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Phenology of Native Angiosperms of South Padre Island, Texas

Robert I. Lonard
Department of Biology, University of Texas-Pan American, Edinburg, Texas

Frank W. Judd
Coastal Studies Laboratory, University of Texas-Pan American, P.O. Box 2591, South Padre Island, Texas

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Robert I. Lonard
Department of Biology, University of Texas-Pan American, Edinburg, Texas 78539

and

Frank W. Judd
Coastal Studies Laboratory, University of Texas-Pan American, P.O. Box 2591, South Padre Island, Texas 78597

Abstract. Flowering and fruiting patterns for 74 species of native angiosperms were studied on South Padre Island, Texas, from May 1984 to May 1986. Four patterns were recognized: 1) a continuous cycle of flowering and fruiting; 2) a cycle limited to spring through autumn; 3) a two season regime, either spring-summer or summer-fall; and 4) a cycle completed in one season or less (spring or fall). Marked year-to-year variation occurred in flowering and fruiting responses within individual species. Only one-fifth of the species exhibited the same monthly patterns in successive years. Number of species in flower or fruit was significantly correlated with mean monthly temperature and photoperiod, but showed no correlation with total monthly precipitation or precipitation with a one month time lag. Insect pollinated species had longer flowering/fruiting periods than wind pollinated species. Flowering and fruiting responses were compared among species common to other Gulf of Mexico islands and with species in common with temperate grasslands.

Key Words. flowering phenology, South Padre Island, Texas

INTRODUCTION

Phenological studies are important in interpreting the floristic relationships of a region. A clearer understanding of the structure and functioning of the ecosystem is effected when phenological information is combined with other biotic and abiotic data. Moreover, knowledge of flowering and fruiting phenophases is fundamental to investigations of angiosperm breeding systems.

Most of the phenological data available for Gulf of Mexico coastal areas are anecdotal information in checklists (Gillespie 1976, Anderson and Alexander 1985) or floristic treatments (Correll and Johnston 1970, Jones 1982, Clewell 1985), or it is applicable to marsh habitats on the coastal mainland (Eleuterius and Caldwell 1984). The only investigation focused specifically on the flowering and fruiting phenology of Gulf of Mexico barrier island plants was conducted in a tropical climate at Veracruz, Mexico, by Castillo and Carabias (1982). Thus, a study was initiated on the flowering and fruiting phenology of native angiosperm species on South Padre Island (a subtropical barrier island), Texas to: 1) provide descriptive information on the flowering and fruiting progression for the bulk of the native angiosperm species occurring on the island; 2) investigate the relationships between climatic factors and flowering and fruiting patterns; and 3) compare the patterns of flowering and fruiting phenologies among species in common between South Padre Island, other Gulf of Mexico barrier islands, Atlantic barrier islands, and various mainland habitats, especially temperate grasslands.

METHODS

Descriptions of the area, vegetation patterns, and edaphic factors were given in Dahl *et al.* (1974), Judd *et al.* (1977), and Judd and Lonard (1985). Temperature, precipitation, and photoperiod data were obtained for Port Isabel, Texas, which is on the mainland adjacent to the southern end of South Padre Island (Orton *et al.* 1967, National Oceanic and Atmospheric Administration 1984, 1985, and 1986). A list of the native species of flowering plants was compiled from information provided by Lonard and Judd (1981).

Flowering and fruiting data for species common to South Padre Island and other insular or coastal mainland areas of the Gulf of Mexico were obtained from Correll and Johnston (1970), Gillespie (1976), Castillo and Carabias (1982), Jones (1982), Eleuterius and Caldwell (1984), Clewell (1985), and Anderson and Alexander (1985). In several cases, authors listed the flowering/fruiting phenophases on a seasonal basis (e.g. spring-summer) rather than giving inclusive months. To quantitatively compare data a maximum of three months was assumed for a season. Flora of the Great Plains (Great Plains Flora Association 1986) was used extensively for phenological comparisons with widely distributed inland species. In addition, Turner (1959), Ashapanek (1962), Wagner (1964), and Lee and Bazzaz (1982) were examined for phenological data concerning specific species.

Phenological data on flowering and fruiting were obtained from three belt transects (5 m wide) extending across the width of the island (Figure 1). The southernmost transect (Number 3) was located in Isla Blanca Park near Brazos-Santiago Pass. Transect Number 2 was oriented parallel to the margin of a hurricane washover 18 km north of Brazos-Santiago Pass. Transect Number 1 crossed all the topographic zones identified by Judd *et al.* (1977), i.e. backshore, primary dunes, secondary dunes and vegetated flats, and tidal flats. It was located 19 km north of Brazos-Santiago Pass.

