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El Niño and displays of spring-flowering annuals in the Mojave and Sonoran deserts

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BOWERS, J. E. (U.S. Geological Survey, 1675 W. Anklam Rd., Tucson, AZ 85745). El Niño and displays of spring-flowering annuals in the Mojave and Sonoran deserts. J. Torrey Bot. Soc. 132: 38–49. 2005.—Although popular and scientific literature frequently assumes a strong connection between El Niño-Southern Oscillation (ENSO) and good displays of spring-flowering annuals in the southwestern United States, such assumptions are based on anecdotal, short-term evidence. The goals of this study were to identify good wildflower years as objectively as possible, to assess the correlation between El Niño and good displays of spring-flowering annuals, and to examine the influence of rainfall amounts on good wildflower years. The terms ''good displays'' and ''good wildflower years'' refer to times or places when populations of showy spring-flowering annuals (often called winter annuals) are abundant, robust, and diverse. In the deserts of southeastern California and southern Arizona, good wildflower years occurred about once every 5 to 7 years in the 20th century. The connection between good wildflower years and traditionally defined El Niño episodes was weak, but when El Niño was redefined in a phenologically meaningful way as any calendar year in which the average Southern Oscillation Index (SOI) between July and December was negative, 21 of 27 good wildflower years in the combined deserts were associated with El Niño. Good wildflower years were 3.6 times more likely after redefined El Niño years than after other years. Rain in the months before good wildflower years was at least 30% greater than the long-term average in the Mojave Desert and at least 50% greater in the Sonoran Desert. A diverse flora of spring-flowering annuals occurred in the region during the late Wisconsin and early Holocene, which was a period of wetter, milder winters and cooler summers. Perhaps some species of spring-flowering annuals persist today in the arid southwestern United States only because frequent El Niño conditions recreate the cool, moist conditions of the late Pleistocene.

Key words: climatic variability, El Niño, ephemerals, herbarium records, Mojave Desert, phenology, Sonoran Desert, spring-flowering annuals, winter annuals.

The idea that good wildflower years in the arid southwestern United States are strongly correlated with El Niño conditions appears in both the popular press (e.g., *New York Times*, March 30, 1998) and in scientific literature (e.g., Venable and Pake 1999, Clauss and Venable 2000) but has not been investigated in a systematic fashion. The phrase ''good wildflower year,'' although imprecise, suggests that populations of showy, spring-flowering annuals (often called winter annuals or ephemerals) are abundant, robust and diverse. Such years are of considerable economic importance, drawing many visitors from other states and countries, and of great biological importance, as well, replenishing seed reserves in the soil (Nelson and Chew 1977, Brown et al. 1979) and promoting reproduction of herbivores (Beatley 1969, French et al. 1974, Brown et al. 1979, Morgan Ernest et al. 2000). Good wildflower years are infrequent because of interannual variability in precipitation and temperature. In dry years, populations of spring-flowering annuals are small (Bowers 1987), and certain species can be difficult to find (although a thorough search will discover many of them in favorable microhabitats). Conventional wisdom suggests that winter frontal storms are crucial for development of good displays in spring (e.g., Shreve 1951, Zabriskie 1979); in recent years, the role of autumn tropical storms has been increasingly emphasized (e.g., Nabhan and Cole 1988).

Most spring-flowering annuals in the arid southwestern United States germinate in response to rain between late September and early December when minimum temperatures are between 8 and 13 °C (Went and Westergaard 1949, Beatley 1974). Abundant germination requires a rain of at least 25 mm; only scattered germination follows storms of 15 to 25 mm (Beatley 1974). Mass germination can also occur between late December and mid-March, given sufficient rain and temperatures > 10 °C (Beatley 1974). Because spring-flowering annuals differ in their temperature requirements for germination, spe-

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cies diversity tends to be greatest when suitable storms are delivered over a range of temperatures (Went 1948, 1949; Juhren et al. 1956, Tevis 1958a, Beatley 1974, Bowers 1987, Rundel and Gibson 1996). Showy species in the Hydrophyllaceae, Polemoniaceae, Onagraceae, Asteraceae and Fabaceae often germinate in autumn when temperatures are relatively warm, whereas inconspicuous species belonging to the Boraginaceae and Brassicaceae emerge in the winter when soils are considerably cooler (Bowers 1987, Rundel and Gibson 1996).

