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## Flowering phenology of six woody plants in the northern Sonoran Desert

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BOWERS, JANICE E. (U.S. Geological Survey, 1675 W. Anklam Road, Tucson, AZ 85745) AND MARK A. DIMMITT (Arizona-Sonora Desert Museum, 2021 N. Kinney Road, Tucson, AZ 85743). Flowering phenology of six woody plants in the northern Sonoran Desert. Bull. Torrey Bot. Club 121: 215–229, 1994. —Climatic and flowering data from a site in the northern Sonoran Desert of southern Arizona were used to define flowering triggers and developmental requirements for 6 woody plants. These formulations were then used to predict flowering dates at a second northern Sonoran Desert site. It was determined that flowering is triggered by rain in *Larrea tridentata* (DC.) Cov., *Fouquieria splendens* Engelm., *Encelia farinosa* A. Gray, *Ambrosia deltoidea* (A. Gray) Payne and *Acacia constricta* Benth., and that flowering is triggered by photoperiod in *Cercidium microphyllum* (Torr.) Rose & Johnst. The base temperature for floral development in *L. tridentata*, *F. splendens*, *E. farinosa*, *A. deltoidea* and *C. microphyllum* is about 10°C. Their mean degree-day requirements range from 414 to 719. *Acacia constricta* requires 522 degree-days above 15°C. Minimum rainfall triggers varied from 9 mm for *Ambrosia* to 20 mm for *Encelia*. Flowering time in *C. microphyllum* may reflect phylogenetic constraints, while flowering time in *F. splendens* may be strongly influenced by pollinator availability. Flowering times of the remaining species seem constrained more by climate than by biotic considerations such as phylogeny, seed germination and competition for pollinators.

Key words: phenology, Sonoran Desert, *Acacia constricta*, *Ambrosia deltoidea*, *Cercidium microphyllum*, *Encelia farinosa*, *Fouquieria splendens*, *Larrea tridentata*.

Plant phenology—seasonal patterns of leafing, flowering and fruiting in relation to climate—has been a topic of scientific study since the eighteenth century (Aitken 1974). Phenology is of great interest in agriculture, where the timing of flower and fruit production can be critical in determining crop yield (Loomis and Connor 1992). It is also a topic of more-than-passing ecological interest, as the timing of flowering and fruiting affects critical aspects of plant life cycles, particularly pollination and seed dispersal, thus setting the stage for later germination and recruitment.

Janzen (1967) has argued that in the tropical dry forests of Central America, dry-season flowering of tree species is “a result of selection for sexual reproduction at the most opportune time in the year, rather than the result of immutable physiological processes which can only occur at that time of year.” He regarded sexual selection as the “ultimate cause” of flowering time, en-

vironmental triggers as the “proximate cause” (Janzen 1967). In the North American deserts, where germination, recruitment and other aspects of plant life cycles are adapted to take advantage of narrow climatic windows (Shreve 1917; Sheps 1973; Sherbrooke 1977, 1989; Ackerman 1979), one might expect that flowering phenology would also be climatically constrained. Most of the dominant species in the northern Sonoran Desert do indeed flower when seasonal soil moisture is greatest (Simpson 1977; Solbrig and Yang 1977). It has been suggested, however, that the flowering time of certain Sonoran Desert dominants is determined by other considerations: pollinator availability for *Fouquieria splendens* (Waser 1979), for instance, or seed germination for phreatophytes and succulents (Solbrig and Yang 1977). Kochmer and Handel (1986) demonstrated that family membership strongly constrains flowering time in the South Carolina flora. In the northern Sonoran Desert, where floristic elements from cool-temperate and warm-subtropical climates mingle (McLaughlin 1989), it is not clear which should dominate—phylogenetic or climatic constraints—in determining phenological patterns. It is also not clear whether species that have evolved under similar climatic regimes will share the same phenological triggers; that is, flower in response to the same environmental cues.

<sup>1</sup> Raymond M. Turner suggested the Tumamoc Hill phenology study. Nohl Lyons helped with computer software. Steven P. McLaughlin, David A. Palzkill, Elizabeth A. Pierson and Raymond M. Turner read the manuscript and offered many helpful comments and suggestions.

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Phenological triggers can be regarded as switches that break bud dormancy and start developmental processes such as leafing and flowering. Once set in motion, these processes advance as a function of temperature, daylength or some combination of the two (Loomis and Connor 1992). Only three environmental triggers for flowering have been identified: photoperiod, temperature and moisture (Rathcke and Lacey 1985; Loomis and Connor 1992). Rains presumably operate by raising soil moisture to some threshold value, at which point, given suitable temperatures, bud dormancy is broken and flower development is initiated. Rainfall amounts are but useful proxies for soil moisture measurements, which often are not available. The flowering triggers for a number of plants native to the eastern United States are known (Jackson 1966), as are those for many crop and ornamental plants (for example, Caprio 1973; Wielgolaski 1973). With a few exceptions, the flowering triggers for plants native to arid regions of the southwestern United States have been examined only in general terms.

In phenological analysis, the trigger date serves as the starting point for calculating the heat units needed for floral development. Heat units are often expressed as degree-days, that is, as the sum of mean daily temperatures above an appropriate base temperature, or threshold. The many variations of this basic method include: 1) summing degree-hours (Lindsey and Newman 1956); 2) summing maximum daily temperature or minimum daily temperature (Bassett et al. 1961); 3) summing the products of mean daily temperature and solar radiation in langley's/day (Caprio 1973); and 4) summing the products of mean daily temperature and hours of daylight above an appropriate threshold (Loomis and Connor 1992). An analysis of several of these methods (White 1979) suggests that while their accuracy does indeed vary, the variation is small and is likely to be of greatest concern in agricultural work, where extremely precise formulation of developmental requirements is desirable.

Table 1 lists 39 Sonoran Desert plant species for which phenological information is available. All these studies were qualitative rather than quantitative. The same is also true of most phenological studies from the Great Basin Desert (Everett et al. 1980; West and Gasto 1978), the Mojave Desert (Beatley 1974; Ackerman et al. 1980), and the Chihuahuan Desert (Kemp 1983). The work of Turner and Randall (1987), which used multiple regression with varying success to

predict leafing and flowering based on rainfall and mean monthly air temperature, is a notable exception.

Our first goal in this study was to define as precisely as possible the phenological triggers and developmental requirements for selected Sonoran Desert plants. We used phenological data gathered at one Sonoran Desert site to determine triggers and heat sums, then, with that information, predicted flowering dates at another Sonoran Desert site. We hypothesized that plants flowering only once a year might be triggered by photoperiod, temperature or some combination of the two (restricted bloomers), and that plants capable of flowering at more than one season would be triggered by rain (repeat bloomers). We were reluctant to invoke a photoperiod or temperature trigger for repeat bloomers because there is no simple scheme that accounts for spring bloom under increasing temperatures and daylengths as well as for autumn bloom under decreasing temperatures and daylengths. An alternative model suggests that repeat bloomers respond in spring to a temperature trigger but in summer to a moisture trigger (Yang and Abe 1974). Considering this explanation needlessly complex, we reasoned that repeat bloomers would flower in response to rain triggers delivered within a certain range of temperatures.

Our second goal was to examine phenological patterns of woody dominants in the northern Sonoran Desert. We expected that the phenological triggers, once identified, would reflect the geographic origins of our species and at the same time accommodate their current biseasonal precipitation regime. We further expected that, in this arid region, the distinction between proximate causes and ultimate causes might prove untenable.