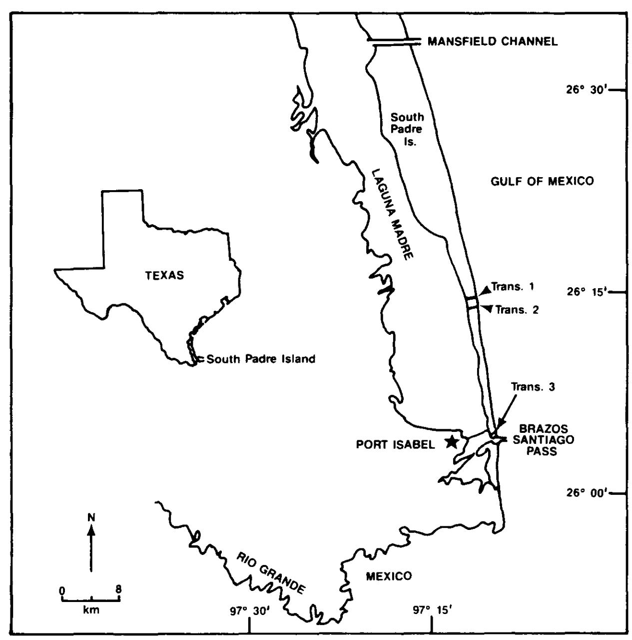

FIG. 1. Map of South Padre Island showing the location of study sites.

The study was initiated 27 May 1984 and terminated 10 May 1986. The transects were censused at 15-day intervals from March through November and at 30-day intervals from December through February. Data recorded were initiation of vegetative growth, time of budding, occurrence of flowering and fruiting, seed dissemination, and senescence. Flowering and fruiting data of native species were selected for presentation in this paper. Flowering and fruiting stages were combined for analysis, because these events were difficult or impossible to separate in many species (Eleuterius and Caldwell 1984). Data were analyzed on a monthly basis. Statistical procedures were those of Sokal and Rohlf (1981). A probability value less than 0.05 was considered significant.

RESULTS

This study was based on observation of the flowering/fruiting phenology of 74 native angiosperm species. The species represented 70 genera and 28 families. Forty-seven species were dicotyledons, and 27 were monocotyledons (Table 1).

Four flowering/fruiting patterns were evident (Table 1): 1) a

Table 1. Flowering and fruiting duration and relationships for 74 species of native angiosperms of South Padre Island, Texas. Entomophilous species = e, anemophilous species = a.