Spring-flowering annuals typically flower between February and April, then disperse seeds in May and June. Survivorship to maturity depends upon adequate rain after germination. If winter and spring are dry, plants die or fail to thrive, and a showy display is unlikely (Beatley 1967, 1974; Burk 1982, Rundel and Gibson 1996). Note, however, that many species are capable of maturing a few fruits and seeds despite dry conditions (Went 1949, Shreve 1951, Tevis 1958b). Long-lived seeds prevent extinction when two or more consecutive years are too dry for plants to complete their life cycle (Wilcott 1974, Venable and Pake 1999).

A connection between El Niño and displays of spring-flowering annuals seems intuitively reasonable. El Niño conditions enhance fall and winter precipitation in the southwestern United States by increasing the frequency with which frontal systems and tropical cyclones enter the region (Andrade and Sellers 1988, Ropelewski and Halpert 1986, Kiladis and Diaz 1989, Webb and Betancourt 1992). These effects can last as long as one year after the event (Webb and Betancourt 1992). In the Sonoran Desert of southern Arizona, 1978, 1983, 1993, and 1998—all El Niño years—were rated as ''good,'' ''great,'' or ''spectacular'' wildflower years (Arizona-Sonora Desert Museum 2000). In the Mojave Desert of southeastern California, ''good'' or ''great'' wildflower displays were reported in several recent El Niño years, including 1973, 1977, 1978, and 1998 (Arizona-Sonora Desert Museum 2000). On the other hand, showy displays can occur locally outside of El Niño episodes as in 1935 (Went and Westergaard 1949) and 1948 (Juhren et al. 1956), and some episodes are too dry for much germination of spring-flowering annuals.

El Niño conditions arise from large-scale interactions between ocean and atmosphere. In the canonical El Niño episode, which lasts for about 18 months, sea-surface warming in the western tropical Pacific Ocean typically begins late in year -1 and reaches a peak in spring and summer of year 0 (Philander 1990). Sea-surface temperatures begin to cool toward the middle of year $+1$, signaling the end of the episode (Philander 1990). One measure of these (and related) changes is the Southern Oscillation Index (SOI), calculated as the standardized difference in sea-level air pressure between Tahiti and Darwin, Australia. The index is negative during El Niño episodes. In recent years, qualitative identification of El Niño episodes has been replaced by quantitative definitions involving duration and distribution of negative SOI values (Trenberth 1997). El Niño-Southern Oscillation (ENSO) conditions recur at 2- to 7-yr intervals (Quinn et al. 1987, Webb and Betancourt 1992) and have a variety of climatic impacts worldwide. El Niño episodes enhance winter precipitation in southern California and Arizona by increasing the frequency of heavy rainfall events and the amount of precipitation during those events (Cayan et al. 1999). Because there is a lag between the onset of sea-surface warming in the tropical Pacific and enhancement of precipitation in the southwestern United States, average rain between October and March, the crucial period for spring-flowering annuals, is most highly correlated with average SOI during the previous July to December (Redmond and Koch 1991).

Investigation of the correlation between El Niño and wildflower displays has been hampered by several factors. Subjective assessments of the display in a given year can be difficult to interpret, for one thing; ''great'' and ''poor'' years are easily distinguished, but the difference between a ''good'' year and one that is merely ''fair'' is not as obvious. For another, spatial variability in timing and amount of precipitation means that a good year in one place might be a poor year in another place only several hundred km away. Moreover, unless some permanent record is made, knowledge of good and poor years is lost as time passes. Finally, unlike spring blooming periods, El Niño episodes do not necessarily fit within a single calendar year, a situation that complicates attempts to correlate the two. The objectives of this study were: (1) to devise an objective means of identifying good wildflower years, (2) to examine the correlation between the timing of ENSO and good wildflower years in the 20th century and (3) to assess the influence of rainfall amounts on displays of spring-flowering annuals. The emphasis throughout was on broad patterns, that is, on years in