**Study Sites.** In the 1980s, we undertook independent phenological studies, one on Tumamoc Hill, the other at the Arizona-Sonora Desert Museum. The Tumamoc Hill study followed 6 native species from 1985 through 1989: *Larrea tridentata* (DC.) Cov., *Fouquieria splendens* Engelm., *Encelia farinosa* A. Gray, *Acacia constricta* Benth., *Cercidium microphyllum* (Torr.) Rose & Johnst. and *Ambrosia deltoidea* (A. Gray) Payne. The Desert Museum study followed 400 native and cultivated species for all or some of the years from 1983 to 1989 (Dimmitt, unpub. data).

Both sites are in the Tucson Mountains, Pima County, Arizona. Tumamoc Hill is a rocky knoll

Table 1. Phenological studies of Sonoran Desert plants.

Species	Source
<i>Acacia constricta</i>	Shreve 1951; Solbrig and Yang 1977
<i>Acacia greggii</i>	Shreve 1951; Solbrig and Yang 1977
<i>Ambrosia deltoidea</i>	Shreve 1951; Halvorson 1970; Solbrig and Yang 1977
<i>Ambrosia dumosa</i>	Shreve 1951; Humphrey 1975
<i>Bursera hindsiana</i>	Humphrey 1975
<i>Bursera microphylla</i>	Shreve 1951; Humphrey 1975
<i>Calliandra eriophylla</i>	Humphrey 1975
<i>Carnegiea gigantea</i>	Johnson 1924; Shreve 1951; Steenberg and Lowe 1977
<i>Cercidium floridum</i>	Turner 1963; Humphrey 1975; Solbrig and Yang 1977
<i>Cercidium microphyllum</i>	Shreve 1951; Turner 1963; Halvorson 1970; Solbrig and Yang 1977
<i>Cordia sonora</i>	Shreve 1951
<i>Echinocereus</i> sp.	Halvorson 1970
<i>Encelia farinosa</i>	Shreve 1951; Humphrey 1975; Solbrig and Yang 1977
<i>Eriogonum fasciculatum</i>	Halvorson 1970
<i>Errazurizia megacarpa</i>	Humphrey 1975
<i>Erythrina flabelliformis</i>	Conn and Snyder-Conn 1981
<i>Euphorbia misera</i>	Humphrey 1975
<i>Ferocactus acanthodes</i>	Halvorson 1970
<i>Forchammeria watsoni</i>	Shreve 1951
<i>Fouquieria columnaris</i>	Humphrey 1974, 1975
<i>Fouquieria splendens</i>	Darrow 1943; Shreve 1951; Humphrey 1975; Solbrig and Yang 1977; Waser 1979
<i>Frankenia palmeri</i>	Humphrey 1975
<i>Ipomoea arborescens</i>	Shreve 1951
<i>Jatropha cardiophylla</i>	Solbrig and Yang 1977
<i>Jatropha cuneata</i>	Humphrey 1975
<i>Justicia californica</i>	Humphrey 1975
<i>Krameria grayi</i>	Halvorson 1970; Solbrig and Yang 1977
<i>Larrea tridentata</i>	Shreve 1951; Halvorson 1970; Yang and Abe 1974; Humphrey 1975; Solbrig and Yang 1977; Abe 1982
<i>Lophocereus schottii</i>	Humphrey 1975
<i>Lycium fremontii</i>	Humphrey 1975
<i>Olneya tesota</i>	Shreve 1951; Turner 1963; Humphrey 1975; Solbrig and Yang 1977
<i>Opuntia acanthocarpa</i>	Halvorson 1970
<i>Opuntia bigelovii</i>	Halvorson 1970; Humphrey 1975
<i>Opuntia phaeacantha</i>	Halvorson 1970
<i>Pachycereus pringlei</i>	Shreve 1951; Humphrey 1975
<i>Prosopis glandulosa</i>	Sharifi et al. 1983; Nilsen et al. 1987
<i>Prosopis velutina</i>	Glendening and Paulsen 1955; Turner 1963; McMillan and Peacock 1964; Halvorson 1970; Solbrig and Cantino 1975
<i>Simmondsia chinensis</i>	Gentry 1958; Halvorson 1970; Humphrey 1975; Solbrig and Yang 1977; Dunstone 1980; De Oliveira 1983; Benzioni and Dunstone 1985
<i>Solanum hindsianum</i>	Humphrey 1975

of andesitic basalt south and east of the main range (Fig. 1). It reaches an elevation of 948 m, with an elevational range of 245 m. The Desert Museum grounds rise from 826 to 882 m in elevation and are on gently sloping, gravelly terrain underlain by sedimentary bedrock.

The climate of both sites is arid. The average annual rainfall during the period of study was 274 mm at Tumamoc Hill, 343 mm at the Desert Museum. About 27 percent of the annual total arrives in winter (December–March), about 51 percent in summer (July–September) (Bowers and Turner 1985). April, May and June are often without rain. Maximum temperatures in sum-

mer frequently exceed 40°C. Winter minima during the period of study were –4°C at Tumamoc Hill, –6°C at the Desert Museum. From 1985 to 1989, the average daily temperature at Tumamoc Hill was 22.8°C. At the Desert Museum, it was 21.7°C during 1983–1987 and 1989.

Vegetation of the Tucson area is typical of the Arizona Upland subdivision of the Sonoran Desert as defined by Shreve (1951). Dominant plants on the rocky slopes of Tumamoc Hill include the 6 species listed above as well as *Carnegiea gigantea*, *Opuntia engelmannii*, *Opuntia versicolor* and *Lycium berlandieri*. The vegetation of the gentle, gravelly slopes on the Desert Museum site

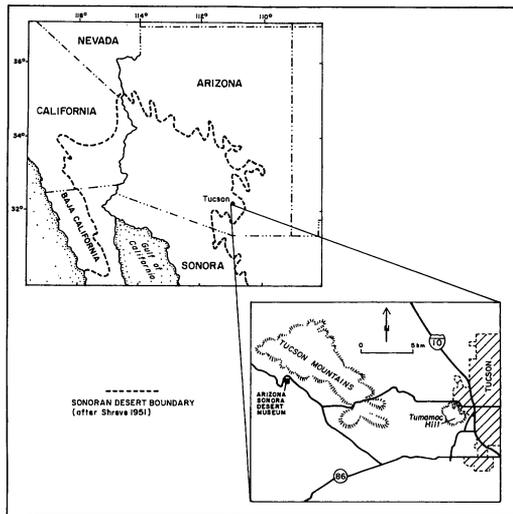


Fig. 1. Location and principal geographic features of the Desert Museum and Tumamoc Hill study sites.

is similar except for the addition of *Simmondsia chinensis* and *Olneya tesota* and the lower frequency of *Acacia constricta*.

