

PHENOLOGY OF *ACACIA BERLANDIERI*, *A. MINUATA*, *A. RIGIDULA*,
A. SCHAFFNERI, AND *CHLOROLEUCON EBANO* IN THE LOWER RIO
 GRANDE VALLEY OF TEXAS DURING A DROUGHT

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ABSTRACT—Flowering and fruiting phenology of *Acacia berlandieri*, *A. minuata*, *A. rigidula*, *A. schaffneri*, and *Chloroleucon ebano* were studied at 3 sites in the Lower Rio Grande Valley of Texas from July 1998 through August 1999. Severe drought conditions prevailed for the 6 months preceding this study, and rainfall was 20% lower during the study than the long-term mean. *Acacia berlandieri* had the longest flowering period (5 months); each of the other 3 *Acacia* species flowered for 3 months. All of the *Acacia* species flowered in winter or spring (at relatively low temperatures and increasing photoperiod). Peak flowering occurred in February in *A. berlandieri*, *A. rigidula*, and *A. schaffneri*. Peak flowering occurred in March in *Acacia minuata*. There was significant variation in percent flowering among months within *A. minuata*, *A. rigidula*, and *A. schaffneri*. Significant variation in percent flowering occurred among species during February, March, and April. *Chloroleucon ebano* flowered in only 1 month (September) following heavy rain. All of the *Acacia* species dropped their fruit before new fruit were developed, but *C. ebano* had mature fruit from the previous year and developing fruit on the same individuals. Few shrubs or trees of any species had fruit from November through April. There were significant differences in percentage of individuals with mature fruit among species in most months, and there was significant variation in percentage of shrubs and trees with mature fruit among sites within species. *Acacia minuata* and *A. schaffneri* showed significant positive correlations between percent fruiting and photoperiod and temperature. We suggest *C. ebano* flowers at higher temperatures than the *Acacia* species and at peak or declining photoperiod rather than during increasing photoperiod.

RESUMEN—La floración y fructificación de *Acacia berlandieri*, *A. minuata*, *A. rigidula*, *A. schaffneri* y *Chloroleucon ebano* se estudiaron en 3 sitios del Valle del Río Bravo de Texas durante julio de 1998 hasta agosto de 1999. Condiciones severas de sequía se presentaron 6 meses antes de la investigación y durante el estudio la lluvia fue 20% menos que el promedio de precipitación a largo plazo. *Acacia berlandieri* tuvo el período de floración más prolongado (5 meses); las otras 3 especies de *Acacia* florecieron durante 3 meses. Todas las especies de *Acacia* florecieron en el invierno y en la primavera (en temperaturas relativamente bajas y en fotoperíodos crecientes). La máxima floración se efectuó en febrero en *A. berlandieri*, *A. rigidula* y *A. schaffneri*. La máxima floración de *A. minuata* fue en marzo. Hubo una diferencia significativa en la proporción de floración entre meses en *A. minuata*, *A. rigidula* y *A. schaffneri*, y una diferencia significativa en la proporción de floración entre especies en febrero, marzo y abril. *Chloroleucon ebano* floreció solamente en septiembre después de una abundante lluvia. Todas las especies de *Acacia* desprendieron su fruta antes del desarrollo de nueva fruta, pero *C. ebano* tenía fruta madura del año anterior junto con fruta desarrollándose en los mismos individuos. Pocos arbustos o árboles de cualquiera de las especies fructificaron desde noviembre hasta abril. Hubo diferencias significativas en el porcentaje de plantas con frutas maduras entre especies en la mayoría de los meses y variación significativa del porcentaje de plantas con frutas maduras dentro de especies entre sitios. *Acacia minuata* y *A. schaffneri* enseñaron correlaciones positivas y significativas entre el porcentaje de fructificación, fotoperíodo y temperatura. Sugerimos que *C. ebano* florece a temperaturas más elevadas que las especies de *Acacia* y en el punto máximo del fotoperíodo o cuando decrece en lugar del fotoperíodo creciente.

Studies of plant phenology are crucial to understanding the resource base of populations, communities, and ecosystems. Indeed, they are the only practical means for distinguishing

rhythmic from contingent activity and for identifying cues for subsequent experimental studies (Bullock and Solis-Magallanes, 1990). There has been only 1 study (Vora, 1990) of