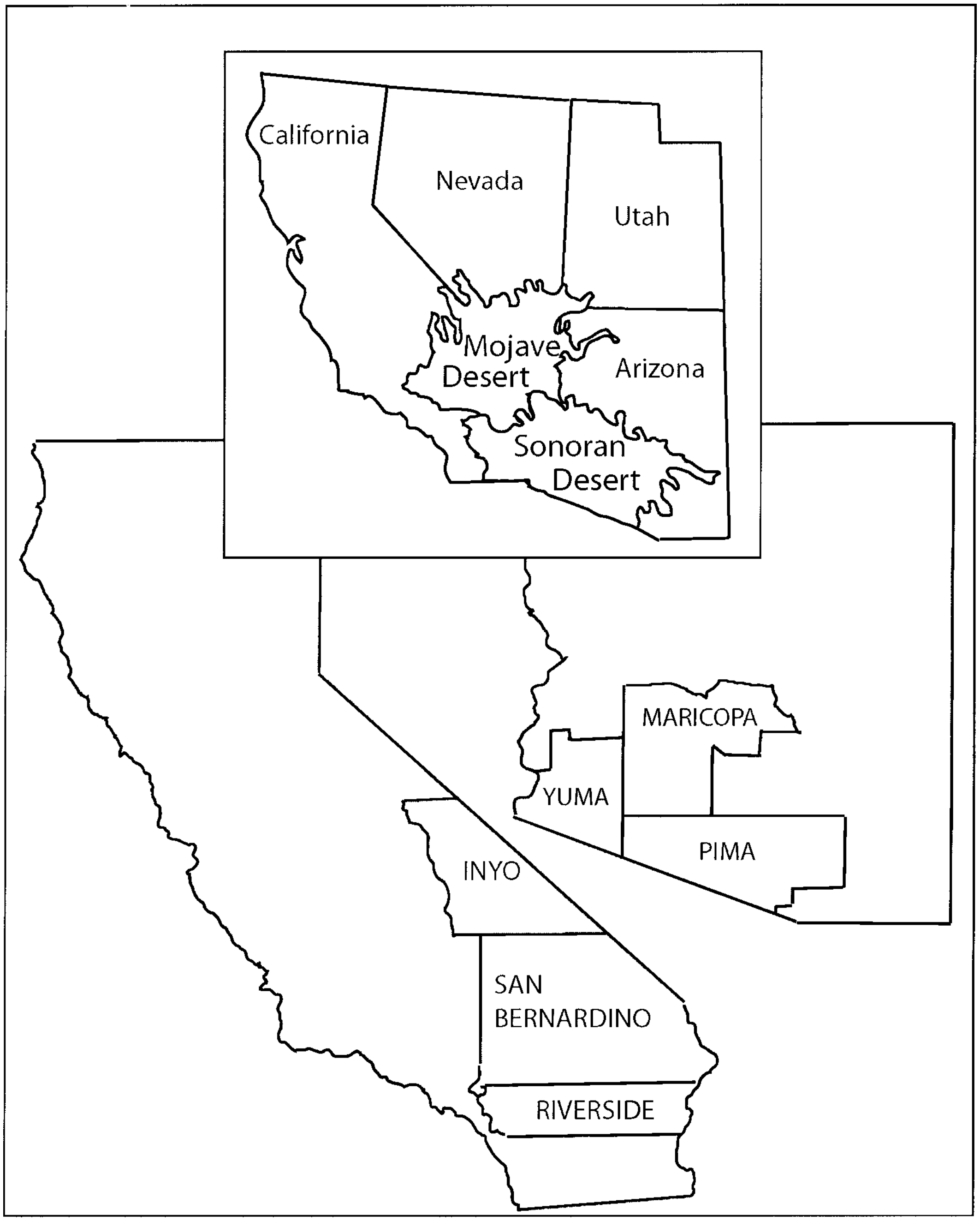

FIG. 1. Map of study area, showing the Sonoran and Mojave deserts in the southwestern United States (top) and the location of counties in California (bottom left) and Arizona (bottom right).

which spring-flowering annuals were diverse, robust and abundant across the desert region.