**Study Species.** *Larrea tridentata* (Zygophyllaceae), an evergreen shrub, flowers in spring in the Mojave Desert and the western Sonoran Desert, where winter rain predominates (Oechel et al. 1972; Boyd and Brum 1983) and in both spring and summer in the eastern Sonoran Desert, where rain is biseasonal (Barbour et al. 1977). Flowering triggers suggested for *Larrea* have been rainfall at all seasons (Shreve 1951; Humphrey 1975; Barbour et al. 1977; Abe 1982), and temperature in spring, moisture in summer (Yang and Abe 1974). *Fouquieria splendens* (Fouquieriaceae) is a drought-deciduous shrub. In the Sonoran Desert, it blooms primarily in spring (March–May) (Waser 1979), but massive autumn flowering occurs under some circumstances (Felger 1980), and winter (January–February) flower is not unknown. Munz (1974) reported flowering in the Mojave Desert from March–July. In the northern Chihuahuan Desert, *Fouquieria* flowers from March–June (Correll and Johnston 1970), occasionally in autumn (Loughmiller and Loughmiller 1984). Photoperiod has been suggested as a likely flowering trigger (Humphrey 1975). *Encelia farinosa* (Asteraceae), a drought-deciduous shrub, blooms mainly in spring (February–May), and given enough rain, from October–January as well. *Acacia constricta* (Fa-

baceae) is a drought-deciduous shrub that blooms in late spring (April–June) and again in summer/autumn (July–October). Floral buds may appear in November or December but rarely receive enough warmth to develop into flowers. *Ambrosia deltoidea* (Asteraceae), a drought-deciduous shrub, flowers early in the spring, usually in February and March. *Cercidium microphyllum* (Fabaceae) is a drought-deciduous tree with smooth, green bark on all branches and twigs. Flowering is in late April and early May. Photoperiod has been suggested as a flowering trigger (Turner 1963).

**Methods.** DETERMINING PHENOLOGICAL TRIGGERS AND DEVELOPMENTAL REQUIREMENTS. *Data Collection.* At Tumamoc Hill, Bowers tagged and numbered 10 individuals each of *C. microphyllum*, *F. splendens*, *E. farinosa*, *A. deltoidea*, *A. constricta*, and *L. tridentata*. The plants grew near the weather station at an elevation of 814 m on a gently sloping bench with a northeast aspect. She made weekly observations during spring and the summer rainy season, less frequent observations at other times of year. Observations, made on the same branch each time, were qualitative records of various phenological stages. For flowers, these were bud initiation, buds present, flowers present, peak flower, none (all flowers gone). For fruits these were abortive, setting, maturing, dropping, none. For leaves these were bud initiation, new leaves, full leaf, leaflets dropping, leaves dropping, none.

At the Desert Museum, Dimmitt and assistants made phenological observations 4 times each month on plant populations located near the weather station at an elevation of about 850 m. His qualitative records of phenological stages, made on irrigated and non-irrigated plants, were population sparsely budding, entire population budding, population sparsely flowering, entire population flowering, population sparsely fruiting, entire population fruiting, population sparsely in leaf, entire population in leaf, population with sparse leaf fall, entire population with leaves falling. Our analysis used data from non-irrigated plants only.

At both sites, rainfall and daily maximum and minimum air temperatures were recorded. We used climatic and flowering data from Tumamoc Hill to define flowering triggers and developmental requirements for the 6 species listed above. With these formulations, we then used climatic data from the Desert Museum to predict flowering dates there.

*Data Analysis.* Phenological analysis is necessarily empirical (Loomis and Connor 1992) and involves comparing the date of flower from year to year with climatic conditions in each year. Although for most species the date of flower will vary from one year to the next, the temperature sum required for flowering should be about the same in every year. If the date of trigger and the date of flower are known, the temperature sum can be readily calculated. If the temperature sum and the date of flower are known, the date of trigger can also be calculated. We knew neither the temperature sum nor the date of trigger for any of our 6 species. Our method, therefore, involved selecting a range of appropriate triggers, then calculating the temperature sum from each trigger to the date of flower. We reasoned that valid triggers would produce temperature sums that converged toward the same value year after year, while spurious triggers would produce values that varied greatly from one year to the next.

Our process of trigger selection is discussed in detail below. For each of our 6 species, we calculated 5 heat sums from the date of each potential trigger to the date of flower as follows:

$$\Sigma (T_d - T_b),$$

where  $T_d$  was the mean daily temperature and  $T_b$  was one of 5 base temperatures. The base temperatures, calculated for every day of record from May 1984–December 1989, were:

- a) the average daily temperature above 0°C  
 $[(T_{\max} + T_{\min}) \div 2]$ ;
- b) the average daily temperature above 5°C  
 $[(T_{\max} + T_{\min}) \div 2 - 5]$ ;
- c) the average daily temperature above 10°C  
 $[(T_{\max} + T_{\min}) \div 2 - 10]$ ;
- d) the average daily temperature above 15°C  
 $[(T_{\max} + T_{\min}) \div 2 - 15]$ ;
- e) the average daily temperature above 20°C  
 $[(T_{\max} + T_{\min}) \div 2 - 20]$ .

If  $T_d < T_b$ , no thermal time was accumulated. For flower dates, we typically used the first date when at least 3 of 10 plants were in bloom. Occasionally, it was necessary to interpolate between observation dates to obtain a meaningful flowering date.

To identify the best base temperature for each species, we used the "least variability method" (Arnold 1959), which involves calculating temperature sums above several different bases. The sums above a given base are averaged for the period of record; the base temperature giving the smallest standard deviation and coefficient of variation is considered to be the appropriate threshold (Arnold 1959).

This process produced three results: 1) a range of triggers capable of initiating flower development, 2) the base temperature below which flower development does not occur, and 3) the mean heat sum required for development after the trigger.

*Rainfall Triggers.* We searched for potential rainfall triggers for all 6 species. We did not expect to find them in *Ambrosia* and *Cercidium*, but did the analysis as a check on our original assumptions. We considered all rains  $\geq 5$  mm as potential triggers. This value is much smaller than the moisture threshold of 25 mm reported for Mojave Desert plants (Beatley 1974) and for trees of tropical dry forest (Opler et al. 1976); however, we did not want to dismiss the possibility that relatively small rains might be effective triggers. When rain fell on several consecutive days, we used the cumulative total as the trigger. For spring-flowering plants, we looked for rain and photoperiod triggers in the preceding autumn and winter (October–February). For summer-flowering plants, we looked for rain triggers in the month before bloom. When 2 or more different rain events seemed equally likely to have triggered a given flower event, we calculated heat sums above the 5 base temperatures for each one, then selected the trigger that produced the base temperature with the lowest standard deviation and coefficient of variation.

*Photoperiod Triggers.* We searched for photoperiod triggers for *Cercidium* and *Ambrosia*, and, as a check on our original assumptions, for *Fouquieria*, as well. First we determined daylength for every day of the year at Tucson, Arizona (about 32°N), by interpolating between the daylength values for 30°N and 35°N given in the Smithsonian Meteorological Tables (List 1951). We selected as photoperiod triggers the following dates for *A. deltoidea*: December 30 (daylength of 10 hours), January 15 (10.21 hours) and February 1 (10.66 hours). For *Cercidium* and *Fouquieria*, which flower somewhat later, we used February 1, February 15 (11.03 hours), March 1 (11.50 hours), and March 15 (11.95 hours).

*Temperature Triggers.* As noted above, winter dormancy of many plants in cold-temperate regions is broken when the mean daily temperature reaches a certain value ( $-0.6^\circ\text{C}$  in the case of *Syringa vulgaris*) (Caprio 1973). In the Seattle-Tacoma area, where the mean daily temperature in winter does not fall below  $-0.6^\circ\text{C}$ , Caprio calculated cumulative degree-days for *Syringa*

*vulgaris* from the end of dormancy, about November 30 (Caprio 1973). In the northern Sonoran Desert, where many winter days are warm enough for growth, it is difficult to find a starting point for the calculation of degree-days for spring-flowering plants. At the same time, the end of dormancy coincides with the beginning of the rainy season, making it impossible to separate the effect of temperature from that of moisture. Because the interactive effects of temperature and moisture seem best suited for laboratory studies, and because of the difficulty in selecting a starting point for degree-day accumulation, we did not search for potential temperature triggers for our 6 species.