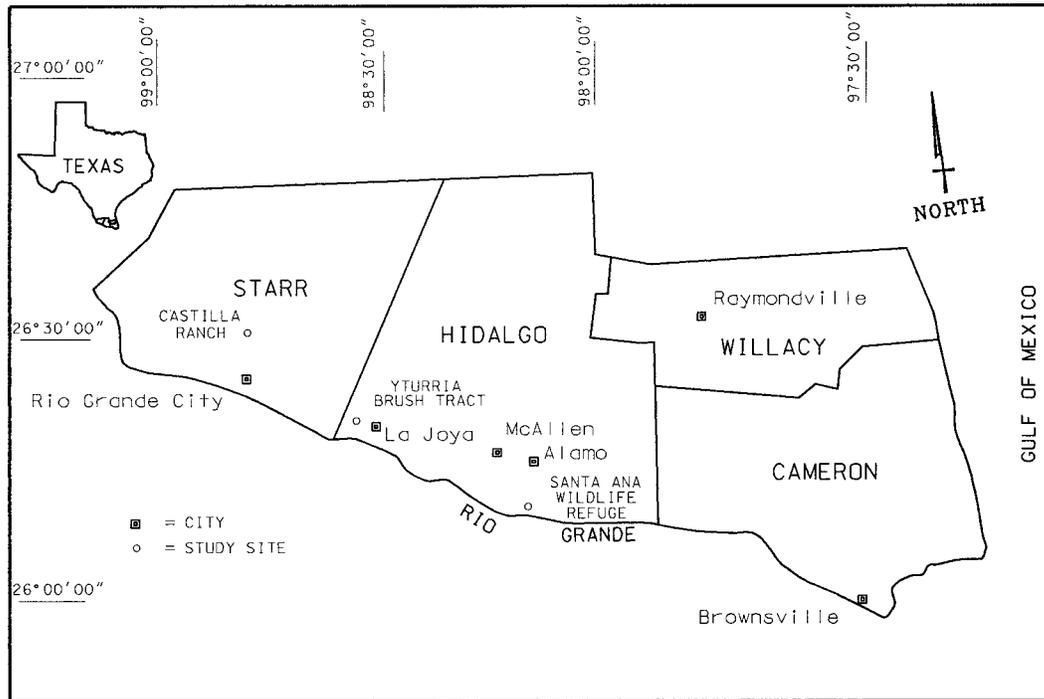


FIG. 1—Map of the Lower Rio Grande Valley of Texas, showing study sites and nearby towns.

the phenology of woody plants in the Lower Rio Grande Valley of Texas (LRGV). Additional, largely anecdotal information is available in floras (Vines, 1960; Correll and Johnston, 1970; Lonard et al., 1991; Everitt and Drawe, 1993; Taylor et al., 1999). Vora (1990) reported on flowering, fruiting, leaf growth, and leaf drop of 19 native species occurring primarily at Santa Ana National Wildlife Refuge, 12.1 km south of Alamo, Hidalgo County, Texas. He did not quantitatively analyze comparisons among species in the characteristics he examined, and he did not quantify the relationships between climatic factors and the reproductive and vegetative responses of the species studied.

The objectives of this study were to: 1) describe and quantify the flowering and fruiting phenology of 4 species of *Acacia* (*A. berlandieri*, *A. minuata*, *A. rigidula*, and *A. schaffneri*) and *Chloroleucon ebano*; 2) quantitatively examine the relationships between climatic factors and the reproductive responses of the species studied; and 3) determine if the magnitude of phenological differences between members of the genus *Acacia* are as great as those between any of the *Acacia* species and *Chloroleucon ebano*.

The null hypotheses tested were: 1) there are no significant differences in the phenologies of the *Acacia* species studied, 2) variation in phenology among the *Acacia* species is less than the variation between any of the *Acacia* species and *Chloroleucon ebano*, and 3) there are no significant correlations between phenological characteristics, such as percentage of individuals in flower, and climatic factors, such as mean monthly temperature or monthly precipitation.

METHODS—Study Area—The study was conducted in Hidalgo and Starr counties of the Lower Rio Grande Valley of Texas (Fig. 1). The LRGV corresponds to the Matamoran Biotic District of the Tamaulipan Biotic Province (Blair, 1950). The climate is semi-arid and subtropical with short, mild winters and long, hot summers (Lonard et al., 1991). The mean length of the frost-free period is 330 days, and frequently an entire winter will pass without a freezing temperature. The normal annual rainfall is 68.2 cm, and the peak of precipitation occurs in September and October (Lonard et al., 1991). Approximately one-third of the total annual precipitation falls during these 2 months. Sixty-nine percent of the annual rainfall is received during the 6-month

period from May through October. Most of the precipitation results from thunderstorms. Often, a single thunderstorm will contribute the rainfall for an entire month. Vegetation of the study sites is brush grassland or thorn woodland (Lonard et al., 1991). The study sites (Fig. 1) were the Castilla Ranch (CR) 11.9 km north of Rio Grande City, Starr County, Texas, Yturria Brush Tract (YBT) 7.1 km west of La Joya, Hidalgo County, Texas, and Santa Ana National Wildlife Refuge (SANWR) 12.1 km south of Alamo, Hidalgo County, Texas.

Description of Species—*Acacia berlandieri* (guajillo) is a semi-evergreen shrub ranging in height from 1.0 to 4.0 m (Lonard et al., 1991; Everitt and Drawe, 1993; Richardson, 1995). Guajillo occurs from southern Texas to Queretaro and Veracruz, Mexico (Turner, 1959; Vines, 1960). It is found on many soil types, but is especially abundant in the LRGV on caliche soils in western Hidalgo and Starr counties. The leaves are fern-like, bipinnately compound, alternate, and have 30 to 50 pairs of leaflets per pinna (Lonard et al., 1991). The flowers are white, and the legumes are 10.2 to 15.2 cm long and contain 5 to 10 dark brown seeds (Taylor et al., 1999).

Acacia minuwata (huisache) is a small, spiny tree or shrub ranging in height from 2.0 to 4.0 m (Lonard et al., 1991; Everitt and Drawe, 1993). It is found from southeastern Texas to the Big Bend and thence southward through southern Texas, Mexico, and Central America into northern South America. Huisache also occurs in southern Florida and the West Indies (Vines, 1960; Cox and Leslie, 1988). Huisache is found on a variety of soil types (Lonard et al., 1991). The leaves are bipinnately compound, alternate, with 2 to 8 pairs of pinnae and 10 to 25 pairs of leaflets per pinna (Lonard et al., 1991). The flowers are yellow to gold, and the fruit can be reddish brown, purple, or black (Everitt and Drawe, 1993). The legumes are 5.1 to 7.6 cm long and the seeds are arranged in 2 rows within them (Everitt and Drawe, 1993; Taylor et al., 1999).

