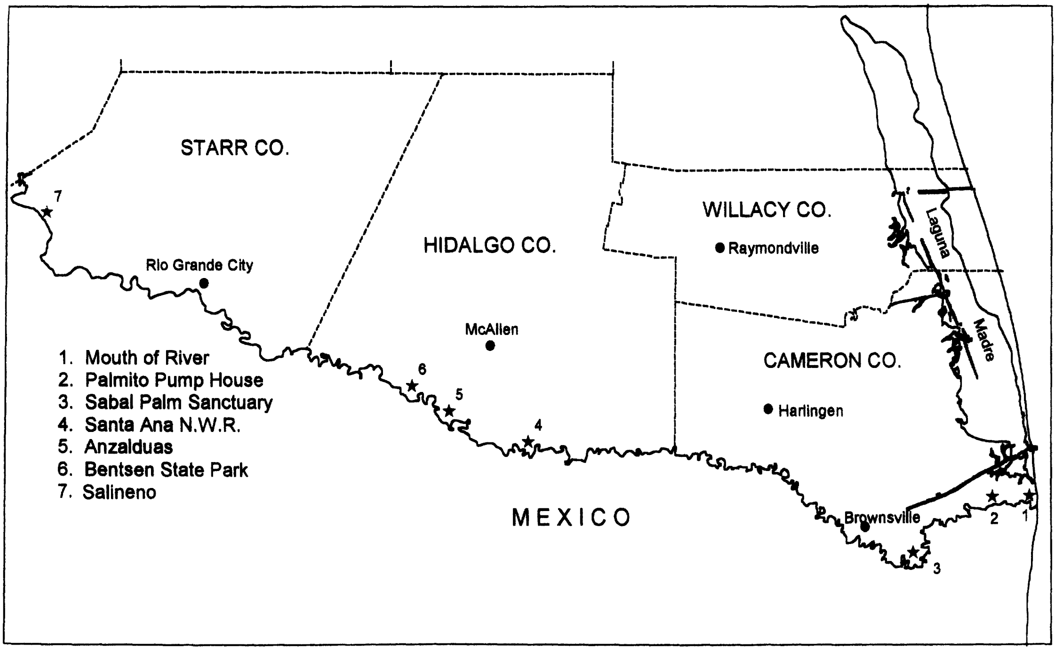

FIG. 1—Locations of study areas along the Rio Grande.

and scored with separation into strata. Trees were 3.0 m or taller, shrubs 1.0 to 2.9 m, and the ground layer less than 1.0 m. We recorded foliage cover and frequency of occurrence and from these data calculated relative cover, relative frequency, and an importance value, which was the sum of relative cover and relative frequency. Importance values were used to determine dominant species. Transects were completed in July 1993 at site 1, in August 1993 at site 2, in September 1993 at site 3, in October 1993 at site 4, in January 1994 at site 5, in July 1995 at site 6, and in August 1995 at site 7. Species similarity was compared among transects and localities using Sorenson's Index of Similarity (Krebs, 1999).

Nomenclature of grasses follows Hatch et al. (1999). Nomenclature of all other species follows Jones et al. (1997).

RESULTS—*Tree Layer*—Spits of sand extend north and south of the Rio Grande at its entry into the Gulf of Mexico. These spits contribute to the barrier island chains off the Texas and Tamaulipas coasts. There were no trees at the mouth of the Rio Grande. Rather, the vegetation was similar to that found along the Laguna Madre shore of the barrier islands.

A comparison of the relative importance of species occurring in the tree layer between localities is shown in Table 1. There was a dominant species or a pair of co-dominant species for each transect (Table 2). Hackberry (*Celtis laevigata*) was dominant at 3 localities, mesquite (*Prosopis glandulosa*) at 2 localities, and cedar elm (*Ulmus crassifolia*) at 1 locality (Table 1). Mesquite was the dominant species on all 3 transects at the Palmito Pumphouse and was the dominant or co-dominant species on 2 transects at Salineño (Table 2). Hackberry was the dominant species on all transects at the Sabal Palm Sanctuary and Bentsen State Park and was the dominant or co-dominant species in all transects at Anzalduas. Hackberry was a co-dominant species in 1 transect at Salineño. Cedar elm and anacua (*Ehretia anacua*) were the dominant species at Santa Ana NWR (Tables 1 and 2). Black willow (*Salix nigra*) was a co-dominant in 1 transect at Anzalduas, and retama (*Parkinsonia aculeata*) was a dominant in 1 transect at Salineño.

A comparison of species similarity among transects at the survey sites is provided in Table 3. The coefficients of similarity vary from 0, when there are no species in common, to 1.0, when all species are the same. The coefficients are generally greater than 0.5 and the mean for coefficients at a given locality is greater than the coefficient for the comparison between 2 transects (Table 4). Species richness

TABLE 1—Comparison of the relative importance of species occurring in the tree layer among transects and localities. Freq. = Frequency, Rel. freq. = Relative Frequency, Rel. cov. = Relative Cover, Imp. val. = Importance Value (the sum of relative frequency and relative cover).