Materials and Methods. STUDY AREA. The Mojave and Sonoran deserts fall within the states of California, Nevada and Arizona in the United States and, in Mexico, in the states of Sonora, Baja California and Baja California Sur (Shreve 1942) (Fig. 1). For this study, three counties in California (Inyo, San Bernardino, Riverside) were selected to represent the Mojave Desert, and three counties in Arizona (Pima,

Table 1. Target species used to define good wildflower years in the Mojave or Sonoran deserts.

Species	Mojave Desert	Sonoran Desert
Abronia villosa S. Watson	X	
Atrichoseris platyphylla A. Gray	X	
Calycoseris wrightii A. Gray	X	X
Camissonia boothii (Douglas) Raven	X	
Camissonia brevipes (A. Gray) Raven	X	X
Camissonia claviformis (Torrey & Frémont) Raven	X	X
Castilleja exserta (A. A. Heller) Chuang & Heckard	X	X
Chaenactis carphoclinia A. Gray		X
Chaenactis fremontii A. Gray	X	
Chaenactis stevioides Hook. & Arn.	X	X
Chorizanthe brevicornu Torrey	X	
Eremalche rotundifolia (A. Gray) E. Greene	X	
Eriastrum diffusum (A. Gray) H. Mason		X
Eriogonum trichopes Torrey		X
Eriophyllum lanosum (A. Gray) A. Gray		X
Eriophyllum wallacei (A. Gray) A. Gray	X	
Erodium texanum A. Gray		X
Eschscholzia californica Cham.		X
Eschscholzia glyptosperma E. Greene	X	
Eschscholzia minutiflora S. Watson	X	
Gilia stellata A. A. Heller	X	X
Langloisia setosissima (Torrey & A. Gray) E. Greene	X	
Lesquerella tenella Nelson		X
Linanthus aureus (Nutt.) E. Greene		X
Linanthus bigelovii (A. Gray) E. Greene		X
Lupinus arizonicus (S. Watson) S. Watson	X	
Lupinus sparsiflorus Benth.		X
Malacothrix coulteri A. Gray	X	
Malacothrix glabrata A. Gray	X	X
Malacothrix sonchoides (Nutt.) Torrey & A. Gray	X	
Mentzelia albicaulis Hook		X
Mentzelia nitens E. Greene	X	

Maricopa, Yuma) were selected to represent the Sonoran Desert (Fig. 1). Although portions of San Bernardino and Riverside counties fall within the Sonoran Desert as mapped by Shreve (1942, 1951) on the basis of vegetation, they are treated as Mojave Desert here because their floristic affinities and rainfall regimes are essentially Mojavean. Annual rainfall in the study region ranges from $<$ 30 mm to $>$ 300 mm. In the western portion, most rain arrives in winter (October to March); the proportion of summer rainfall increases toward the east, reaching about 50% (Turner 1994, Turner and Brown 1994, Turnage and Mallery 1941). Plant cover is typically sparse, often no more than 10% to 30% (Shreve 1951). Shreve (1951) estimated that nearly 400 species of spring-flowering annuals could be found in the desert regions of southern California. About half that many occur in Arizona (Kearney and Peebles 1960). Throughout the Mojave and Sonoran deserts, spring-flowering annuals comprise a substantial portion of local floras, about 30% to 40% (Venable and Pake 1999, Raven and Axelrod 1978).

OBJECTIVE IDENTIFICATION OF GOOD WILDFLOWER YEARS. The general strategy was to examine the frequency of showy spring-flowering annuals throughout the 20th century in the Mojave and Sonoran deserts. Two phases were involved: selection of ''target'' species and determination of their frequency through time. The criteria used for target species were showy (i.e., large, colorful, or zygomorphic) flowers or inflorescences, broad geographic distribution, and common frequency. Altogether, 49 species were selected for analysis (Table 1). This method of assessing quality of bloom was based on two observations: first, that showy species are represented by more individuals in more locations in good wildflower years than in other years, and, second, that plant collectors tend to be most active in seasons and years when many species are in flower. As a result, the chance that a particular species will be represented in herbarium collections should increase in good wildflower years. Although the method considered only a small proportion of spring-flowering annuals in the region, it emphasized those most likely to contribute to showy displays. By definition, inconspicuous species make little visual contribution. In addition, those inconspicuous species of greatest ecological importance (e.g., *Plantago*, *Pectocarya*) are present in most years (Venable and Pake 1999), therefore do not distinguish good wildflower years from other years. Uncommon or narrowly distributed species might be showy but are too infrequently collected to be of use in defining broad, regional patterns.