Acacia rigidula (black brush) is a white-spined, multiple-stemmed shrub that grows to a maximum height of 3.0 m (Lonard et al., 1991). It often occurs in association with guajillo. Black brush occurs from southern Texas southward to Jalisco, San Luis Potosi, and Veracruz, Mexico (Vines, 1960; Correll and Johnston, 1970). In the LRGV it is found on clay or gravelly soils (Richardson, 1995). The leaves are alternate, bipinnately compound with 1 or 2 pairs of pinnae and 2 to 4 pairs of leaflets per pinna (Lonard et al., 1991). The flowers are white or yellowish. The legume is black to reddish black, 5.1 to 8.9 cm long, and constricted between the seeds (Richardson, 1995; Taylor et al., 1999).

Acacia schaffneri (huisachillo) is a spiny, rounded shrub that grows to a maximum height of about 2.0 m (Lonard et al., 1991). Huisachillo occurs from Ci-

TABLE 1—Species present at study sites in the Lower Rio Grande Valley of Texas.

Species	Castilla Ranch	Santa	
		Ana NWR	Yturria Tract
<i>Acacia berlandieri</i>		X	X
<i>Acacia minuwata</i>	X	X	
<i>Acacia rigidula</i>	X	X	X
<i>Acacia schaffneri</i>	X		X
<i>Chloroleucon ebano</i>		X	X

bolo Creek (north and east of San Antonio) west to Eagle Pass and then south into Mexico to Puebla and Colima. It also is found in the West Indies, South America, and the Galapagos Islands (Vines, 1960). In the LRGV it occurs on sandy and clay soils (Richardson, 1995). Leaves are alternate, bipinnately compound with 2 to 5 pairs of pinnae and 10 to 15 pairs of leaflets per pinna (Lonard et al., 1991). Flowers are yellow, and the fruit is a linear, black, pubescent legume about 4 to 13 cm long and constricted between the seeds (Correll and Johnston, 1970; Lonard et al., 1991; Everitt and Drawe, 1993; Richardson, 1995).

Chloroleucon ebano (Texas ebony) is a tree growing up to 15 m in height (Richardson, 1995) but usually is less than 10 m tall (Lonard et al., 1991). It has zigzag branches with stout stipular spines. Texas ebony ranges from a line connecting Laredo, San Antonio, and Sinton in Texas southward into Tamaulipas and Nuevo Leon, Mexico (Vines, 1960). The leaves are alternate or fasciated and bipinnately compound with 3 to 6 pairs of leaflets per pinna. The species occurs on sandy loam soils in the LRGV (Lonard et al., 1991). The flowers are white, and the fruit is a thick-walled woody legume.

Field Methods—All 5 species were not present together at any of the study sites (Table 1). Ten individuals from each of the species present at a site were marked for study. Shrubs (*A. berlandieri*, *A. rigidula*, and *A. schaffneri*) were 1.5 m in height or taller. *Acacia minuwata* and *Chloroleucon ebano* were 3 m or taller. Shrubs and trees of these heights were known to be capable of possessing fruit. Distance between marked individuals ranged from 8 m to 2,320 m. In no case did canopies overlap. All plants selected were healthy. Plants were marked with colored flagging and 2 aluminum tags bearing a unique identification number.

Data were collected biweekly from July 1998 through August 1999. Flowering events were evaluated using methods described by Gill and Mahall (1986). Buds were categorized as new, growing, or static. Flowering was documented when buds were in anthesis. Fruiting was documented when flowers

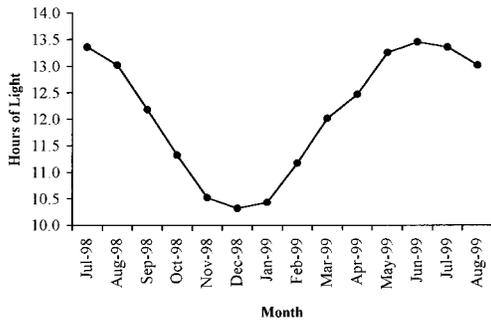


FIG. 2—Mean hours of light per month, July 1998 through August 1999, for McAllen, Texas.

exhibited the formation of a legume. Fruits were categorized as immature, mature and closed, and mature and open. Dehiscent fruits were recorded as mature and open as long as there were seeds adhering to the pods (Friedel et al., 1994).

Daily air temperatures, precipitation, and photoperiod were obtained from the National Climatic Data Center for McAllen, Texas. Local cooperative observer reports for Rio Grande City and La Joya were obtained from the National Weather Service, Brownsville, Texas. Long-term precipitation data were obtained from the office of the Texas State Climatologist.

Statistical Methods—Statistical methods used follow Sokal and Rohlf (1981). Percentage of individuals flowering and percentage of individuals with mature, but not open fruit were compared among species within months and among months within species using *G*-tests for goodness of fit for more than 2 classes. Chi-square tests were used to compare percentage of individuals flowering and percentage of individuals with mature fruit between sites within guajillo, huisache, huisachillo, and Texas ebony. *G*-

tests were used to compare among sites in black brush. Product-moment correlation coefficients were calculated for percentage of individuals flowering and percentage of individuals with mature fruit versus mean monthly photoperiod, mean monthly temperature, and monthly precipitation. Lag-time effects of rainfall on flowering and fruiting were examined by conducting correlation tests for percentage flowering or fruiting for a given month versus rainfall during the previous month. Significance was accepted if probability was ≤ 0.05 in any test.

RESULTS—Climatic Data—Mean daily photoperiod at McAllen, Texas ranged from 10 h and 32 min in December 1998 to 13 h and 45 min in June 1999 (Fig. 2). The study sites differed in latitude from McAllen by less than 15 min (Fig. 1), so photoperiod at the study sites varied only slightly.