Location	Species	Freq.	Rel. freq.	% Cover	Rel. cov.	Imp. val.
Palmito Pumphouse	*Prosopis glandulosa*	77.8	70.0	19.63	93.6	163.6
	Phragmites australis	33.3	30.0	1.35	6.4	27.2
Sabal Palm Sanctuary	*Celtis laevigata*	73.3	37.9	56.29	63.6	101.5
	Leucaena pulverulenta	26.7	13.8	10.41	11.8	25.6
	Arundo donax	20.0	10.3	6.27	7.1	17.4
	Phragmites australis	20.0	10.3	5.27	6.0	16.3
	Salix nigra	13.3	6.9	2.47	2.8	9.7
	Acacia minuata	13.3	6.9	1.47	1.7	8.6
	Sabal mexicana	6.7	3.5	3.00	3.4	6.9
	Diospyros texana	6.7	3.5	1.40	1.6	5.1
	Parkinsonia aculeata	6.7	3.5	1.37	1.5	5.0
	Salix exigua	6.7	3.5	0.60	0.1	3.6
Santa Ana NWR	*Ulmus crassifolia*	53.3	25.8	20.93	39.7	65.5
	Ehretia anacua	46.7	22.6	9.49	18.0	40.6
	Celtis laevigata	20.0	9.7	7.35	13.9	23.6
	Diospyros texana	26.7	12.9	1.31	2.5	15.4
	Salix exigua	13.3	6.4	3.69	7.0	13.4
	Celtis pallida	13.3	6.4	3.05	5.8	12.2
	Baccharis neglecta	6.7	3.2	4.33	8.2	11.4
	Cocculus diversifolius	13.3	6.4	0.61	1.1	7.5
	Tillandsia usneoides	6.7	3.2	1.37	2.6	5.8
	Sideroxylon celastrinum	6.7	3.2	0.63	1.2	4.4
Anzalduas	*Celtis laevigata*	58.3	30.7	21.90	38.2	68.9
	Fraxinus berlandieriana	36.7	19.3	8.23	14.3	33.6
	Salix exigua	35.0	18.4	4.68	8.2	26.6
	Salix nigra	16.7	8.8	9.25	16.1	24.9
	Ehretia anacua	21.7	11.4	5.77	10.1	21.5
	Phragmites australis	6.7	3.5	4.77	8.3	11.8
	Prosopis glandulosa	8.3	4.4	1.83	3.2	7.6
	Diospyros texana	6.7	3.5	0.93	1.6	5.1
Bentsen State Park	*Celtis laevigata*	77.8	46.7	41.40	62.4	109.1
	Acacia minuata	22.2	13.3	8.33	12.5	25.8
	Salix nigra	11.1	6.7	11.11	16.7	23.4
	Prosopis glandulosa	22.2	13.3	0.57	0.9	14.2
	Arundo donax	11.1	6.7	3.07	4.6	11.3
	Fraxinus berlandieriana	11.1	6.7	1.77	2.7	9.4
	Cocculus diversifolius	11.1	6.7	0.13	0.2	6.9
Salineño	*Prosopis glandulosa*	50.0	22.2	34.04	36.1	58.3
	Parkinsonia aculeata	50.0	22.2	17.25	18.3	40.5
	Fraxinus berlandieriana	33.3	14.8	18.42	19.5	34.3
	Celtis laevigata	41.7	18.5	14.50	15.4	33.9
	Celtis pallida	25.0	11.1	3.29	3.5	14.6
	Acacia minuata	8.3	3.7	4.92	5.2	8.9
	Condalia hookeri	8.3	3.7	1.83	1.9	5.6
	Cocculus diversifolius	8.3	3.7	0.03	<0.1	3.7

TABLE 2—Summary of dominant species by vegetation layer, location, and transect.