Species	*Duration of flowering/ fruiting (no. months)*		*Mode of pollination*
Continuous (10-12 month) flowering and fruiting:			
Philoxerus vermicularis (L.) R. Br.	Jan-Jun; Aug-Dec	(11)	e
Sesuvium portulacastrum L.	Mar-Jun	(11)	e
Cassia fasciculata Michx. var. *ferrisiae* (Britt.) Turner	Jan-May; Jul-Dec	(11)	e
Rhynchosia americana (Mill.) Metz.	Jan-Dec	(12)	e
Sophora tomentosa L.	Jan-Dec	(12)	e
Linum alatum (Small) Winkler	Jan-Dec	(12)	e
Polygala alba Nutt.	Jan-Dec	(12)	e
Croton punctatus Jacq.	Jan-Dec	(12)	e
Euphorbia cordifolia Ell.	Jan-Dec	(12)	e
Opuntia compressa (Salisbury) MacBride var. *fusco-atra* (Eng.) Winiger	Jan-Dec	(12)	e
Oenothera drummondii Hook.	Jan-Dec	(12)	e
Samolus ebracteatus H.B.K.	Jan-Dec	(12)	e
Polypremum procumbens L.	Apr-Jan	(10)	e
Ipomoea pes-caprae (L.) Sweet var. *emarginata* Hallier f.	Apr-Jan	(10)	e
Physalis viscosa L. var. *spathulifolia* (Torr.) Gray	Jan-Dec	(12)	e
Oldenlandia boscii (DC.) Chapm.	Jan-Dec	(12)	e
Borrichia frutescens (L.) DC.	Jan-Dec	(12)	e
Erigeron myrionactis Small	Jan-Dec	(12)	e
Eupatorium betonicifolium Mill.	Jan-Dec	(12)	e
Gaillardia pulchella Fouq. var. *picta* (Sweet) Gray	Jan-Dec	(12)	e
Heterotheca subaxillaris (Lam.) Britt. and Rusby	Jan-Dec	(12)	e
Machaeranthera phyllocephala (DC.) Shinners	Jan-Dec	(12)	e
Ratibida penduncularis (T. and G.) Barnh.	Jan-Dec	(12)	e
Solidago sempervirens L. var. *mexicana* (L.) Fern.	Jan-Dec	(12)	e
Dichanthelium nodatum (Hitchc. and Chase) Gould	Jan-Dec	(12)	a
Eragrostis secundiflora Presl.	Apr-Jan	(10)	a
Dichromena colorata (L.) Hitchc.	Mar-Jan	(11)	e
Eleocharis obtusa (Willd.) Schult.	Jan-Dec	(12)	a
Fuirena simplex Vahl	Jan-Dec	(12)	e
Scirpus americanus Pers. var. *longispicatus* Britt.	Feb-Dec	(11)	a
Commelina erecta L. var. *angustifolia* (Michx.) Fern.	Feb-Dec	(11)	e
Primarily spring through autumn (7-9 months) flowering and fruiting:			
Salicornia bigelovii Torr.	May-Oct	(6)	?
Salicornia virginica L.	May-Nov	(7)	?
Batis maritima L.	Apr-Nov	(8)	?
Cakile geniculata (Robins.) Millsp.	Feb-Aug; Dec	(8)	e
Baptisia leucophaea Nutt. var. *laevicaulis* Canby	Mar-Sep	(7)	e
Galactia canescens Benth.	Apr-Nov	(8)	e
Prosopis reptans Benth. var. *cinerascens* (Gray) Burkhart	May-Jan	(9)	e
Calylophus australis Towner and Raven	Mar-Oct	(8)	e
Eustoma exaltatum (L.) G. Don	May-Nov	(7)	e
Ipomoea stolonifera (Cyr.) Gmel.	Apr-Dec	(9)	e
Agalinus maritima Raf.	Mar-Nov	(9)	e
Bacopa monnieri (L.) Wettst.	May-Dec	(8)	e
Buchnera floridana Gand.	May-Nov	(7)	a
Iva angustifolia DC.	Jun-Dec	(7)	a
Aristida longespica Poir. var. *geniculata* (Raf.) Fern.	May-Dec	(8)	a
Spartina patens (Ait.) Muhl.	May-Nov	(7)	a
Spartina spartinae (Trin.) Hitchc.	Jan; Apr-Oct	(8)	a
Sporobolus virginicus (L.) Kunth	Apr-Nov	(8)	a
Uniola paniculata L.	Apr-Nov	(8)	a
Fimbristylis castanea (Michx.) Vahl	Jun-Dec	(7)	a

Table 1. Continued

Species	Duration of flowering/ fruiting (no. months)		Mode of pollination
Two season flowering and fruiting; either spring-summer, or summer-fall (4-6 months):			
Suaeda linearis (Ell.) Moq.	Jun-Nov	(6)	?
Lythrum alatum Pursh var. *lanceolatum* (Ell.) T. and G. *ex* Rothrock	Apr-Sep	(6)	e
Limonium nashii Small	Jul-Nov	(5)	e
Sabatia arenicola Greenm.	Jan-Jun	(6)	e
Lycium carolinianum Walt. var. *quadrifidum* (Dun.) C. L. Hitchc.	Aug-Jan	(6)	e
Stemodia tomentosa (Mill.) Greenm. and Thomps.	Apr-Sep	(6)	e
Distichlis spicata (L.) Greene	Aug-Nov	(4)	a
Panicum amarum Ell.	Aug-Nov	(4)	a
Paspalum distichum L.	Aug-Nov	(4)	a
Paspalum monostachyum Vasey	Sep-Dec	(4)	a
Schizachyrium scoparium (Michx.) Nash var. *littoralis* (Nash) Gould	Jul-Dec	(6)	a
Sporobolus tharpii Hitchc.	Jun-Nov	(6)	a
Caldium jamaicense Crantz	Apr-Jul	(4)	a
Juncus megacephalus M.A. Curtis	May-Aug	(4)	a
Sisyrinchium biforme Bickn.	Mar-Jun; Dec-Jan	(6)	e
One season flowering and fruiting (1-3 months), spring or fall:			
Schrankia latidens (Small) K. Schum.	May-Jun	(2)	e
Hydrocotyle bonariensis Lam.	May-Jun	(2)	e
Flaveria brownii A.M. Powell	Nov-Dec	(2)	e
Andropogon glomeratus (Walt.) B.S.P.	Oct-Nov	(2)	a
Monanthochloe littoralis Engelm.	Mar-May	(3)	a
Muhlenbergia filipes M. A. Curtis	Oct-Nov	(2)	a
Triplasis purpurea (Walt.) Chapm.	Oct-Nov	(2)	a
Spiranthes vernalis Engelm. and Gray	May	(1)	e