Because of the distance between study sites (Fig. 1), it was possible that rain might have occurred at 1 site and not at another. The National Climatic Data Center nearest the study sites was McAllen, Texas (Fig. 1). Consequently, we used data for McAllen, Texas in our rainfall comparisons (Fig. 3), but we also compared these official data with local climatological observer reports for SANWR, Rio Grande City (near CR), and La Joya (near YBT). These comparisons showed that monthly rainfall totals were generally similar among the sites, i.e., less than 1.5 cm difference in all but 3 months. In September 1998, CR received 3.5 cm more rainfall than the other 2 study sites, and in October 1998, CR received 2.6 cm more rain than

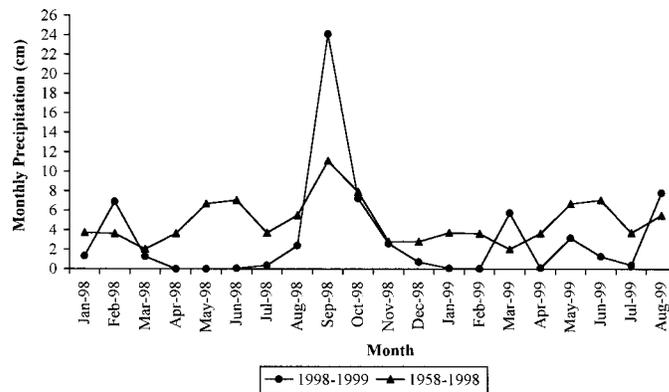


FIG. 3—Monthly precipitation at McAllen, Texas from January 1998 through August 1999 compared to the 40-year monthly precipitation means.

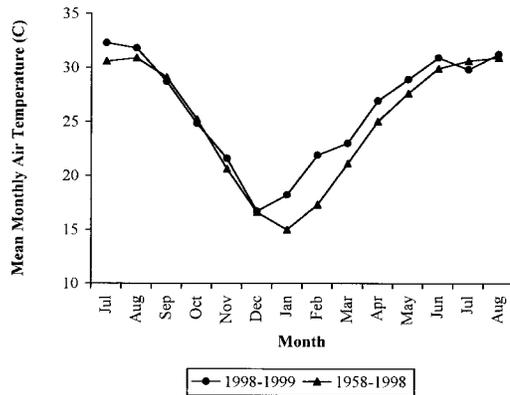


FIG. 4—Mean monthly air temperatures at McAllen, Texas from July 1998 through August 1999 compared with the 40-year mean monthly temperatures.

the other sites. In August 1999, CR received 3.0 cm less rain than the other 2 sites. There was less than 1.0 cm difference in monthly rainfall totals of the SANWR and YBT sites in all months.

Comparison of monthly precipitation for the 6 months preceding the beginning of the study with the 40-year mean (Fig. 3) shows that 5 of the 6 months had precipitation totals lower than the 40-year means for those months. In the 4 months preceding onset of the study, there was a total of only 1.35 cm of rainfall, whereas on average, there is 19.43 cm. Thus, prior to the beginning of the study, rainfall was 93% below average (i.e., drought conditions prevailed). After the study began, rainfall in July and August 1998 continued to be lower than the long-term average (Fig. 3). Rainfall in September 1998 was markedly higher than usual, after which it was equal to or lower than normal in all months except March and August 1999. During the 14 months of the study, the rainfall total was 56.01 cm, which is 20% lower than the long-term average of 69.91 cm for the same time period. If we consider the 6 months preceding the study and the 14 months of study, clearly, drought conditions prevailed during these 20 months.

Mean monthly air temperatures in 1998 and 1999 were equal to or above the long-term averages in all months except July 1999 (Fig. 4). From January through June 1999, mean monthly air temperatures were consistently greater than the long-term means. Freezing temperatures (-1.67°C) occurred at Rio

Grande City, which is near the CR site, on 26 and 27 December 1998, 10 and 11 January 1999, and 13, 14, and 22 February 1999. La Joya (near the YBT site) experienced a low of -1.11°C on 26 December 1998 and a low of 0.56°C on 27 December 1998. A low of 0.0°C occurred at this site on 11 January 1999 and 13 February 1999.

Flowering—On a calendar-year basis, guajillo and huisachillo were the first species to flower (in January 1999; Fig. 5). In February 1999, all 4 *Acacia* species were in flower, but Texas ebony was not. Ebony was seen in flower only in September 1998. The 4 *Acacia* species continued flowering into March, but by April, huisachillo had ceased flowering. The percentage of individuals in each of the species in flower in April was low ($<10\%$ in all cases). No species was in flower in May, but 2.5% of the guajillo flowered in June. Guajillo had the longest flowering period, but the percentage of individuals flowering was consistently low. Each of the other 3 species of *Acacia* flowered for 3 months. The peak of flowering occurred in February in guajillo, black brush, and huisachillo (Fig. 5). In huisache, the peak of flowering occurred in March. For months when 2 or more species were in flower (January, February, March, and April 1999), *G*-tests were performed to determine if there was significant variation among species. There was significant variation among species in February 1999 ($G = 198.686$, $P < 0.001$), March 1999 ($G = 89.650$, $P < 0.001$), and April 1999 ($G = 11.665$, $P < 0.025$). *G*-tests on the monthly percentage of individuals flowering within species among months showed significant variation in huisache ($G = 7.988$, $P < 0.025$), black brush ($G = 17.068$, $P < 0.001$), and huisachillo ($G = 18.418$, $P < 0.001$).