Location and transect	Dominants ground layer	Dominants shrub layer	Dominants tree layer
Mouth of Rio Grande			
1	*Monanthochloae littoralis*	*Avicennia germinans*	Not present
2	*Monanthochloae littoralis*	Not present	Not present
3	*Monanthochloae littoralis*	Not present	Not present
Palmito Pumphouse			
1	*Monanthochloae littoralis*	*Prosopis glandulosa* *Zanthoxylum fagara*	*Prosopis glandulosa*
2	*Monanthochloae littoralis*	*Celtis pallida*	*Prosopis glandulosa*
3	*Borrichia frutescens*	*Zanthoxylum fagara* *Celtis pallida*	*Prosopis glandulosa*
Sabal Palm Sanctuary			
1	*Panicum maximum*	*Celtis laevigata*	*Celtis laevigata*
2	*Panicum maximum*	*Cocculus diversifolius*	*Celtis laevigata*
3	*Panicum maximum*	*Zanthoxylum fagara* *Mimosa asperata*	*Celtis laevigata*
Santa Ana NWR			
1	*Panicum maximum*	*Celtis pallida* *Zanthoxylum fagara*	*Ulmus crassifolia*
2	*Panicum maximum*	*Zanthoxylum fagara*	*Ulmus crassifolia*
3	*Chromolaena odorata* *Cocculus diversifolius*	*Celtis pallida*	*Ehretia anacua*
Anzalduas			
1	*Panicum maximum*	*Celtis pallida*	*Salix nigra* *Celtis laevigata*
2	*Panicum maximum*	*Celtis pallida*	*Celtis laevigata*
3	*Panicum maximum*	*Celtis pallida*	*Celtis laevigata*
Bentsen State Park			
1	*Panicum maximum*	*Celtis pallida*	*Celtis laevigata*
2	*Panicum maximum*	*Celtis pallida*	*Celtis laevigata*
3	*Panicum maximum*	*Celtis pallida*	*Celtis laevigata*
Salineño			
1	*Pennisetum ciliare*	*Opuntia engelmannii*	*Celtis laevigata* *Prosopis glandulosa*
2	*Pennisetum ciliare*	*Celtis pallida*	*Prosopis glandulosa*
3	*Pennisetum ciliare*	*Celtis pallida*	*Parkinsonia aculeata*

was 0 at the mouth of the river and increased rapidly as distance from the Gulf coast increased (Table 4). Species richness was greatest at the Sabal Palm Sanctuary and Santa Ana NWR.

Mesquite, hackberry, anacua, and cedar elm occurred throughout the 50-m wide strip of riparian vegetation adjacent to the Rio Grande (Table 5). Only black willow seemed limited to the river's edge. However, when all transects where black willow occurred were examined (Table 6), it was clear this species also occurred at considerable distances from the river. Conversely, sandbar willow (*Salix exigua*), which was never a dominant species, occurred at more locales than black willow and was not found farther than 16 m from the river's edge.

The dominant species in the tree layer were represented by all stages of life. Hackberry was found in the shrub layer (Tables 2 and 7) and ground layer (Tables 2 and 10) at most locales where it was dominant. Cedar elm and anacua

TABLE 3—Within-site variation in species similarity (Sorenson's Index of Similarity) in the tree layer.

	Comparisons			
Location	Transects 1 & 2	Transects 2 & 3	Transects 1 & 3	$\bar{x}$
Palmito Pumphouse	1.000	1.000	1.000	1.000
Sabal Palm Sanctuary	0.667	0.545	0.667	0.626
Santa Ana NWR	0.500	0.545	0.615	0.571
Anzalduas	0.600	0.667	0.727	0.665
Bentsen State Park	0.500	0.250	0.667	0.472
Salineño	0.833	0.909	0.769	0.830

occurred in the shrub and ground layers at Santa Ana NWR. Mesquite occurred in the shrub layer at Palmito Pumphouse and in the ground layer at Salineño. Black willow occurred in the shrub layer at Anzalduas. Retama is the only tree that was not also present in the shrub or ground layers.

Shrub Layer—The relative importance of species occurring in the shrub layer is compared among localities in Table 7. There was a dominant or a pair of co-dominant species for each transect (Table 2). The only shrub present at the mouth of the Rio Grande was black mangrove (*Avicennia germinans*) (Table 7). There was greater variation in dominants in the shrub layer compared to the tree layer, but granjeno (*Celtis pallida*) was a dominant or co-dominant species at all locations except the mouth of the Rio Grande and the Sabal Palm Sanctuary. Colima (*Zanthoxylum fagara*) was second to granjeno as a dominant shrub (Tables 2 and 7). It was a dominant or co-dominant at 3 locations.

TABLE 4—Site variation in tree layer species richness and between-site variation using Sorenson's Index of Similarity.

Location	# of species	Sorenson's index
Mouth of Rio Grande	0	
Palmito Pumphouse	2	0.000
Sabal Palm Sanctuary	10	0.167
Santa Ana NWR	10	0.300
Anzalduas	8	0.444
Bentsen State Park	7	0.471
Salineño	8	0.667

TABLE 5—Site variation in location of dominant tree species relative to the Rio Grande River.