The presence of 28 Sonoran Desert species in three Arizona counties was determined from herbarium collections at the University of Arizona and Arizona State University; in particular, a record was made of every year from 1900 to 1999 in which each species was collected. Year of collection for 31 Mojave Desert species in three California counties was similarly determined from specimens deposited in the herbarium at Rancho Santa Ana Botanic Garden and from specimens listed in an online data base compiled from the herbaria at the University of California at Berkeley (University of California 2001). Because the online data base included very few target species collected after 1989, the period of record for the Mojave Desert was truncated at 1989, making it 10 years short of a century. County records were combined to make separate pools for the Mojave and Sonoran deserts. The number of target species present in each year was determined, and the long-term mean and its standard deviation were calculated. To eliminate biases arising from temporal variation in collecting effort, the annual data were transformed using a detrending routine (SYSTAT 1998). Good wildflower years were defined as those in which the detrended number of target species equaled or exceeded one standard deviation.

A check of the method was made by comparing objectively and subjectively identified wildflower years. For the Mojave Desert, subjective classifications were taken from *Desert Magazine* (Palm Desert, California) between 1940 and 1960; for the Sonoran Desert, from the Arizona-Sonora Desert Museum (2000) web page between 1964 and 1999. Such subjective classifications are published to alert the public to times and places of wildflower displays. In the case of *Desert Magazine*, I evaluated written descriptions to decide whether spring-flowering annuals were abundant, diverse and widespread in any particular year. If these conditions seemed to be met, the year was considered a good wildflower year. The Arizona-Sonora Desert Museum web page described individual years as poor, fair, good, great or spectacular; for the purpose of comparison, I categorized good, great and spectacular years as good wildflower years. This analysis provided a series of years subjectively classified as good or not good for wildflowers. I determined the correlation between these subjective ratings and my own objective ratings by calculating simple matching dichotomy coefficients (SYSTAT 1998).

CLIMATIC ANALYSES. Climatic analyses were designed to answer three questions. Was there a correlation between traditionally designated El Niño episodes and good wildflower years? Did particular seasonal patterns of SOI precede good wildflower years regardless of El Niño designations? Finally, if seasonal SOI was used to redefine El Niño years in a phenologically meaningful way, was there a correlation between redefined El Niño years and good wildflower years?

The association between El Niño events and good wildflower years from 1900 to 1999 was examined separately for the Mojave and Sonoran deserts by compiling a table of El Niño episodes as defined by climatologists and of periods between episodes (''interims''). Designation of episodes followed Quinn et al. (1987), Webb and Betancourt (1992) and Trenberth (1997). If a good wildflower year occurred during or immediately after (within 12 months of) an episode or interim, the association with that episode or interim was considered positive. The number of positive associations for the entire period was summed separately for episodes and interims. Clumping of wildflower years within El Niño episodes and interims prevented the use of appropriate statistical tests such as contingency table analysis.

The difference between good and other wildflowers years in seasonal SOI was examined using a series of independent *t*-tests with Bonferroni-adjusted *P* values. To increase sample size (number of good wildflower years), the Mojave and Sonoran deserts were pooled for this analysis such that a good wildflower year in either desert was treated as a good wildflower year in the pooled sample. Seasonal SOI was calculated by averaging monthly values within each of the following seasons: January to December before spring bloom, January to June before spring bloom, July to December before spring bloom, May to April before and during spring bloom, and October to April before and during spring

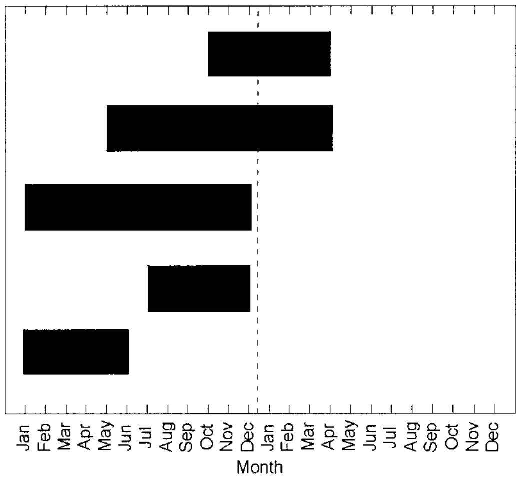

FIG. 2. Schematic representation of periods used in calculating seasonal SOI in the months before spring bloom. Year of spring bloom is right of the vertical dashed line.

bloom (Fig. 2). A separate *t*-test was performed for each season. SOI values were provided by the Climatic Research Unit, University of East Anglia, United Kingdom (Climatic Research Unit 2003).