**PREDICTING FLOWER DATES AT THE DESERT MUSEUM.** We used the formulations from the Tumamoc Hill data set to predict flowering dates at the Desert Museum. Given the variability inherent in our data, we predicted a range of flowering dates rather than a single date for each species in each year. We used the mean date  $\pm$  2 standard deviations, which approximates the 95% confidence limits. For example, our formulation for *L. tridentata* suggested that it will flower given a triggering rain of 20 mm and a heat sum thereafter of  $443 \pm 62$  degree-days above  $10^{\circ}\text{C}$  ( $\pm$  2 SD). Examining the Desert Museum weather record, we found a potential rain trigger in a storm of 25 mm on December 6–8, 1986. Summing degree-days above  $10^{\circ}\text{C}$  from the day after this event, we reached the heat sum less 2 SD (381) on April 6, 1987; the mean heat sum (443) on April 12, 1987; and the heat sum plus 2 SD (505) on April 16, 1987. The predicted range of flower, therefore, was April 6–16.

After predicting flower dates for every year of record for all 6 species, we noted for each flowering event at the Desert Museum the first date when the entire population was in flower (full flower). When full flower was not achieved, we noted the first date when some of the population was in flower. Phenological data for *Acacia constricta* were not available for 1988 and 1989, nor for *Ambrosia deltoidea* in 1989. Finally, we compared the predicted dates of flower with the observed dates, then reevaluated our initial formulations.

**Results. DERIVING PHENOLOGICAL FORMULAS ON TUMAMOC HILL.** *Larrea tridentata.* The dates of flower during our study were April 4, 1985; March 31, 1986; March 26, 1987; October 1, 1987; March 14, 1988; December 13, 1988; April 21, 1989, August 25, 1989; and November 17,

1989. The lowest coefficient of variation, 0.069, was achieved with a base temperature of  $10^{\circ}\text{C}$  (Fig. 2). At flowering, mean degree-days above  $10^{\circ}\text{C}$  were  $443 \pm 31$ . Triggering rains varied from 20–30 mm. Flowering in *Larrea* apparently requires a triggering rain of at least 20 mm and a heat sum thereafter of about 443 degree-days above  $10^{\circ}\text{C}$ .

*Fouquieria splendens.* The dates of flower during our study were April 10, 1985; April 7, 1986; April 24, 1987; April 13, 1988; and March 30, 1989. In addition, on October 23, 1987, we noted a number of plants in flower at the base of Tumamoc Hill about 200 m below our study site. The lowest coefficient of variation, 0.090, was achieved with a base temperature of  $10^{\circ}\text{C}$  (Fig. 2). At flowering, mean degree-days above  $10^{\circ}\text{C}$  were  $514 \pm 47$ . Triggering rains varied from 11–46 mm. Photoperiod did not seem to be an effective trigger. Spring flower in *F. splendens* apparently is triggered by the first cool-season rain of at least 10 mm and requires a heat sum thereafter of about 515 degree-days above  $10^{\circ}\text{C}$ . We had too little data to predict when *F. splendens* will bloom in autumn; heavy, soaking rains when temperatures are cool but not cold seem to be a prerequisite.

*Encelia farinosa.* The dates of flower during our study were April 4, 1985; March 31, 1986; April 17, 1987; May 20, 1988; and April 21, 1989. The lowest coefficient of variation, 0.104, was achieved using a base temperature of  $10^{\circ}\text{C}$  (Fig. 2). At flowering, mean degree-days above  $10^{\circ}\text{C}$  were  $414 \pm 43$ . Triggering rains varied from 21–26 mm. Bloom in *E. farinosa* is triggered by cool-season rains of at least 20 mm and requires a heat sum thereafter of about 415 degree-days above  $10^{\circ}\text{C}$ .

*Acacia constricta.* The dates of flower during our study were April 30, 1985; April 29, 1986; May 15, 1987; May 20, 1988; August 3, 1988; September 26, 1988; May 5, 1989; and August 11, 1989. The lowest coefficient of variation, 0.132, was achieved with a base temperature of  $15^{\circ}\text{C}$  (Fig. 2). At flowering, mean degree-days above  $15^{\circ}\text{C}$  were  $522 \pm 69$ . Triggering rains varied from 11–27 mm. Flowering in *A. constricta* is triggered by a rain of at least 11 mm followed by a heat sum of about 522 degree-days above  $15^{\circ}\text{C}$ . The first cool-season rain triggers spring flower.

*Ambrosia deltoidea.* The dates of flower during our study were March 20, 1985; February 17,

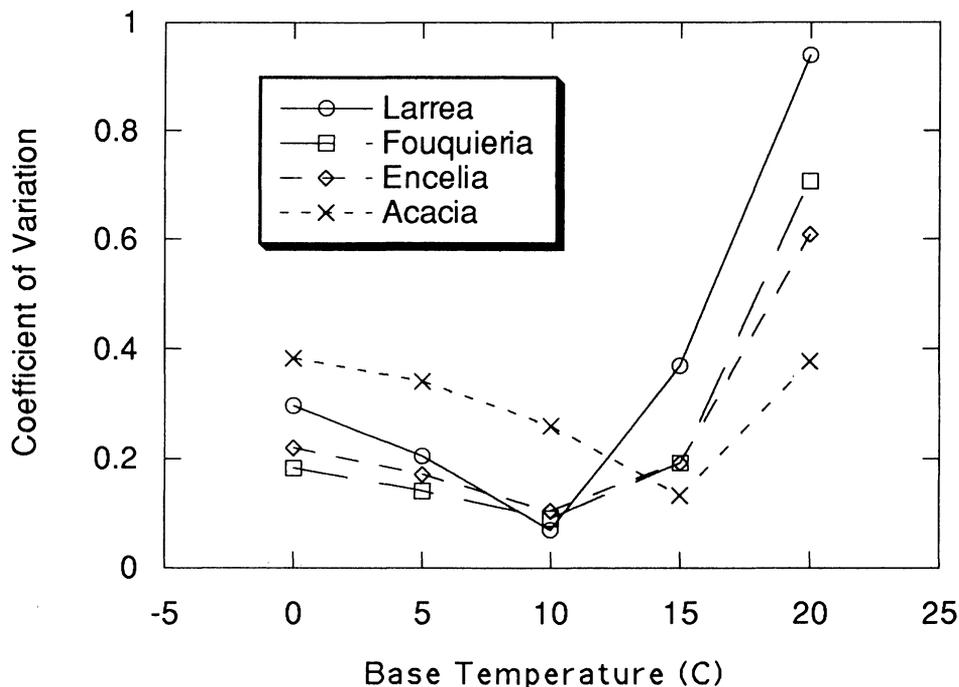


Fig. 2. Relationship between base temperature and the coefficient of variation for mean degree-days for four woody plant species. Mean degree-days calculated from rainfall triggers to date of flower.