Location	Dominant species tree layer	Distance from river
Palmito Pumphouse	*Prosopis glandulosa*	2–24 m
Sabal Palm Sanctuary	*Celtis laevigata*	10–50 m
Santa Ana NWR	*Ulmus crassifolia*	16–50 m
	Ehretia anacua	10–50 m
Anzalduas	*Salix nigra*	6–16 m
	Celtis laevigata	11–42 m
Bentsen State Park	*Celtis laevigata*	5–23 m
Salineño	*Celtis laevigata*	3–23 m
	Prosopis glandulosa	21–40 m

Species similarity is compared among the transects at the study sites in Table 8. Black mangrove was present only in transect 1 at the mouth of the Rio Grande; thus, all comparisons showed no species in common at this site. Omitting the mouth of the Rio Grande, coefficients of similarity are generally greater than 0.4, but there are 3 exceptions. The means at a given site (Table 8) were greater than the coefficients in between-site comparisons (Table 9), except for the comparison between Bentsen State Park and Salineño. Thus, generally, there was greater similarity in species between transects at a site than between sites.

Species richness was lowest at the mouth of the river and highest at the localities in the middle portion of the study area (Table 9). All of the dominant shrubs were present in the ground layer except for *Cocculus diversifolius*

TABLE 6—Site variation in location of *Salix* species relative to the Rio Grande River.

Location	*Salix* species	Distance from river (m)
Sabal Palm Sanctuary	*S. exigua*	0–1
	S. nigra	39–43
Santa Ana NWR	*S. exigua*	0–5
Anzalduas	*S. exigua*	6–16
	S. nigra	6–16
Bentsen State Park	*S. nigra*	0–10

TABLE 7—Comparison of the relative importance of species occurring in the shrub layer among transects and localities. Freq. = Frequency, Rel. freq. = Relative Frequency, Rel. cov. = Relative Cover, Imp. val. = Importance Value (the sum of relative frequency and relative cover).

Location	Species	Freq.	Rel. freq.	% Cover	Rel. cov.	Imp. val.
Mouth of Rio Grande	*Avicennia germinans*	66.7	100.0	3.97	100.0	200.0
Palmito Pumphouse	*Celtis pallida*	55.5	27.8	6.99	30.2	58.0
	Zanthoxylum fagara	33.3	16.9	5.81	25.1	41.8
	Phaulothamnus spinescens	22.2	11.1	5.07	21.9	33.0
	Prosopis glandulosa	33.3	16.7	2.08	9.0	25.7
	Ziziphus obtusifolia	22.2	11.1	1.01	4.3	15.4
	Boerhavia scandens	22.2	11.1	0.90	3.9	15.0
	Forestiera angustifolia	11.1	5.6	1.32	5.7	11.3
Sabal Palm Sanctuary	*Celtis laevigata*	33.3	16.0	1.87	26.7	42.7
	Cocculus diversifolius	46.7	22.6	1.30	18.6	41.2
	Malvaviscus drummondii	46.7	22.6	1.24	17.7	40.3
	Zanthoxylum fagara	13.3	6.4	0.76	10.9	17.3
	Sabal mexicana	13.3	6.4	0.57	8.2	14.6
	Mimosa asperata	13.3	6.4	0.44	6.3	12.7
	Salix exigua	13.3	6.4	0.36	5.2	11.6
	Sesbania drummondii	6.7	3.2	0.23	3.3	6.5
	Celtis pallida	6.7	3.2	0.11	1.6	4.8
	Wissadula amplissima	6.7	3.2	0.08	1.1	4.3
	Lippia alba	6.7	3.2	0.03	0.4	3.6
Santa Ana NWR	*Zanthoxylum fagara*	46.7	24.6	3.36	29.5	54.1
	Celtis pallida	46.7	24.6	1.38	12.1	36.7
	Salix exigua	20.0	10.5	1.75	15.4	25.9
	Condalia hookeri	6.7	3.5	2.23	19.6	23.1
	Ehretia anacua	13.3	7.0	0.80	7.0	14.0
	Baccharis neglecta	10.0	5.3	0.67	5.9	11.2
	Ulmus crassifolia	13.3	7.0	0.40	3.5	10.5
	Buddleja sessiliflora	6.7	3.5	0.27	2.4	5.9
	Diospyros texana	6.7	3.5	0.18	1.6	5.1
	Baccharis salicifolia	6.7	3.5	0.20	1.8	4.6
	Forestiera angustifolia	6.7	3.5	0.13	1.1	4.6
	Celtis laevigata	6.7	3.5	0.01	0.1	3.6
Anzalduas	*Celtis pallida*	48.3	33.7	4.62	57.8	91.5
	Cocculus diversifolius	30.0	20.9	0.22	2.7	23.6
	Zanthoxylum fagara	13.3	9.3	0.80	10.4	19.3
	Baccharis neglecta	6.7	4.7	1.00	12.5	17.2
	Ehretia anacua	6.7	4.7	0.53	6.6	11.3
	Salix exigua	8.3	5.8	0.26	3.3	9.1
	Lantana urticoides	6.7	4.7	0.33	4.1	8.8
	Acacia minuata	6.7	4.7	0.16	2.0	6.7
	Salix nigra	8.3	5.8	0.06	0.8	6.6
	Serjania brachycarpa	8.3	5.8	0.02	0.2	6.0
Bentsen State Park	*Celtis pallida*	66.7	40.0	13.60	80.5	120.5
	Cocculus diversifolius	44.4	26.7	0.37	2.2	28.9
	Celtis laevigata	33.3	20.0	0.87	5.1	25.1
	Condalia hookeri	11.1	6.7	1.33	7.9	14.6
	Buddleja sessiliflora	11.1	6.7	0.73	4.3	11.0
Salineño	*Celtis pallida*	50.0	40.0	4.91	53.3	93.3
	Opuntia engelmannii	25.0	20.0	2.63	28.5	48.5
	Celtis laevigata	25.0	20.0	1.23	13.3	33.3
	Acacia minuata	16.7	13.4	0.33	3.6	17.0
	Condalia hookeri	8.3	6.6	0.12	1.3	7.9