continuous cycle of flowering and fruiting; 2) a cycle limited to spring through autumn; 3) a two season regime, either spring-summer or summer-fall; and 4) a cycle completed in one season or less (i.e. spring or fall). Thirty-one species (41.9%) flowered and fruited more or less continuously during the year (10-12 months). Twenty species (27%) flowered and fruited during the spring, summer, and fall (7-9 months). Fifteen species (20.3%) flowered and fruited for two seasons, either spring and summer or summer and fall (4-6 months). Eight species (10.8%) flowered and fruited during only one season, usually either in the spring or the fall, and always for a duration of three months or less. Twisted lady's tresses (*Spiranthes vernalis* Engelm. and Gray) and gulf muhly (*Muhlenbergia filipes* M.A. Curtis) had the shortest flowering and fruiting responses. These were 1.0 and 1.5 months, respectively.

Table 1 identifies the mode of pollination and lists the beginning and ending months of flowering and fruiting response. Twenty-three species (31.1%) were anemomophilous, 47 species (63.5%) were entomophilus, and the mode of pollination was unclear for four species (5.4%). Mean duration of flowering and fruiting for insect pollinated species was 9.3 (s.d. = 3.2) months, and the mean for wind pollinated species was 6.3 (s.d. = 3.2) months. Duration of flowering and fruiting was significantly longer for insect pollinated species ($t = 3.689$, 58 df, $p < 0.001$).

Table 2 provides a comparison of the mean duration of flowering and fruiting for six Gulf of Mexico coastal sites, mainland Texas, and the Great Plains states with South Padre Island, Texas. Only species in common between South Padre Island and each of the other sites were included in the analyses. The mean duration of flowering and fruiting for shared species was significantly greater for South Padre Island in all the comparisons, except for Vera Cruz, Mexico (Castillo and Carabias 1982). Thirteen species were common to the Vera Cruz location and South Padre Island, and the means for both were approximately 10 months. Only 20.3% of the South Padre Island species exhibited the same flowering and fruiting initiation and cessation dates (i.e. months) in two years.

A comparison among months of the number of species in flower and/or fruit is given in Table 3. The number of species flowering or fruiting was different in successive years for each of the months. However, there was no significant difference in the mean number of species in flower and/or fruit per month for the two years (1984-85, $N = 12$, $X = 42.7$, s.d. = 13.1; 1985-86, $N = 12$, $X = 47.1$, s.d. = 12.2; $t = 0.838$, 22 df, $p > 0.4$). Furthermore, the pattern of flowering and fruiting was similar for the two years. A peak occurred in October, and the lowest number of species in flower or fruit was in February in each of the years.

Table 2. Comparison of mean duration of flowering and fruiting between South Padre Island, Texas, angiosperms and species in common at other sites. N = number of species shared, s.d. = standard deviation, t = student's t value.

Location (Citation)	*N*	*X Duration (months)*	*s.d.*	*t*	*Probability*
Great Plains States					
(Great Plains Flora Association 1986)	13	4.2	1.21		
vs				3.285	<0.01
South Padre Island, Texas	13	7.8	3.87		
Texas					
(Correll and Johnston 1970)	66	6.5	2.59		
vs				3.025	<0.01
South Padre Island, Texas	66	8.1	3.33		
Mississippi Tidal Marshes					
(Eleuterius and Caldwell 1984)	22	4.0	1.50		
vs				5.461	<0.001
South Padre Island, Texas	22	7.9	3.05		
Florida Panhandle					
(Clewell 1985)	42	4.3	2.09		
vs				5.250	<0.001
South Padre Island, Texas	42	7.7	3.59		
Dog Island, Florida					
(Anderson and Alexander 1985)	26	3.5	1.90		
vs				4.104	<0.001
South Padre Island, Texas	26	6.8	3.64		
Mustand Island, Texas					
(Gillespie 1976)	45	6.4	3.20		
vs				3.665	<0.001
South Padre Island, Texas	45	8.9	3.09		
Texas Coastal Bend					
(Jones 1982 and Gould and Box 1965)	51	7.5	2.69		
vs				3.119	<0.01
South Padre Island, Texas	51	9.2	2.84		
Vera Cruz, Mexico					
(Castillo and Carabias 1982)	13	10.0	2.38		
vs				0.268	>0.5
South Padre Island, Texas	13	9.6	3.50		