1986; April 2, 1987; March 14, 1988; and April 14, 1989. The lowest coefficient of variation, 0.099, was achieved with a base temperature of 10°C (Fig. 3). The photoperiod triggers produced higher coefficients of variation than the rainfall triggers (Fig. 3). Contrary to our expectations, rainfall, not photoperiod, apparently triggers flowering in this species. The curve produced by the rainfall triggers is rather flat, which suggests that the actual base temperature may be a few degrees higher or lower than 10°C. Alternatively, another temperature summation method might provide more robust results. At flowering, mean degree-days above 10°C were  $472 \pm 47$ . Triggering rains varied from 15–27 mm. *Ambrosia deltoidea* apparently flowers in response to the first cool-season rain of 15 mm or more and requires a heat sum thereafter of about 472 degree-days above 10°C.

*Cercidium microphyllum*. The dates of flower during our study were April 30, 1985; April 15, 1986; May 15, 1987; May 1, 1988; and April 21, 1989. The lowest coefficient of variation, 0.067, was achieved using a rainfall trigger and a base temperature of 0°C (Fig. 4); however, the resulting curve suggests that this is a spurious result. If one uses mean daily temperatures to calculate

temperature sums, and one selects a range of base temperatures that extend above and below the actual base, a graph plotting coefficient of variation versus base temperature will necessarily produce a V-shaped curve (see, for example, Lindsey and Newman 1956; Arnold 1959; White 1979). In the case of *C. microphyllum*, the only combination of trigger and base temperature to produce an appropriately V-shaped curve was February 15 and 10°C, with a coefficient of variation of 0.100 (Fig. 4). For *C. microphyllum*, the best trigger is apparently a daylength of about 11 hours. At flowering, mean degree-days above 10°C were  $719 \pm 72$ . *Cercidium microphyllum* apparently flowers when daylengths reach about 11 hours and degree-days above 10°C thereafter reach about 719.

**PREDICTED VERSUS OBSERVED FLOWER DATES.**  
*Larrea tridentata*. Our initial set of predicted flower dates fell within  $\pm 2$  SD of the target for only 4 of 12 flowering events. In several cases, the difference between predicted and observed dates of flower suggested that we had selected the wrong triggers. For example, the March 1983 bloom was apparently triggered by a rain of 13 mm from November 9–11, and the September 1986 bloom was apparently triggered by a storm

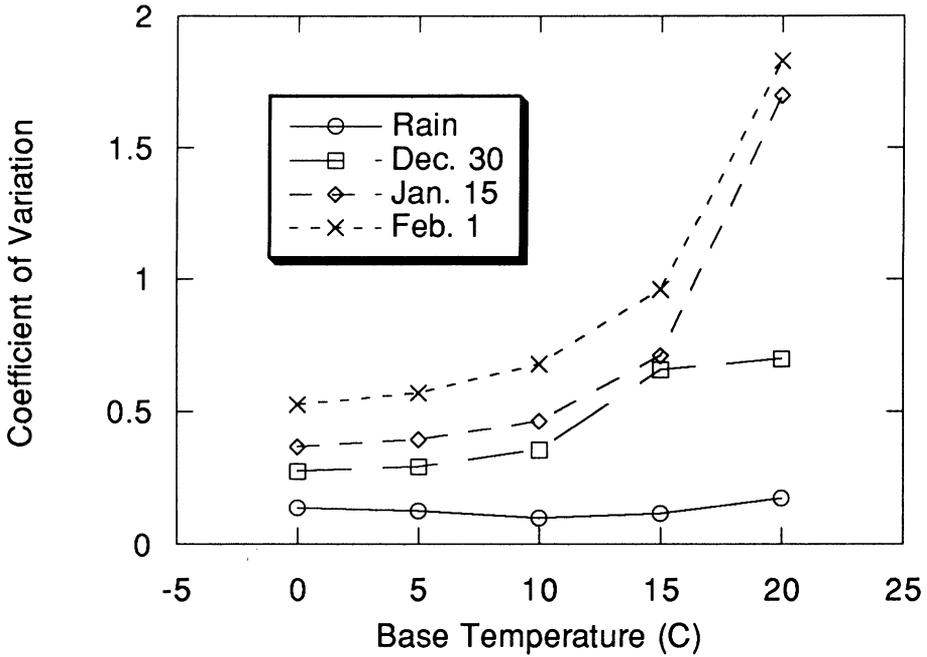


Fig. 3. Relationship between base temperature and the coefficient of variation for mean degree-days for *Ambrosia deltoidea*. Mean degree-days calculated from rainfall triggers and three daylength triggers to date of flower.

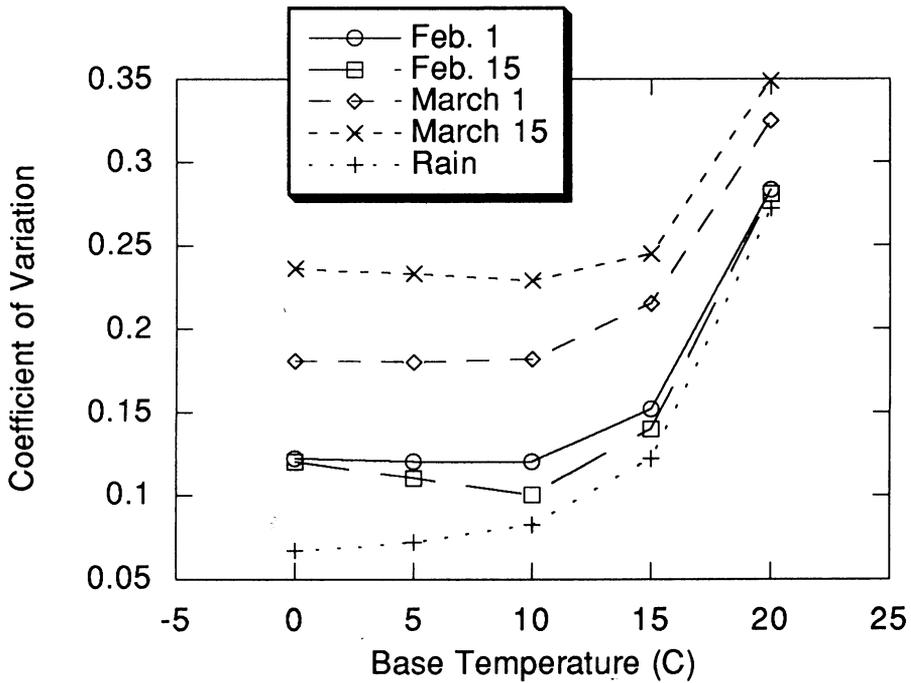


Fig. 4. Relationship between base temperature and the coefficient of variation for mean degree-days for *Cercidium microphyllum*. Mean degree-days calculated from rainfall triggers and four daylength triggers to date of flower.