TABLE 8—Within-site variation in species similarity (Sorenson's Index of Similarity) in the shrub layer.

Location	Comparisons: Transects 1 & 2	Transects 2 & 3	Transects 1 & 3	$\bar{x}$
Mouth of Rio Grande	0.000	0.000	0.000	0.000
Palmito Pumphouse	0.500	0.286	0.571	0.452
Sabal Palm Sanctuary	0.571	0.429	0.500	0.500
Santa Ana NWR	0.533	0.545	0.571	0.550
Anzalduas	0.500	0.250	0.200	0.317
Bentsen State Park	0.571	0.667	0.857	0.698
Salineño	0.400	0.400	0.750	0.517

TABLE 9—Site variation in shrub layer species richness and between-site variation using Sorenson's Index of Similarity.

Location	# of species	Sorenson's index
Mouth of Rio Grande	1	
		0.000
Palmito Pumphouse	7	
		0.000
Sabal Palm Sanctuary	6	
		0.211
Santa Ana NWR	13	
		0.435
Anzalduas	10	
		0.267
Bentsen State Park	5	
		0.600
Salineño	5	

and *Mimosa asperata,* and, thus, it appears that most of the dominant shrubs were reproducing.

Ground Layer—The relative importance of species occurring in the ground layer is compared among localities in Table 10. There was a dominant species in all transects except transect 3 at Santa Ana NWR, where there was a pair of co-dominants (Table 2). Salt tolerant species were dominant at the mouth of the Rio Grande and the Palmito Pumphouse. At the Sabal Palm Sanctuary, Santa Ana NWR, Anzalduas, and Bentsen State Park the introduced grass *Panicum maximum* was the dominant in all but 1 transect (Table 2). At Salineño, buffel grass (*Pennisetum ciliare,* an introduced grass) was dominant in the ground layer.

There is high similarity in the ground layer species present among transects at the mouth of the Rio Grande (Table 11). At the Palmito Pumphouse and Sabal Palm Sanctuary there is great variation in the similarity of species present. At all other sites, coefficients of similarity are 0.5 or greater in comparisons among transects at a site (Table 11). In all cases, the means for coefficients at a site are greater than the coefficient for comparisons between sites (Table 12). Thus, there is greater similarity in species within a site than between sites.

DISCUSSION—Shelford (1974) included the lower reach of the Rio Grande in the Southern Grassland Biome and mapped the vegetation as an Acacia-Grassland community. Frye et al. (1984) showed a 32-km stretch of the Rio Grande in Starr County as part of a Mesquite-Blackbrush (*Prosopis glandulosa—Acacia rigidula*) association, but most of the lower reach of the Rio Grande in Starr, Hidalgo, and Cameron counties is mapped as cropland. A 15-km stretch westward from the mouth of the river in Cameron County is mapped as "Other Native and/or Introduced Grasses" or as "Marsh/Barrier Island". This section of the river in eastern Cameron County is in Thomas' (1969) Gulf Prairies and Marshes vegetational area. The separation of the Gulf Prairies and Marshes from the South Texas Plains vegetational area is based on the absence of trees in the Gulf Prairies and Marshes. We found that trees were indeed absent at the mouth of the river and that the vegetation was typical of that found on the tidal flats of South Padre Island (Judd et al., 1977).

Diamond et al. (1987) identified 4 series that could occur along the lower reach of the Rio Grande: Texas Palmetto (*Sabal mexicana*) Series, Sugarberry-Elm (*Celtis laevigata—Ulmus* sp.) Series, Texas Ebony-Anacua (*Chloroleucon ebano–Ehretia anacua*) Series, and Mesquite-Huisache (*Prosopis glandulosa—Acacia minuata*) Series. The Texas Palmetto Series is a distinct community, and we found that at least 1 of the species in each of the other 3 series (i.e., *Celtis laevigata, Ehretia anacua,* and *Prosopis glandulosa*) was dominant at places along the lower reach of the Rio Grande.