Variation in Flowering Among Sites—There was marked variation in flowering among sites only in guajillo. Guajillo began flowering at the YBT site in January, but did not flower at SANWR until April. Except for guajillo, the differences in onset and duration of flowering among sites involved low percentages of individuals for a month or less. Onset of flowering in huisache was the same at the CR and SANWR sites (i.e., in February), but 5% of the individuals flowered in April at CR, when there were no individuals in flower at SANWR. Black brush was present at all 3 study sites, and onset of flowering was in February at all of the sites. Five

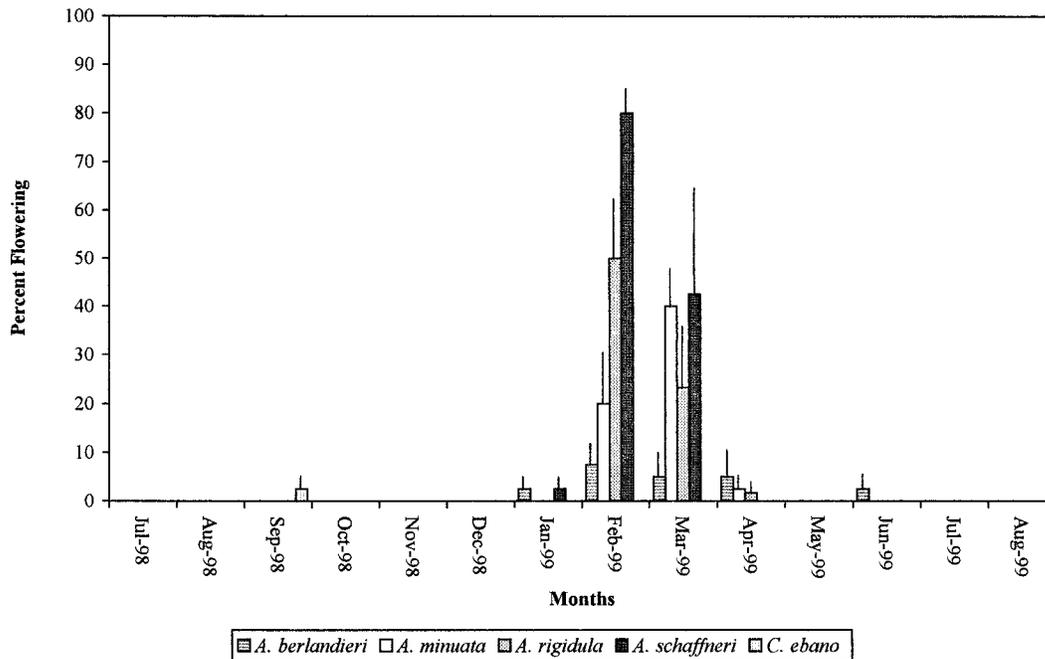


FIG. 5—Percent flowering compared among species for all sites. Sample size for each 2-week census = 20 for *Acacia berlandieri*, *A. minyata*, *A. schaffneri*, and *Chloroleucon ebano*. Sample size for *A. rigidula* = 30 for each census. Means for 2 censuses each month shown by bars. Vertical lines depict 1 SE.

percent of the individuals flowered at SANWR in April, but there was no flowering in black brush at the CR and YBT sites in April.

Five percent of huisachillo at CR were in flower in January, but huisachillo did not flower at YBT until March. Texas ebony flowered at the YBT site in September 1998, but not at SANWR.

Correlation Between Flowering and Climatic Factors—All of the *Acacia* species flowered in winter or spring months, i.e., at low temperatures and increasing photoperiod. However, only 1 correlation was significant (Table 2).

There was a significant positive correlation between precipitation and flowering in huisache.

Texas ebony only flowered in 1 month (September 1998) so it was not possible to calculate a correlation coefficient for flowering and temperature, precipitation, or photoperiod. However, it is noteworthy that the flowering occurred after the heavy rains that fell in September 1998 (Fig. 3).

There was no evidence of lag-time effect of rainfall on flowering. The correlation between percent flowering and rainfall during the previous month was not significant ($P > 0.05$) for

TABLE 2—Correlation coefficient (r) for percent flowering versus mean monthly photoperiod, monthly precipitation, and mean monthly temperature. Student's t -value = t . NS = not significant ($P > 0.05$). Only months when the species were in flower were included in the analyses.

Species	Photoperiod			Precipitation			Temperature		
	r	t	P	r	t	P	r	t	P
<i>Acacia berlandieri</i>	0.334	0.501	NS	-0.007	0.010	NS	0.422	0.658	NS
<i>Acacia minyata</i>	0.298	0.441	NS	0.872	2.519	<0.05	0.095	0.135	NS
<i>Acacia rigidula</i>	-0.070	0.099	NS	0.120	0.171	NS	-0.043	0.061	NS
<i>Acacia schaffneri</i>	-0.096	0.136	NS	0.188	0.271	NS	-0.092	0.131	NS

TABLE 3—Dates of flowering, fruiting, and fruit maturation for *Acacia berlandieri*, *A. minuwata*, *A. rigidula*, *A. schaffneri*, and *Chloroleucon ebano* among sites in the Lower Rio Grande Valley of Texas during 1999. An asterisk indicates that a stage was not seen at a given site. NA = not applicable (these species produce fruits that are indehiscent). CR = Castilla Ranch; SANWR = Santa Ana NWR; YBT = Yturria Brush Tract.