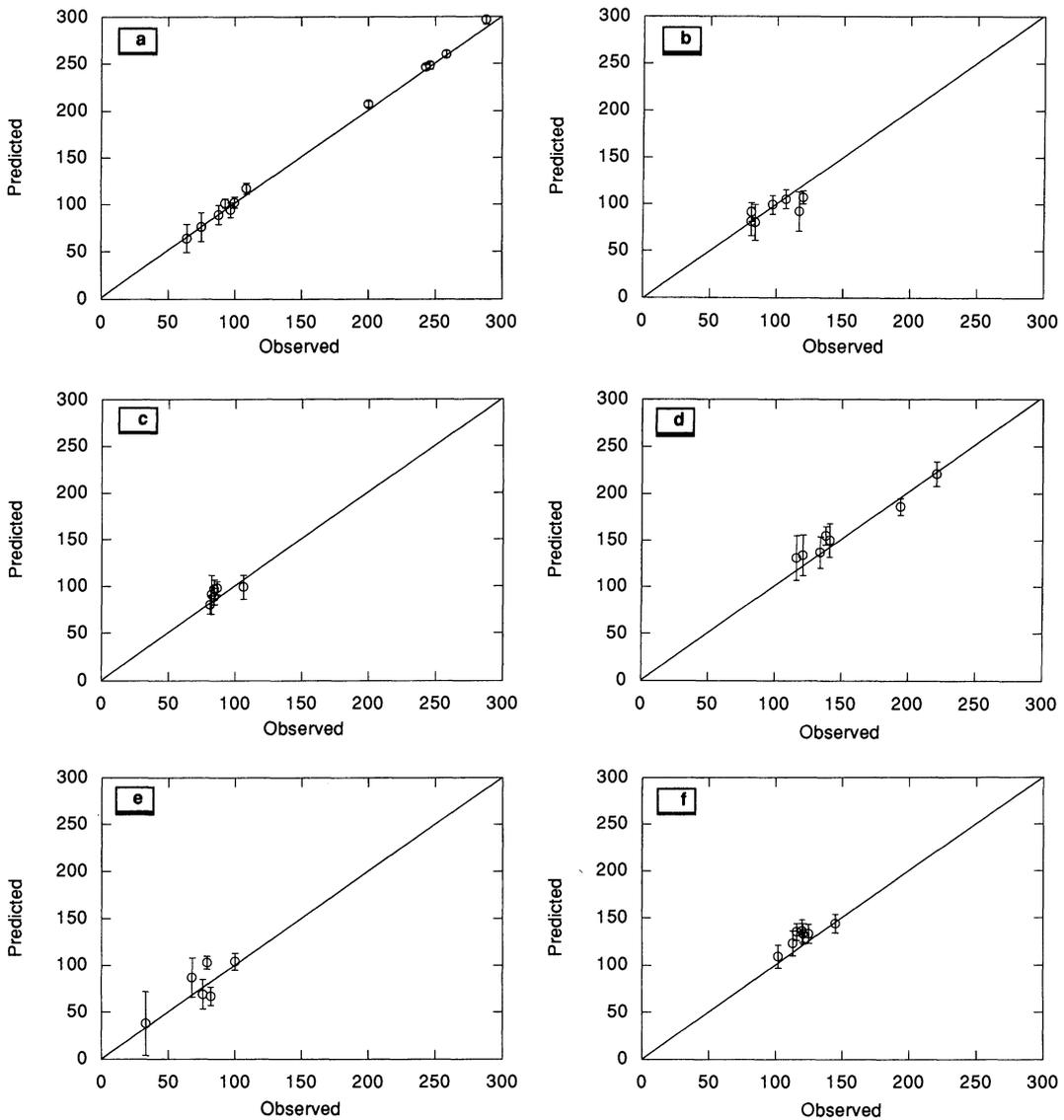


Fig. 5. Predicted versus observed flower dates for six woody plant species at the Arizona-Sonora Desert Museum, 1982–1989. Dates are plotted as ordinal numbers from first day of year to last day of year. The line has a slope of 1 and denotes a 1:1 correspondence between predicted and observed flower dates. The error bars represent the range in predicted flower dates on either side of the mean. a, *Larrea tridentata*; b, *Fouquieria splendens*; c, *Encelia farinosa*; d, *Acacia constricta*; e, *Ambrosia deltoidea*; f, *Cercidium microphyllum*.

of 12 mm from August 11–12. Both triggers were smaller than expected. When we used rains  $\geq 12$  mm as the trigger, we correctly predicted the date of flower for 8 of 12 flowering events. In the 4 remaining cases, the observed flowering dates fell outside the predicted range by only 3 or 4 days, and there were no alternative rainfall triggers. Figure 5a shows the predicted dates of flower plotted against the observed dates. Linear regression of mean predicted dates versus observed

dates suggests that our climatic formulation explains a high proportion of the variance in flowering dates ( $R^2 = 0.998$ ).

*Fouquieria splendens*. Our predicted flower dates fell within  $\pm 2$  SD of the target for 5 of 7 flowering events. In the 2 remaining cases, we could find no other likely triggers. The autumn preceding the spring 1983 flowering season was wetter than normal; this may have hampered our

efforts to identify a single rainfall trigger. The lack of summer flowering in our area suggests that high temperatures inhibit floral development. Figure 5b shows the predicted dates of flower plotted against the observed dates. Linear regression of mean predicted dates versus observed dates suggests that our climatic formulation explains only a modest proportion of the variance in flowering dates ( $R^2 = 0.558$ ). Dropping the 1983 flowering event from the regression, however, shows that for the remaining years, our climatic formulation explains much of the variance ( $R^2 = 0.806$ ).

*Encelia farinosa*. Our predicted dates of flower fell within  $\pm 2$  SD of the target for 6 of 8 flowering events. In the 2 remaining cases, the observed flowering dates were only a few days short of the predicted range, and we could find no other likely triggers. Figure 5c shows the predicted dates of flower plotted against the observed dates. Linear regression of mean predicted dates versus observed dates suggests that our climatic formulation explains a high proportion of the variance in flowering dates ( $R^2 = 0.995$ ). We could not determine a date of flower for spring 1984 because bloom was recorded as continuous between November 1983 and April 1984. The lack of summer flowering suggests that high temperatures inhibit floral development.

*Acacia constricta*. Our initial set of predicted flower dates fell within  $\pm 2$  SD of the target for only 4 of 7 flowering events. It seemed likely that we had selected the wrong trigger in at least 2 cases. We had not considered rains before November 1 as potential triggers for spring flowering; when we used heavy October rains as triggers for spring flower in 1984 and 1985, we correctly predicted 6 of 7 events. For the remaining event, the observed date of flower was 7 days outside the predicted range; we could find no other likely trigger. Figure 5d shows the predicted dates of flower plotted against the observed dates. Linear regression of mean predicted dates versus observed dates suggests that our climatic formulation explains a high proportion of the variance in flowering dates ( $R^2 = 0.970$ ). The relative high base temperature ( $15^\circ\text{C}$ ) may account for the lack of early spring flowering.

*Ambrosia deltoidea*. Our initial set of predicted flower dates fell within  $\pm 2$  SD of the target for only 2 of 6 flowering events. Examining the weather record, we found that 3 flowering events had evidently been triggered by smaller rains than

expected. When we used rains  $\geq 9$  mm as the trigger, we correctly predicted 5 of 6 events. We could find no other likely rainfall trigger for the remaining flowering event. Figure 5e shows the predicted dates of flower plotted against the observed dates. Linear regression of mean predicted dates versus observed dates suggests that our climatic formulation explains a modest proportion of the variance in flowering dates ( $R^2 = 0.659$ ). We suspect that much of the remaining variance results from a mismatch in dates of flower between Tumamoc Hill and the Desert Museum; the unisexual flowers are inconspicuous, and determination of full flower is more subjective than for showy species such as *Larrea* and *Encelia*. The lack of summer flowering suggests that high temperatures inhibit floral development, or that there is a chilling requirement.