McLendon (1991) identified the Hackberry-Huisache Association as the riparian association of South Texas. He listed the most common dominants as sugar hackberry (*Celtis laevigata*) and huisache (*Acacia minuata*). Included among the subdominants were cedar elm, anaqua, mesquite, Texas persimmon (*Diospyros*

TABLE 10—Comparison of the relative importance of species occurring in the ground layer among transects and localities. Freq. = Frequency, Rel. freq. = Relative Frequency, Rel. cov. = Relative Cover, Imp. val. = Importance Value (the sum of relative frequency and relative cover).

Location	Species	Freq.	Rel. freq.	% Cover	Rel. cov.	Imp. val.
Mouth of Rio Grande	*Monanthochloe littoralis*	44.4	10.8	28.71	47.5	58.3
	Batis maritima	88.9	21.6	9.75	16.1	37.7
	Suaeda linearis	66.7	16.2	9.81	16.2	32.4
	Salicomia virginica	66.7	16.2	2.03	3.4	19.6
	Spartina alterniflora	33.3	8.1	6.17	10.2	18.3
	Borrichia frutescens	44.4	10.8	3.52	5.8	16.6
	Lycium carolinianum	55.6	13.5	0.41	0.7	14.2
	Distichlis spicata	11.1	2.7	0.04	0.1	2.8
Palmito Pumphouse	*Monanthochloe littoralis*	100.0	9.9	12.93	26.4	36.3
	Borrichia frutescens	88.9	8.7	7.25	14.9	23.6
	Maytenus phyllanthoides	88.9	8.7	2.51	4.9	13.6
	Prosopis reptans	66.7	6.3	2.05	4.5	10.8
	Panicum maximum	44.5	4.7	2.48	4.9	9.6
	and 25 additional species with importance values below 8.					
Sabal Palm Sanctuary	*Panicum maximum*	100.0	37.9	44.64	73.1	111.0
	Panicum hirsutum	13.3	5.4	6.89	12.3	17.7
	Rivina humilis	33.3	8.0	3.45	7.9	15.9
	Celtis laevigata	26.7	7.7	0.55	1.1	8.8
	and 18 additional species with importance values below 8.					
Santa Ana NWR	*Panicum maximum*	60.0	6.9	10.29	24.2	31.1
	Tillandsia usneoides	40.0	4.6	5.43	13.0	17.6
	Cocculus diversifolius	53.3	5.7	1.76	5.5	11.2
	Salvia coccinea	46.7	4.8	1.78	5.0	9.8
	Chromolaena odorata	26.7	2.6	1.90	6.1	8.7
	and 30 additional species with importance values below 8.					
Anzalduas	*Panicum maximum*	73.3	34.4	41.78	66.0	100.4
	Pennisetum ciliare	21.7	10.1	13.39	21.4	31.5
	Cyperus odoratus	21.7	10.1	3.69	5.8	15.9
	Eriochloa punctata	15.0	7.5	3.07	4.3	11.8
	and 8 additional species with importance values below 8.					
Bentsen State Park	*Panicum maximum*	100.0	53.0	66.97	96.3	149.3
	Blue-green algal mat	22.2	11.7	0.33	0.5	12.2
	Pennisetum ciliare	22.2	11.7	0.23	0.3	12.0
	and 4 additional species with importance values below 8.					
Salineño	*Pennisetum ciliare*	58.3	7.3	23.98	43.3	50.6
	Paspalum lividum	33.3	4.3	5.39	9.3	13.6
	Setaria leucopila	41.7	4.9	5.85	9.7	14.6
	Cynodon dactylon	33.3	4.3	4.95	8.5	12.8
	Ruellia nudiflora	33.3	4.3	2.43	4.4	8.7
	and 30 additional species with importance values below 8.					

texana), and Texas ebony. Twelve common ground-cover species were identified, but no dominants were listed. Mist flower (*Chromolena odorata*) was the only species listed as common by McLendon (1991) that was a dominant in the ground layer at 1 of our sites (Santa Ana NWR). McLendon (1991) did not include the lower Rio Grande Valley in his description of the vegetation of South Texas, so he did not apply the Hackberry-Huisache Association to the riparian vegetation of the Rio Grande. However, we found that sugar hackberry was a dominant tree at 4 of 7 sites on the Rio Grande, but huisache was not dominant in the

TABLE 11—Within-site variation in species similarity (Sorenson's Index of Similarity) in the ground layer.