Results from the previous analysis were used to redefine El Niño years for the purpose of this study. This was not an attempt to redefine El Niño climatologically but an effort to reorganize the salient fact of El Niño (negative SOI) in a way that had meaning for spring-flowering annuals. Specifically, an aperiodic and temporally diffuse phenomenon (ENSO) was redefined so that it could be compared with a periodic and temporally limited phenomenon (spring bloom). El Niño years were redefined using the seasonal SOI that produced the highest *t*-statistic.

The association between redefined El Niño years and good wildflower years was examined for the combined Mojave and Sonoran deserts. Presence/absence of redefined El Niño was compared with presence/absence of good wildflower years in each year from 1900 to 1999. An odds-ratio test was used to determine the independence of good wildflower years from redefined El Niño years. The connection between SOI and spring displays in redefined El Niño years was also examined graphically. After redefined El Niño years were categorized as good for wildflowers or not (deserts pooled), monthly SOI was averaged across all years within each category and plotted to show changing patterns from

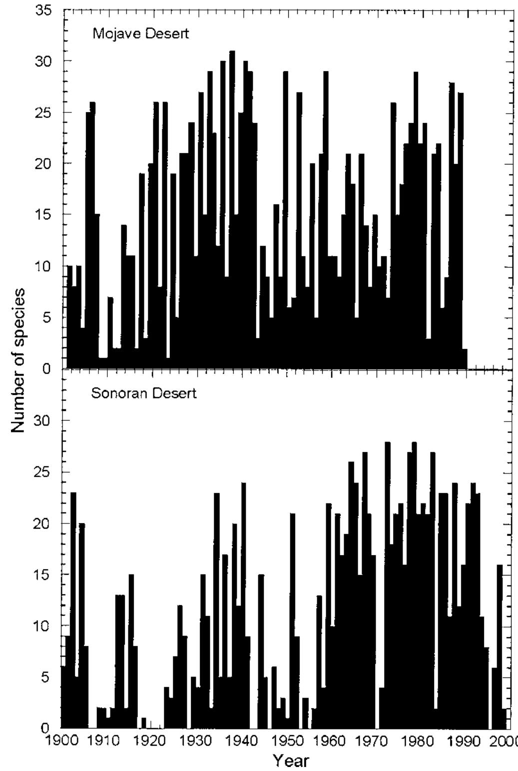

FIG. 3. Number of target species collected in the Mojave and Sonoran deserts between 1900 and 1999.

January to December in both the year before and the year of spring bloom.

To assess the amount of moisture needed to ensure a good wildflower year, total rain for autumn (September to December) and spring (January to March) was determined for every year of record for four stations in California (Needles, Brawley, Death Valley, Independence) and three stations in Arizona (Tucson, Mesa, Gila Bend). Stations were selected on the basis of spatial distribution and duration of record. For every good wildflower year, the percent difference from the long-term average was calculated. In addition, patterns of seasonal rain were examined by averaging September to December, January to March, and September to March rain across the California or Arizona stations, then plotting frequency (number of years) in 20 mm rainfall classes.

Results and Discussion. IDENTIFICATION OF GOOD WILDFLOWER YEARS. The average number of target species collected/year was 14.6 $\pm$ 9.2 and 10.9 $\pm$ 9.1 in the Mojave and Sonoran deserts, respectively (Fig. 3). Good wildflower years were those in which the detrended species number was >9.2 (Mojave Desert) or >9.1 (Sonoran Desert). In the Mojave Desert, good wildflower years occurred about 20% of the time, in the Sonoran Desert, about 14% of the time (Fig. 4). Possibly some good years were missed and some other years were incorrectly identified as good; however, objective and subjective ratings agreed 91% and 92% of the time for the Mojave and Sonoran deserts, respectively, showing that good wildflowers years as defined by this study closely matched those identified by other sources. Probabilities of good and bad years can be estimated from climatic records (e.g., Sheve 1951, Philippi 1993, Clauss and Venable 2000) but rely on somewhat circular logic; the objective method allows estimates to be made on a botanical basis.