Table 3. Comparison among months, for two years (May-April), of number of species in flower and/or fruit and mean monthly temperature, mean monthly photoperiod and total monthly precipitation.

	Number of species in flower/fruit		*Temperature (C)*		*Precipitation (mm)*		*Photoperiod (hrs light)*
Month	*84-85*	*85-86*	*84-85*	*85-86*	*84-85*	*85-86*	*84-85 & 85-86*
May	38	54	25.8	26.3	98.3	111.0	13.42
Jun	53	58	27.6	28.3	3.3	21.3	13.75
Jul	53	58	28.4	27.6	36.6	45.7	13.59
Aug	52	57	28.7	28.3	23.1	15.5	13.04
Sep	52	50	26.5	28.4	666.0	188.7	12.30
Oct	56	59	26.0	24.8	44.5	100.1	11.54
Nov	55	54	21.1	22.8	1.8	39.9	10.88
Dec	42	35	20.7	15.7	40.1	33.0	10.54
Jan	32	30	12.3	15.8	72.4	20.1	10.72
Feb	16	25	13.9	17.6	32.5	37.3	11.29
Mar	25	36	20.9	20.2	22.4	1.8	12.01
Apr	39	49	23.4	24.5	40.6	42.4	12.78

Table 3 provides data for the correlation of flowering and fruiting with temperature, precipitation, and photoperiod. There was a strong positive correlation ($r = 0.809$, $t = 6.455$, 22 df, $p < 0.001$) between mean monthly temperature and number of species in flower and/or fruit. Conversely, the correlation between total monthly precipitation and number of species flowering or fruiting was not significant ($r = 0.154$, $t = 0.713$, 22 df, $p > 0.4$). Lack of correlation also held when a time lag of 30 days was introduced, i.e. when the number of species flowering or fruiting was compared with the previous month's precipitation total ($r = 0.258$, $t = 1.224$, 21 df, $p > 0.4$). Although photoperiod does not change annually, flowering and fruiting responses of the two years were compared separately. In 1984-85, there was no correlation between photoperiod and number of species flowering or fruiting ($r = 0.303$, $t = 1.006$, 10 df, $p > 0.4$), but in 1985-86 there was a positive correlation ($r = 0.647$, $t = 2.682$, 10 df, $p < 0.05$).

DISCUSSION

Flowering and fruiting phenophases were influenced by a variety of abiotic (i.e. photoperiod, temperature, precipitation, etc.) and biotic factors. In temperate grasslands various authors (Ashapanek 1962, Dickinson and Dodd 1976, Kebart and Anderson 1987) have shown that either precipitation or a combination of long-term mean monthly temperatures were important factors in determining flowering responses. These factors were important for individual species as well as for all species within a given community.

Clearly, temperature was a major factor affecting the flowering and fruiting phenology of the native angiosperms of South Padre Island, Texas. This study was initiated five months after a severe freeze occurred in the lower Rio Grande Valley of Texas. Fifty-three to 55 consecutive hours of freezing or below freezing temperatures were recorded with a minimum of -8.8 C. Extensive damage occurred to stands of blackmangrove [*Avicennia germinans* (L.) Stearn] on South Padre Island and elsewhere along the coast (Lonard and Judd 1985). Furthermore, the effects of the freeze on the flowering and fruiting responses of herbaceous species on South Padre Island were evident into the spring and summer of 1984. For example, yellow sophora (*Sophora tomentosa* L.) did not flower until November 1984, but this species flowered and fruited continuously in 1985. It was not until September 1984 that flowering and fruiting responses were similar in the same months in 1985. Additionally, when mean monthly temperatures dropped to 20 C or below from December to March the flowering and fruiting responses declined dramatically. Finally, the duration of flowering for species shared between South Padre Island and more northern locales was significantly longer at South Padre Island. The long flowering/fruiting periods reflect the subtropical environment of South Padre Island and a frost-free period of approximately 330 days.