	Comparisons			
Location	Transects 1 & 2	Transects 2 & 3	Transects 1 & 3	$\bar{x}$
Mouth of Rio Grande	0.933	0.923	0.857	0.904
Palmito Pumphouse	0.667	0.265	0.265	0.399
Sabal Palm Sanctuary	0.320	0.615	0.154	0.363
Santa Ana NWR	0.698	0.681	0.682	0.687
Anzalduas	0.833	0.555	0.500	0.629
Bentsen State Park	0.571	0.571	0.500	0.547
Salineño	0.565	0.571	0.619	0.585

TABLE 12—Site variation in ground cover species richness and between-site variation using Sorenson's Index of Similarity.

Location	# of species	Sorenson's index
Mouth of Rio Grande	8	
		0.108
Palmito Pumphouse	29	
		0.200
Sabal Palm Sanctuary	21	
		0.304
Santa Ana NWR	35	
		0.292
Anzalduas	13	
		0.200
Bentsen State Park	7	
		0.182
Salineño	37	

tree or shrub layers at any of the sites. Indeed, we found huisache in the tree and shrub layers at only 2 sites. Species that McLendon (1991) listed as subdominants of the Hackberry-Huisache Association were all present in the riparian vegetation of the Rio Grande.

Clover (1937) did not consider the riparian vegetation separate from that of the lower Rio Grande Valley in general. However, she reported that there were communities dominated by huisache near the Rio Grande, and she mentioned a heavily wooded area along the Rio Grande in Cameron County, where trees reached a height of 17 m or more. She identified the canopy at this site as consisting of *Celtis laevigata, Ulmus crassifolia, Chloroleucon ebano, Sapindus saponaria* var. *drummondii*, and *Fraxinus berlandieriana*. Blair (1950) reported that the most luxuriant brush in the lower Rio Grande Valley occurred on the immediate floodplain of the Rio Grande, and he stated that large cedar elms dominated the floodplain in some places and there was usually an alternation of cedar elm and brush species as dominants. Clearly, Blair (1950) was aware that cedar elm was patchily distributed along the Rio Grande and that dominant species varied among sites. We found that cedar elm was dominant at only 1 of the 7 locations we investigated. It is surprising that neither Clover (1937) nor Blair (1950) mentioned sugar hackberry as a dominant species.

Clover (1937) discussed the "Boscaje de Palma" as a distinct community and identified *Sabal mexicana* as the dominant species. She singled out *Arundo donax* for special recognition, reporting that it was 6 m tall and added to the tropical appearance of the locality. Clover (1937) reported that it was difficult to tell what species ranked second or third in dominance and listed 8 species as prominent. She listed a total of 74 species collected along a transect from the river's edge into the densest growth of the palm forest. Our transects at the Sabal Palm Sanctuary were just to the east of the palm grove proper and there were only a few scattered palms along the transects. However, it was clear that the sabal palm community was distinct from other riparian communities in the lower Rio Grande and deserves special recognition.

Jahrsdoerfer and Leslie (1988) recognized and mapped 5 plant communities in the floodplain of the lower Rio Grande between the mouth of the river and Falcon Dam: 1) Clay Loma and Wind Tidal Flats, 2) Sabal Palm Forest, 3) Midvalley Riparian Woodland, 4) Upper Valley Flood Forest, and 5) Chihuahua Thorn Forest or Falcon Woodland. Our mouth of the Rio Grande transects were in vegetation roughly similar to Jahrsdoerfer's and Leslie's Wind Tidal Flats. We both found *Borrichia frutescens* was a dominant, but Jahrsdoerfer and Leslie (1988) did not mention *Monanthochloe littoralis*. Our Palmito Pumphouse site corresponds to their Clay Loma designation, and the ground layer species that they listed were present at the Palmito Pumphouse site, but the shrub and tree species they listed as characteristic, i.e., fiddlewood (*Citharexylum brachyanthum*) and Texas ebony, while present, were not dominant. Rather, mesquite, granjeno, and colima (*Zanthoxylum fagara*) were the dominant trees and shrubs.

Jahrsdoerfer's and Leslie's (1988) Sabal Palm Forest clearly corresponds to the Boscaje de Palma of Clover (1937). There is little question that this community is unique, although our transects were on the eastern margin of the forest and we found that *Celtis laevigata, Cocculus diversifolius, Zanthoxylum fagara* and *Mimosa asperata* were more important than *Leucaena pulverulenta, Ehretia anacua,* and *Chloroleucon ebano.*

Our Santa Ana NWR and Anzalduas sites correspond with Jahrsdoerfer's and Leslie's (1988) Midvalley Riparian Woodland. There is considerable agreement in dominant species. Jahrsdoerfer and Leslie (1988) stated that this community was essentially a bottomland, hardwood site with stands of cedar elm, Berlandier ash (*Fraxinus berlandieriana*), and sugar hackberry mixed with mesquite and granjeno. We found that granjeno was a dominant in the shrub layer and that sugar hackberry and cedar elm were dominants in the tree layer. Berlandier ash and mesquite were present, but of low importance at both sites.