Species	Site	First flowers	First immature fruit	First mature fruit	First dehiscence
<i>A. berlandieri</i>	SANWR	24 April	*	*	*
<i>A. berlandieri</i>	YBT	14 February	27 March	*	*
<i>A. minuwata</i>	CR	13 February	27 March	22 May	NA
<i>A. minuwata</i>	SANWR	28 February	28 March	23 May	NA
<i>A. rigidula</i>	CR	13 February	27 March	8 May	8 May
<i>A. rigidula</i>	SANWR	14 February	13 March	9 May	22 May
<i>A. rigidula</i>	YBT	14 February	28 March	9 May	23 May
<i>A. schaffneri</i>	CR	16 January	27 February	22 May	NA
<i>A. schaffneri</i>	YBT	14 February	27 February	5 June	NA
<i>C. ebano</i>	SANWR	*	8 November	9 May	*
<i>C. ebano</i>	YBT	12 September	25 September	*	*

each of the *Acacia* species (*A. berlandieri*, $r = -0.154$, 4 *df*; *A. minuwata*, $r = -0.183$, 1 *df*; *A. rigidula*, $r = -0.829$, 1 *df*; *A. schaffneri*, $r = -0.841$, 1 *df*). Texas ebony was in flower for only 1 month, so it could not be tested for lag-time rainfall effect.

Fruiting—Dates when various stages of fruit development were first observed are provided in Table 3. In guajillo, flowers were produced at both sites where the species occurred, and immature fruit were developed at the YBT site. However, no fruit developed at the SANWR site, and the immature fruit at the YBT site failed to reach maturity. In huisache, fruit development began in late March and took about 56 days to develop to maturity. Fruit produced in 1998 was retained on the trees through November 1998. Black brush had immature fruit by mid to late March and took about 39 days to develop mature fruit. The fruit began to dehisce soon after maturing (Table 3). Huisachillo had immature fruit in late April and took about 84 days to develop mature fruit. Fruit produced in 1998 were retained on the trees through February 1999. Texas ebony had immature fruit in early November and it took 182 days for the fruit to reach maturity at SANWR.

The percentage of fruiting is compared among species in Fig. 6. Guajillo had mature, unopened fruit on the trees in only 3 of the 14 months of the study. Conversely, Texas ebony had mature fruit in 13 of the months. Hui-

sachillo had mature fruit present in 12 months, and black brush and huisache had mature fruit on the trees in 9 months. All of the *Acacia* species had dropped their fruit before new fruits were developed, but Texas ebony had mature fruit from the previous year and developing fruit on the same individuals. Few individuals of any species had fruit from November through April.

There were significant differences among species in percentage of individuals with mature fruit in all months except November 1998, February 1999, and April 1999. If Texas ebony is removed so that the comparisons are only among the *Acacia* species, the results are the same, i.e., there are significant differences among species in the percentage of individuals with mature fruit in all months except November 1998, February 1999, and April 1999.

There was significant variation in fruiting within species among sites. For example, mature fruits were never seen in guajillo at SANWR, but mature fruits were present at YBT in July, August, and November 1998 (developed from flowering that occurred prior to the beginning of this study) (Table 4). In huisache, the percentage of individuals with mature fruit was significantly greater ($\chi^2 = 4.00$, $P < 0.05$) at SANWR than at CR in all months during which fruit was present except for September 1998 and May 1999 (Table 4). Similarly, there was significant variation in fruiting of black

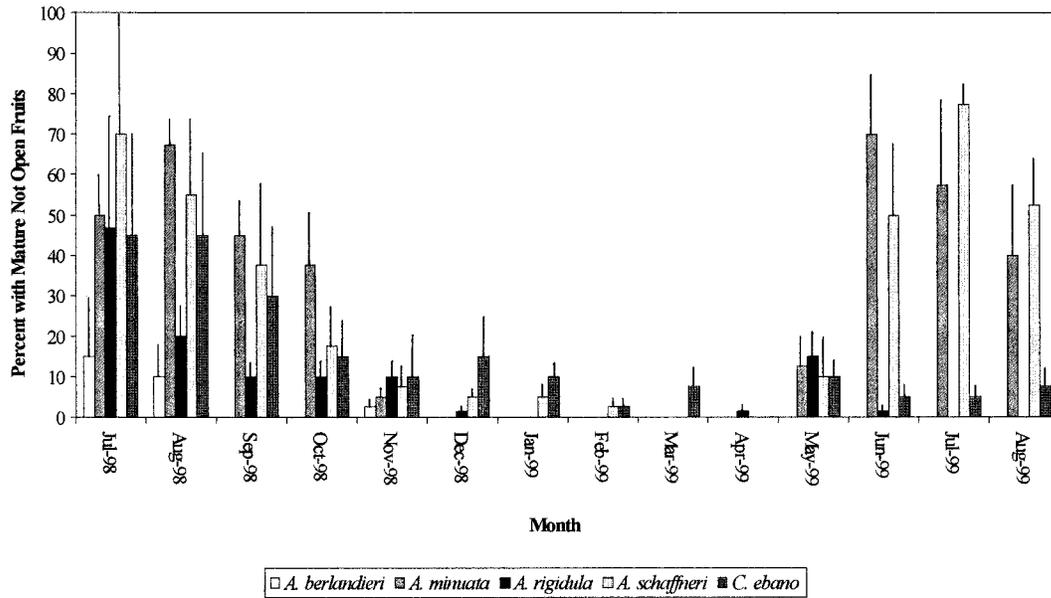


FIG. 6—Percent fruiting compared among species for all sites. Sample size for each 2-week census = 20 for *Acacia berlandieri*, *A. minuta*, *A. schaffneri*, and *Chloroleucon ebano*. Sample size for *A. rigidula* = 30 for each census. Means of 2 censuses each month shown by bars. Vertical lines depict 1 SE.

TABLE 4—Comparison of percentage of individuals with mature (but not open) fruit among species and locations in the Lower Rio Grande Valley of Texas from July 1998 through August 1999.