Apparently, the only Sonoran Desert shrub for which chilling requirements are known is *Simmondsia chinensis*. Flower buds, typically formed in autumn (Gentry 1958), remain dormant until they have undergone at least 20 days of chilling at temperatures no higher than  $20^\circ\text{C}$  (Dunstone 1980; Benzioni and Dunstone 1985; Ferriere et al. 1989), a requirement easily met in most winters in our area. None of our 6 species has been reported to require vernalization. Those that bloom in autumn (*L. tridentata*, *A. constricta*, *F. splendens*, *E. farinosa*) do so following a lengthy period of high summer temperatures and are unlikely to require chilling. *Ambrosia deltoidea* is perhaps somewhat more likely to require vernalization; if so, its needs were met at our study sites in every year of record.

*Cercidium microphyllum*. Our predicted dates of flower fell within  $\pm 2$  SD of the target for 4 of 7 events. For 1 event, the observed date of flower was 1 day outside the predicted range; for one other, it was 7 days outside. Figure 5f shows the predicted dates of flower plotted against the observed dates. Linear regression of mean predicted dates versus observed dates suggests that our climatic formulation explains a moderately high proportion of the variance in flowering dates ( $R^2 = 0.755$ ).

**Discussion.** PHENOLOGICAL PATTERNS IN THE NORTHERN SONORAN DESERT. Our results demonstrate that flowering in *L. tridentata*, *F. splendens*, *E. farinosa*, *A. deltoidea* and *A. constricta* is triggered by rain, and that flowering in *C. microphyllum* is triggered by photoperiod. The base temperature for floral development in *L. triden-*

*tata*, *F. splendens*, *E. farinosa*, *A. deltoidea* and *C. microphyllum* is about 10°C. Their mean degree-day requirements range from 414 to 719. *Acacia constricta* requires 522 degree-days above 15°C. Minimum rainfall triggers varied from 9 mm for *Ambrosia* to 20 mm for *Encelia*. (These values exclude the spring 1984 flowering season, which, as we discuss below, followed an unusually wet autumn).

We were most successful at predicting flower in *L. tridentata*, *F. splendens*, *E. farinosa*, *A. constricta* and *A. deltoidea*. Longer phenological records or more frequent observations might enable us to predict bloom in *C. microphyllum* more accurately. We found several different causes for lack of agreement between predicted and observed flower dates. In many cases, the discrepancy was fairly small, and we could find no other likely trigger. Our decision not to search for temperature triggers may have slightly biased our results for certain species. Because Bowers studied individuals while Dimmitt studied populations, there was a lack of consistency in defining phenological stages. For *C. microphyllum*, for example, the dates of early flower (1–3 of the marked plants in bloom) at Tumamoc Hill corresponded roughly to dates of full flower (most plants in bloom) at the Desert Museum. Some of the discrepancies between predicted and observed flower dates no doubt reflect the variability produced by our two different methods of data collection.

In other cases, predicted and observed flower dates differed because we had selected the wrong trigger. For the rain-triggered species, we were able to define fairly precisely the heat sum required to bring the plants into flower; however, the relatively short phenological record at Tumamoc Hill gave us only a limited number of rain triggers to choose from. Refining our formulations, therefore, often involved identifying the smallest possible trigger. For example, using rains  $\geq 20$  mm as a trigger for *L. tridentata*, we initially selected the storm of 47 mm from January 30–February 4, 1986 as a more likely trigger than that of 15 mm on November 28, 1985. It appeared that the smaller storm had indeed triggered the flowering event of March 5, 1986, and we revised our formulation accordingly.

In some years, unusual climatic events foiled our best efforts at prediction. One example is the early spring flowering of *A. deltoidea* in 1984, which can be attributed only to a 2-mm rain on October 20, 1983. The early date of flower may be a result of the El Niño event of the previous fall, when rains totaling 200 mm fell between

September 29 and October 4, 1983. This may be further evidence that flowering occurs not in response to rainfall as such but to threshold levels of soil moisture. A few of our predicted flowering events failed to materialize. We expected a rain of 62 mm from July 14–19, 1985 to trigger flowering in *L. tridentata*, for example, but it did not. This was the first storm after a long drought at moderate to high temperatures, and perhaps there was not enough moisture in the soil for the trigger to be effective.

In a few cases, we cannot explain the discrepancy between predicted and observed dates. One example is the late March 1985 bloom of *A. deltoidea*. The only likely trigger was the 27-mm storm in early December 1984, but these rains should not have produced flowers until April 6–April 20, 1985.

Duration of bloom varied considerably from year to year in our study. At the Desert Museum, flowering of *Encelia*, *Larrea* and *Ambrosia* was severely truncated in 1979. Apparently, flowering is almost invariably initiated given the appropriate trigger; however, given insufficient soil moisture, its duration may be curtailed. For the spring 1989 flowering season, the preceding November–February rains had been scant (only 30 mm), and the 22-mm rain in late March, while sufficient to trigger flowering, evidently did not provide enough soil moisture to sustain a normal period of bloom. That same spring, only 5 of 10 marked *Cercidium* plants bloomed on Tumamoc Hill. As Shreve (1951) noted, *C. microphyllum* may fail to flower altogether during extremely dry years, as happened in 1956 (Turner 1963), when only 51 mm of rain fell during the previous November–March.

*Larrea tridentata* had the most protracted period of bloom of our six species. The average over the 7 years of study was 59 days. The longest duration of flower at the Desert Museum, 88 days, was in spring 1983; that year, after the initial trigger of 11 mm on November 17–19, 1982, there were 5 more potentially triggering rains. Perhaps each rain triggered a new flush of bloom; alternatively, prolonged high soil moisture may have produced a continuous state of bloom as a result of internal resource allocation. To decide between these two hypotheses, it would be necessary to count and mark individual flowers throughout the blooming period.

For the purposes of analysis, we assumed that a single rain, as long as it was large enough, could trigger flowering in our 6 species. This may indeed be the case for *F. splendens* and *L. triden-*

*tata*. Humphrey (1975) reported normal spring flowering in both species after a dry winter in which only 20 mm of rain fell between October 1968 and March 1969. Most of it was apparently delivered in a single storm on January 25 (Humphrey 1975); clearly, this one event sufficed to trigger flowering in *Fouquieria* and *Larrea*. (Such incidents may account for the widespread belief that *F. splendens* flowers every year regardless of rain.) Other species may require additional rain after the trigger. Given the poor showing by *Encelia* and *Ambrosia* in spring 1989, it seems likely that they do need supplemental rains, and that the minimum amount, excluding the trigger, is close to 30 mm.

On our two study sites, the general sequence of flowering was *Ambrosia*, *Larrea*, *Encelia*, *Fouquieria*, *Cercidium* and *Acacia*. This order reflects the different phenological requirements of the six species. *Ambrosia deltoidea* has a relatively high heat-sum requirement (472 degree-days above 10°C), but because light rains are more frequent than heavy ones in our area (Shreve 1914), its small rainfall trigger (9 mm) evidently produces early bloom in most years. *Encelia*, on the other hand, has a larger trigger (20 mm), which might force it to bloom much later than *Ambrosia* if not for its low heat-sum requirement (414 degree-days above 10°C). *Fouquieria* and *Larrea* require similar rainfall triggers (12 and 13 mm), but the lower heat-sum requirements of *Larrea* (443 degree-days above 10°C) enable it to flower as much as a month before *Fouquieria* (514 degree-days above 10°C).