Our Bentsen State Park locality corresponds with the Upper Valley Flood Forest of Jahrsdoerfer and Leslie (1988). They reported that mesquite and granjeno were the dominant woody species. We found that granjeno was indeed the dominant shrub, but sugar hackberry was the dominant tree species. Mesquite comprised less than 20% of the tree species cover (Table 1).

Our Salineño locality occurred in the Chihuahuan Thorn Forest of Jahrsdoerfer and Leslie (1988). They reported that the community included black willow, Montezuma bald cypress (*Taxodium mucronatum*), Texas ebony, and mesquite. We found that mesquite, sugar hackberry, and retama (*Parkinsonia aculeata*) were the dominant trees. We did not find black willow at this site, but it did occur in the area. Texas ebony was also present in the area, but there were no bald cypress here.

Vora (1990) placed the vegetation of Santa Ana NWR into 9 communities: 1) Rio Grande riparian, 2) River bank, 3) Recent accretions, 4) Aquatic, 5) Seasonally flooded, 6) Former resaca bottoms, 7) Floodplain–bottomland, 8) Floodplain–chaparral, and 9) Upland brush. His map of the refuge shows communities 1, 2, 3, 7, and 8 bordering on the Rio Grande at 1 or more locations. Vora's (1990) description of the Rio Grande riparian community makes clear that he limited this community to the slope of the river bank, i.e., between the water's edge and the top of the bank. He reported that the vegetation was dense and composed of dry-land willow (*Baccharis neglecta*), seepwillow (*B. salicifolia*), black willow, and sandbar willow. We found dry-land willow, seepwillow, and black willow growing on the slope of the river bank and on top of the bank for distances as great as 50 m from the water's edge at 4 study sites. Only black willow was dominant in any of our transects (1 at Anzalduas). The frequency of *Salix* and *Baccharis* species was too low at most sites for them to achieve dominance.

There is considerable overlap in the species present in Vora's (1990) other communities (i.e., in 2, 3, 7, and 8) so it is difficult to determine the basis of his community designations. For example, the overstory dominants of the River bank community are sugar hackberry and black willow, while those of the Recent accretions community are sugar hackberry, huisache, and retama.

Our transects at Santa Ana NWR were in the community identified as Floodplain–bottomland by Vora (1990). We had close agreement with the dominant tree species, i.e., cedar elm and anacua. We found that the dominant shrubs were granjeno and colima, and Vora (1990) also listed these as 2 of 4 dominant shrub species. Vora (1990) reported that the ground cover consisted principally of *Rivina humilis* and tree seedlings, but we found that *Panicum maximum, Chromolaena odorata,* and *Cocculus diversifolius* were the dominants in the ground cover. *Rivina humilis* was third in importance in 1 transect and fourth in a second transect. Thus, the only major differences are in the ground layer, where it appears that the introduced grass *Panicum maximum* was displacing native species as the dominant.

Butterwick and Strong (1976) studied the riparian vegetation of the Rio Grande in the stretch of the river immediately below Falcon Dam in the Falcon thorn woodland. They sampled 4 line transects at a site 1 km WSW of Santa Margarita, Starr County, Texas. Transects 1 and 2 were on a terrace adjacent to the river that was often inundated by rising water. The dominant species of Transect 1 were *Fraxinus berlandieriana* and *Acacia minuata.* On Transect

2, the dominant species based on relative cover were *Acacia minuata, Celtis laevigata,* and *Celtis pallida.* Retama was fourth in importance on Transect 1 and fifth in importance on Transect 2. Transects 3 and 4 were on the next higher terrace at the same location and were rarely inundated. Mesquite was dominant on Transect 3. On Transect 4, mesquite was the dominant based on relative cover, but granjeno was dominant based on density. Butterwick and Strong (1976) called this a Mesquite-Granjeno Association.

Butterwick and Strong (1976) did not quantify the ground cover, but they listed species that were common in ground cover. For example, they identified 3 grass species as common on Transects 1 and 2 and 4 grass species as common on Transects 3 and 4. Buffel grass was not mentioned for any of the transects, but we found it was the dominant species at Salineño.

Our transects traversed both terraces identified by Butterwick and Strong (1976), and we found that mesquite, sugar hackberry, and retama were dominants in the tree layer, while granjeno and prickly pear were dominant in the shrub layer. In comparing Butterworth's and Strong's (1976) data to our results, the Sorenson's index was 0.777. This value is only slightly lower than the mean of 0.83 that we obtained for between-transect comparisons at this site and it is greater than any of the between-site indices. Thus, there is relatively close agreement in our findings, except for the ground layer, where it appears that buffel grass is replacing native grasses.

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