Species and locations	Jul 98	Aug 98	Sep 98	Oct 98	Nov 98	Dec 98	Jan 99	Feb 99	Mar 99	Apr 99	May 99	Jun 99	Jul 99	Aug 99
<i>Acacia berlandieri</i>														
Santa Ana NWR					5									
Yurria Brush Tract	30	20												
<i>Acacia minuta</i>														
Castilla Ranch	40	60	40	15							15	45	20	10
Santa Ana NWR	60	75	50	60	10						10	95	95	70
<i>Acacia rigidula</i>														
Castilla Ranch	30	25	10								25			
Santa Ana NWR	10	5	5	10	5						5			
Yurria Brush Tract	100	30	15	20	25	5					15	5		
<i>Acacia schaffneri</i>														
Castilla Ranch	40	25	5								20	80	80	30
Yurria Brush Tract	100	85	70	35	15	10	10	5				20	75	75
<i>Chloroleucon ebano</i>														
Santa Ana NWR	20	15									20	10	10	15
Yurria Brush Tract	70	75	60	30	20	30	20	5	15					

TABLE 5—Correlation coefficients (r) for percent individuals with mature but not open fruits versus mean monthly photoperiod, monthly precipitation, and mean monthly temperature. Student's t -value = t . NS = not significant ($P > 0.05$). Correlation coefficients are based on sample sizes of 14 (14 months of fruiting data).

Species	Photoperiod			Precipitation			Temperature		
	r	t	P	r	t	P	r	t	P
<i>Acacia berlandieri</i>	0.327	1.199	NS	-0.194	0.685	NS	0.438	1.688	NS
<i>Acacia mininata</i>	0.701	3.405	<0.01	0.207	0.733	NS	0.804	4.684	<0.001
<i>Acacia rigidula</i>	0.344	1.269	NS	-0.011	0.038	NS	0.459	1.790	NS
<i>Acacia schaffneri</i>	0.715	3.543	<0.01	0.081	0.282	NS	0.782	4.346	<0.05
<i>Chloroleucon ebano</i>	0.226	0.803	NS	0.251	0.898	NS	0.390	1.467	NS

brush among the 3 sites where it occurred in all months during which fruiting was seen ($\chi^2 = 10.97$, $P < 0.005$) except for September 1998 (Table 4). YBT had the highest percent fruiting of black brush in 1998, but in May 1999, the CR site had the highest percentage of fruiting. Huisachillo had significantly greater percentage fruiting from July 1998 through February 1999 at the YBT site ($\chi^2 = 5.00$, $P < 0.05$), but in May and June 1999, the CR site had significantly higher fruiting ($\chi^2 = 20.00$, $P < 0.001$ in May; $\chi^2 = 36.00$, $P < 0.001$ in June) (Table 4). In July 1999, there was no significant variation between the sites, and in August 1999, the YBT site had the greater percentage of individuals with fruit ($\chi^2 = 19.29$, $P < 0.001$). In Texas ebony, there was significant variation between sites in the percentage of individuals with mature fruit in each of the months ($\chi^2 = 5.00$, $P < 0.05$) (Table 4).

Correlation Between Fruiting and Climatic Factors—Correlations between percent fruiting and photoperiod, monthly precipitation, and mean monthly temperature showed that significant positive relationships were present in huisache and huisachillo for percent fruiting and photoperiod and temperature (Table 5). In addition, there was a significant positive correlation in Texas ebony between the percentage of individuals with mature open (dehisced) fruit and precipitation ($r = 0.729$, $t = 3.689$, $P < 0.05$, 12 df). There was no evidence of a time-lag effect of precipitation on percentage of individuals with mature but unopened fruit. The correlation was not significant for any species (*A. berlandieri*, $r = -0.936$, 1 df , $P > 0.2$; *A. mininata*, $r = -0.061$, 7 df , $P > 0.5$; *A. rigidula*, $r = -0.352$, 6 df , $P > 0.2$; *A. schaffneri*, $r =$

-0.121 , 9 df , $P > 0.5$; *C. ebano*, $r = -0.191$, 11 df , $P > 0.5$).

DISCUSSION—Rainfall in the 6 months prior to the beginning of this study was 93% below average, and during the 14 months of study, rainfall was 20% below the long-term average. Thus, the phenology we observed cannot be considered typical for the species studied. Nevertheless, it is important to know how climatic variation affects phenology, and this study provides such information for a drought year. However, caution must be exercised when attempting to formulate generalizations based on these data.

Having recording rain gauges at each of the study sites might have improved the information on the relationship of rainfall and flowering and fruiting, but the costs were prohibitive for us. Local climatological reports showed that generally there was less than 1.5 cm difference in the rainfall total for a month among the 3 sites.

There was broad overlap in the flowering periods of the *Acacia* species. All 4 species flowered in February and March. Texas ebony flowered only in September, when none of the *Acacias* were in flower. The flowering durations that we observed differed considerably from reports in floras. For example, Jones (1975) reported that guajillo can be found in flower from February through December (i.e., in every month except January) in the Coastal Bend area of southern Texas. We found guajillo in flower from January through April and then in June. Thus, the flowering we observed was for a shorter time. Correll and Johnston (1970) reported guajillo flowers in spring and

often again later, following rains in drought years. Local rainfall might have been responsible for the flowering that we observed in June.

Both Everitt and Drawe (1993) and Taylor et al. (1999) reported huisache flowers from February through March in southern Texas, while Jones (1975) indicated a 2 month longer duration of January through April. Vora (1990) reported huisache flowered at SANWR from January through March. We found that huisache flowered from February through April. Thus, there was greater similarity in our observations and published reports of flowering in huisache than there was in comparisons for guajillo. Published reports for black brush all showed flowering begins in February, but they differed in the termination of flowering. Jones (1975) and Taylor et al. (1999) indicated flowering ends in April, while Everitt and Drawe (1993) and Correll and Johnston (1970) reported that flowering extends into July. We found that flowering extended from February through April; thus, our data support those of Jones (1975) and Taylor et al. (1999). Only Jones (1975) gave a duration for flowering for huisachillo (February through April). Both Correll and Johnston (1970) and Everitt and Drawe (1993) stated huisachillo flowers in spring and might flower again later in drought years. We found flowering began and ended a month earlier than reported by Jones (1975).