El Nino Episodes and Displays of Spring-Flowering Annuals. Between 1900 and 1999, there were 27 El Niño episodes and 27 interims. In the Mojave and Sonoran deserts respectively, 60% (12 of 20) and 57% (8 of 14) of good wildflower years happened during or immediately after El Niño episodes. Thus, in either desert, slightly more than half of good wildflower years could be ascribed to the influence of climatologically defined El Niño events. The association was surprisingly weak given the strong popular belief that El Niño brings about showy wildflower displays (*New York Times*, March 30, 1998). Also surprising was that many El Niño episodes apparently did not give rise to remarkable spring displays. In the Mojave Desert, 61% (14 of 23 episodes before 1990) were not associated with good wildflower displays. The proportion was slightly higher in the Sonoran Desert, 70% (19 of 27 episodes before 2000). One reason for the inconsistency of ENSO effects is that El Niño episodes vary in magnitude, spatial coverage, onset and duration (Philander 1990). Between 1951 and 1994, for example, El Niño began in any month from February to September and lasted for 7 to 19 months (Trenberth 1997). Variability in timing, distribution, and strength means that El Niño increases the likelihood of a wet winter from even odds to 75% at most (Redmond 1998), resulting in a less-than-perfect relation between El Niño episodes and good wildflower years.

SOI and Displays of Spring-Flowering Annuals. The phasing of El Niño events–that is, the time of year when SOI shifts into negative values–has profound biological implications. If El Niño is to enhance cool-season precipitation in time to promote abundance and diversity of spring-flowering annuals, sea-surface temperatures in the tropical Pacific must shift from cool to warm several months before the start of the winter rainy season. In this study, two measures of seasonal SOI differed between good and other wildflower years: the May to April before and during spring bloom (t = 3.0, Bonferroni-adjusted P = 0.02), and the July to December before spring bloom (t = 3.5, Bonferroni-adjusted P = 0.005). In the May to April before and during good wildflower years, average SOI was −0.48 (S.D. = 0.800). During other years, it was considerably greater, 0.05 (S.D. = 0.774). Similarly, the average July-to-December value was −0.57 (S.D. = 0.816) before good wildflower years and 0.09 (S.D. = 0.830) before other years. These results provided a phenological basis for redefining El Niño as any calendar year when average SOI from July to December was negative; 57 such years occurred in the 20th century. There was good consensus between reorganized SOI values and traditional El Niño episodes: 24 of 27 El Niño episodes were represented among the redefined El Niño years.

Of 27 good wildflower years in the Mojave and Sonoran deserts, 21 followed redefined El Niño years (Fig. 4). Good wildflower years were 3.6 times more likely in redefined El Niño years than in other years ($P < 0.05$). The widely perceived connection between El Niño and spring-flowering annuals certainly exists but is obscured by the traditional definition of El Niño episodes. The link is much more obvious when El Niño is restated in terms of negative SOI some two to nine months before spring bloom. Note, however, that 36 of 57 redefined El Niño years were not followed by good wildflower displays. Figure 5 suggests that on average such years are characterized by moderately rather than strongly negative SOI in the summer and autumn before spring bloom.