We did find some variation in flower sequence from year to year. On Tumamoc Hill in 1987 *Larrea* flowered about a week before *Ambrosia*. Both events were triggered by the same December storm, but the smaller heat-sum requirement of *Larrea* evidently resulted in its flowering earlier that spring. In 1989, *F. splendens* flowered 3 weeks before *Larrea* and *Encelia* on Tumamoc Hill, perhaps because it was able to respond to a January storm of 15 mm accompanied by cold temperatures (-2°C, -1°C, 0°C) whereas the others were not. Because the next potential trigger was the 26-mm storm of March 25, flowering of *Larrea* and *Encelia* was unusually delayed that spring. In contrast, Opler et al. (1976) found that in Costa Rica the sequence of flowering among 12 tropical trees and shrubs was constant from year to year and site to site. Flowering in their species was invariably triggered by the first end-of-dry season rain of 25 mm or more (Opler et al. 1976). The flowering requirements of our spe-

cies are more diverse; consequently the flowering sequence is more likely to vary from year to year.

**EVOLUTION OF FLOWERING TIMES IN THE NORTHERN SONORAN DESERT.** The spring flowering peak in the northern Sonoran Desert has been noted often (MacDougal 1908; Halvorson 1970; Solbrig and Yang 1977). *Larrea*, *Fouquieria*, *Ambrosia*, *Cercidium* and *Encelia* generally reach peak flower between the beginning of March and the end of April. On Tumamoc Hill, other common nonsucculent perennials that flower during the March–April peak include *Acourtia wrightii*, *Bahia absinthifolia*, *Baileya multiradiata*, *Brickellia coulteri*, *Carlwrightia arizonica*, *Glandularia gooddingii*, *Hibiscus coulteri*, *Krameria grayi*, *Menodora scabra*, *Porophyllum gracile* and *Trixis californica*.

Janzen (1967) argued that the dry-season flowering peaks in the lowlands of Central America are ultimately due to biotic rather than climatic factors. In the North American deserts, flowering peaks are determined to a much greater extent by what Janzen called “immutable physiological processes.” Most of the dominant species in the Sonoran, Mojave and Chihuahuan deserts (except perhaps phreatophytes and plants with specialized water-storage organs) depend heavily on the seasonal availability of soil moisture to bring flowers and fruits from initial to final stages (Beatley 1974; Simpson 1977; Solbrig and Yang 1977; Kemp 1983). In many cases, a significant rain is the trigger that initiates flowering. For these reasons, flowering time for most species must coincide with the seasons of greatest soil moisture.

Photoperiod seems most likely to trigger flowering where the environment is predictable. In deserts, which are inherently unpredictable, rainfall is more efficient than daylength at coordinating phenological events with environmental conditions. The exception in our study is *Cercidium microphyllum*; blooming during the dry season, it is apparently cued to one of the few predictable climatic features of the northern Sonoran Desert.

Flowering times of some desert plants may be constrained by the need to produce seeds in time for germination in the summer rainy season, as Solbrig and Yang (1977) suggested. *Encelia farinosa* and *A. deltoidea* disperse seeds in late spring but do not germinate until the following winter or autumn, and *Larrea* disperses seed from spring to autumn but seldom germinates except in late summer or autumn (Rivera and Freeman 1979).

It seems unlikely that flowering times in these species have been determined by seed germination needs. *Cercidium microphyllum*, *A. constricta* and *F. splendens* also disperse seeds in late spring but germinate in response to summer rains. The two legumes, *Cercidium* and *Acacia*, have hard seed coats that prevent germination for at least a year (Shreve, 1951; McAuliffe 1990). Seeds of *F. splendens* remain highly viable for two years after dispersal (Dimmitt, unpubl. data). Germination needs do not seem a likely constraint on flowering times in these species, either.

Waser (1979) concluded that flowering time in *F. splendens* in the Sonoran Desert has been largely determined by pollinator availability, specifically the northward migration of hummingbirds in spring. Additional indirect evidence comes from the Chihuahuan Desert, where *F. splendens* grows under a summer rainfall regime yet continues to flower in spring (Henrickson 1972). Production of flowers during a relatively dry season argues for strong selective pressure of some sort, such as the arrival of migrating hummingbirds. (Climatic summaries from the northern Chihuahuan Desert [Schmidt 1975; Brown 1982] suggest that winter rains there are usually reliable enough and large enough to trigger spring flowering in *F. splendens*.) Many other species of *Fouquieria* bloom at virtually any season given sufficient rain and warm enough temperatures (Henrickson 1972), and this too suggests strong selective pressure for spring bloom in *F. splendens*.

With the exception of *F. splendens*, it seems likely that pollinators have had little influence on flowering times of the species studied here. *Acacia constricta* offers few rewards to any pollinator (Simpson 1977). *Ambrosia deltoidea* is wind pollinated. *Encelia* and *Larrea* bloom opportunistically in response to rains. Some pollinators, apparently cued by the same triggers as their hosts (Simpson et al. 1977), time their emergence to coincide with flowering peaks: for instance, of the 22 solitary bees that feed only on *Larrea* pollen or nectar, 20 are active only in spring (Hurd and Linsley 1975).

Competition for pollinators may cause some species to shift flowering times, as Waser (1983) has demonstrated for *Ipomopsis aggregata*, a perennial herb. We know of no similar shifts in the northern Sonoran Desert, where climate forces sympatric species to overlap largely in their blooming periods. In fact, rather than avoiding competition for pollinators, two sympatric leguminous trees, *C. microphyllum* and *Olneya te-*

*sota*, flower in the late spring dry season and share a major pollinator, the solitary bee *Centris pallida* (Jones 1978). The other Sonoran Desert species of *Cercidium* also flower in spring, as do many leguminous trees of the region (Wiggins 1964); spring flowering of *C. microphyllum* may represent a phylogenetic constraint.

The dominant trees and shrubs of temperate-zone plant communities may not have coexisted long enough to affect one another's flowering times (Kochmer and Handel 1986). In the Sonoran Desert, Pleistocene and Holocene macrofossils show that community composition has varied continuously as species have responded differently to climatic fluctuations (Van Devender et al. 1990). Today, for example, *L. tridentata* and *E. farinosa* are common associates in the Puerto Blanco Mountains, Arizona, but *E. farinosa* has been there for at least 10,200 years while *L. tridentata* did not arrive until about 3400 years ago (Van Devender 1990).

The plant communities of the northern Sonoran Desert include species of various affinities. *Encelia* and *Ambrosia* reach their centers of greatest diversity in the winter-wet, summer-dry climates of California and Baja California (Wiggins 1964). *Fouquieria* and *Cercidium* have speciated most heavily in the summer-wet, winter-dry climates of Sonora, Sinaloa, Chihuahua, Coahuila, Durango and Zacatecas (Henrickson 1972; Shreve 1935). We expected that the phenologies of these species in our study area would reflect their origins and at the same time accommodate the prevalent biseasonal rainfall regime. The phenological triggers we found, however, do not align themselves in any simple way with place of origin. Plants with subtropical affinities can be cued to rain triggers (*Fouquieria*, *Acacia*) or to photoperiod triggers (*Cercidium*). Plants of cool-temperate affinity can respond to cool-season rain triggers (*Encelia*, *Ambrosia deltoidea*) or to both cool-season and warm-season rain (*Ambrosia dumosa*) (Ackerman et al. 1980). The phenological strategies of woody dominants in the northern Sonoran Desert can be characterized as a "grab-bag" in that species with a variety of triggers and heat requirements coexist. Flowering times and phenological triggers of the dominant species, though strongly constrained by climate, are nonetheless unique.

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