The greatest differences in our observations of flowering and published reports occurred in Texas ebony. Both Correll and Johnston (1970) and Everitt and Drawe (1993) reported that flowering in Texas ebony principally takes place in April through July, but rarely might extend to November. Jones (1975) reported flowering occurs from May through October, and Taylor et al. (1993) found that flowering extended from June through August. Vora (1990) reported that Texas ebony flowered at SANWR from May through September. We observed flowering only in September, but flowering occurs for a longer time in the area because we found mature, unopened fruit present at SANWR from May through August 1999. These fruit must have developed from a brief flowering that occurred in a 2-week interval between our censuses in late April and early May. The combined data from published sources suggests flowering generally is initiated

later in the year in Texas ebony (April) than in the *Acacia* species (January or February). Texas ebony might have a higher threshold of temperature and require a longer photoperiod for flowering than the *Acacia* species.

The study by Vora (1990) was based on 2 years of data. All the other sources compared above were floras or identification books. The periods over which flowering data were obtained were not given. Data they included might have been based on herbarium records, published work, personal observations, or a combination of these.

Observations that flowering in *Acacia* species often occurs later in a drought year after rains (Correll and Johnston, 1970; Everitt and Drawe, 1993) and the absence of a correlation between photoperiod and flowering in any of the species in this study suggest photoperiod does not limit flowering. However, *Acacia* species other than guajillo did not flower at photoperiods above 12.5 h of light, and all of the *Acacia* species flowered when photoperiod was increasing. Conversely, literature records and our observations suggest that Texas ebony flowers at peak or declining photoperiod. Flowering at increasing photoperiods might be a generic characteristic of acacias. Milton and Moll (1982) reported that 3 species of Australian acacias flowered during winter and spring in South Africa. This pattern also held for arid and semi-arid Australian acacias of temperate origin (Friedel et al., 1994). We need several years of data on flowering to establish the relationship between flowering and photoperiod in southern Texas acacias.

Except for guajillo, *Acacia* species we studied flowered at mean air temperatures below 25°C, while literature records and our observations suggest Texas ebony flowers at mean air temperatures above about 26°C. Thus, air or soil temperature might be a major factor separating the flowering of black brush, huisache, and huisachillo from that of Texas ebony. Because photoperiod and temperature vary synchronously, it is difficult to determine their separate influences. Lonard and Judd (1989) suggested that photoperiod and temperature might act together to influence phenology.

Vora (1990) reported that plant growth and reproduction in the LRGV were keyed to rainfall and soil moisture for most of the 19 species he studied. Similarly, statements by Correll and

Johnston (1970) and Everitt and Drawe (1993) that flowering in guajillo and huisachillo might occur after the usual flowering period following rains in drought years suggest that rainfall might profoundly affect the flowering of acacias and Texas ebony. Such was not the case for acacias in this study. The heavy rains in September 1998 did not trigger flowering in any of the *Acacia* species. The low percentage of flowering seen in guajillo in June 1999 after cessation of flowering in late April 1999 could not be tied to a rainfall event. Conversely, the low percentage of flowering in Texas ebony in September 1998 corresponded with the heavy rainfall occurring that month.

The significant positive correlation between percentage of individuals flowering and monthly precipitation in huisache shows that rainfall during the flowering period can increase flower production. Similarly, heavy rains in spring near the end of the usual flowering period might lengthen flowering in acacias or increase the number of flowers per individual.

The drought apparently influenced the timing and duration of flowering slightly in the *Acacia* species during the period of observation in this study and it might have been responsible for the shortness and low percentage of flowering in Texas ebony.

Hypothesis 1 was falsified. There were significant differences in the flowering and fruiting phenologies of *Acacia* species. Guajillo had a longer flowering period than the other acacias, with a low percentage of individuals in flower at any point in time. Huisache, huisachillo, and black brush were similar in the timing of flowering, but there were significant differences among the species in the level of flowering. There were significant differences among species in the percentage of shrubs and trees with mature fruit in all but 3 of the 14 months. *Acacia* species also differed in the duration that mature fruit was present on the plants.

Variation in flowering phenology within *Acacia* species among sites was slight except for guajillo. Variation in fruiting phenology within species among locales was greater and involved all 4 *Acacia* species and Texas ebony. Causes of this variation are likely complex and involve interactions of temperature, soil composition, and soil moisture.

Hypothesis 2 was supported. There was great

difference in the timing of flowering of Texas ebony compared to the *Acacia* species, and Texas ebony was apparently more affected by the drought. We suggest that water deficiency in the magnitude observed in this study does not prevent or delay flowering in the *Acacia* species, but it might slow or prevent fruit development.

Hypothesis 3 was falsified. There was a significant positive correlation between monthly rainfall and percentage of individuals in flower in huisache. The hypothesis also was falsified for correlation between the percentage of individuals with mature fruit and photoperiod and temperature. There was a significant positive correlation in Texas ebony between the percentage of trees with mature, open (dehiscid) fruit and precipitation. We suggest that the extremely thick woody legume of Texas ebony requires heavy rainfall to effect dehiscence and that this anatomical trait, therefore, ensures that seeds are dropped at a time propitious for germination (i.e., when there is sufficient soil moisture to support germination and seedling growth).

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