Precipitation did not appear to be a significant factor influencing flowering and fruiting responses of the South Padre Island flora. Although, other investigators in the tropics (Opler *et al.* 1976, Castillo and Carabias 1982) found that precipitation was important in initiating sexual reproduction. For example, Castillo and Carabias (1982) reported that maximum flower production occurred during the months of highest precipitation on the barrier island at Vera Cruz, Mexico. Furthermore, they noted that the months of major flower production differed in successive years, and that flower production was correlated with differences in annual precipitation.

Precipitation may not be a limiting factor for flower and fruit production on South Padre Island as long as successive years of drought do not lower the water table. Judd *et al.* (1977) reported that depth to the water table in the secondary dunes and vegetated flats zone of South Padre Island was less than 1.0 m (except on tall dunes). It is likely that capillary action is sufficient to move water from the water table to roots, and that moisture is not a limiting factor on South Padre Island unless there is an extended drought.

Effect of photoperiod on flowering and fruiting responses was unclear. In 1984-85, no correlation was found between mean photoperiod for a given month and the number of species flowering or fruiting, but in 1985-86 a significant positive correlation occurred. The marked difference may have been due to differences in other light parameters, such as intensity, or to a factor (such as temperature) or factors that were correlated with photoperiod. Apparently, many tropical species are "short day" or "day-neutral" with respect to the photoperiod stimulus for anthesis (Opler *et al.* 1976). Studies are needed to separate the effects of temperature and photoperiod on flowering and fruiting of South Padre Island species.

Mean duration of flowering and fruiting was longer for insect pollinated species than for wind pollinated species. Rabinowitz *et al.* (1981) reported similar results in Missouri. The long duration for insect pollinated species was probably due to the virtual absence of freezing temperatures on South Padre Island. Thus, insects can be active year-round.

The flowering/fruiting response on South Padre Island exhibited marked year-to-year variation. Only 20% of the species were found in flower or fruit in the same months in successive years. Castillo and Carabias (1982) reported similar results for the flora of a barrier island at Vera Cruz, Mexico. They attributed the difference between years to differences in precipitation. Apparently, the differences were largely due to the freeze in December 1983 and its rather long-lasting effects into 1984.

Three dominant species on South Padre Island had longer flowering/fruiting durations than conspecific populations in temperate zones of the Gulf Coast or at mainland locations. Sea oats (*Uniola paniculata* L.), the dominant species of the backshore and primary dunes, initiated flowering as early as April and fruited until November. However, on a South Carolina barrier island, sea oats initiated anthesis in early July and concluded fruiting by late August (Wagner 1964). Seacoast bluestem [*Schizachyrium scoparium* var. *littorālis* (Nash) Gould], the dominant species of the secondary dunes and vegetated flats topographic zone, initiated flowering in July and fruited until early December. In central Oklahoma, a conspecific population flowered and fruited from August to early November (Ashapanek 1962). The robust annual prairie senna [*Cassia fasciculata* var. *ferrisiae* (Britt.) Turner] has high importance in the primary dune zone and was in flower or fruit every month except June. Lee and Bazzaz (1982) found that Illinois populations began flowering in late July and fruited until early October when frosts killed the plants. Apparently, little or no seed dormancy requirements were necessary for prairie senna. Seeds germinated shortly after dispersal; thus, the species acted essentially as a perennial on South Padre Island. A similar situation existed in bigelow glasswort (*Salicornia bigelovii* Torr.), a common annual species on the margins of the tidal flats.

Two observations made during this study merit comment. Bitter panicum (*Panicum amarum* Hitchc. & Chase), which occurred in exposed sites in the backshore zone and along the windward base of the primary dunes, typically flowered and fruited from mid-September to late November. However, plants in a partially shaded site, protected from prevailing winds, and receiving precipitation from a roof drip-line flowered and fruited from August to March. Although it is not native to the flora of South Padre Island, cherry tomato (*Lycopersicon esculentum* var. *cerasiforme* Mill.) is of interest to horticulturists. Plants of this species flowered and fruited from April to June in the crevices between the granite boulders that form the jetty at Brazos-Santiago Pass. The plants were only a few meters above mean high tide and eventually were killed by an unusually high tide.

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