Patterns of spring bloom doubtless reflect sources of climatic variability besides ENSO. Precipitation in the southwestern United States shows strong interdecadal fluctuations that can be ascribed to regional and global patterns of atmospheric circulation and sea-surface temperature (Cayan et al. 1998). Such decadal patterns might account at least in part for clustering of good wildflower years (Fig. 4). One source of decadal variability is the Pacific Decadal Oscillation (PDO), a measure of relative sea-surface temperatures in the northern Pacific Ocean

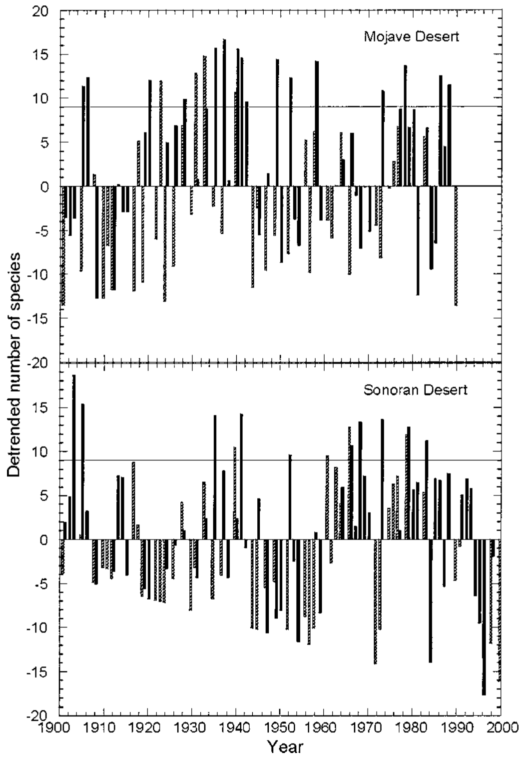

FIG. 4. Good and other wildflower years in the Mojave and Sonoran deserts during the 20th century. Good wildflower years were those in which detrended number of target species was > 9.2 (Mojave Desert) or > 9.1 (Sonoran Desert) (horizontal lines). Dark bars show number of species in springs following redefined El Niño years; light bars show number of species in springs following other years. Redefined El Niño years were calendar years in which average SOI from July to December was negative.

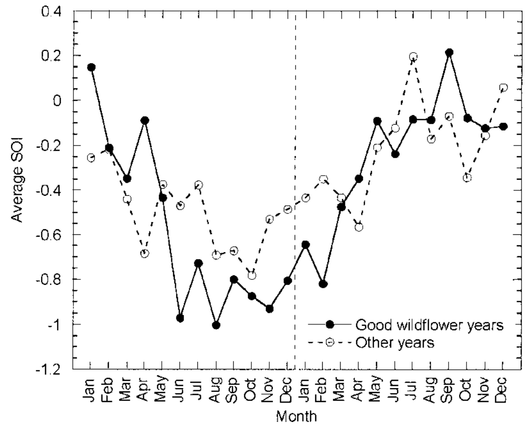

FIG. 5. Average monthly SOI in redefined El Niño years with (closed circles) and without (open circles) good wildflower displays in the Mojave and Sonoran deserts. Redefined El Niño years were calendar years in which average SOI from July to December was negative. Year of spring bloom is right of the vertical dashed line.

(McCabe and Dettinger 1999). Enhanced winter precipitation in the southwestern United States is correlated with positive PDO values, droughts with negative values. PDO conditions can strengthen the climatic effects of ENSO (Gershunov et al. 1999, McCabe and Dettinger 1999). During the 1950s, for example, prolonged negative PDO and frequent positive SOI combined to produce severe winter drought, and as a result there were few good displays of spring-flowering annuals.

In the late Wisconsin and early Holocene (10,000 to 12,000 yr BP), a period of wetter, milder winters and cooler summers than today (Van Devender et al. 1990, 1991), a diverse flora of spring-flowering annuals occurred in *Pinus-Juniperus* woodlands throughout much of the present-day Sonoran Desert (Van Devender 1987, Van Devender et al. 1991, Van Devender and Wiens 1993, McAuliffe and Van Devender 1998) (Fig. 6). Spring-flowering annuals are rare in the midden record before 12,000 yr BP (Fig. 6); the phenomenon is probably real rather than an artifact of preservation (McAuliffe and Van Devender 1998). Starting about 8,000 to 9,000 yr BP, the regional climate became drier, especially in winter, and woodlands retreated upslope to be replaced by desert-scrub (Van Devender and Spaulding 1979, Betancourt et al. 1993, Spaulding 1995). This period of winter drought lasted through the mid-Holocene and was most likely accompanied by increased summer rainfall (Davis and Shafer 1992, McAuliffe and Van Devender 1998, Betancourt et al. 2001). The diversity of spring-flowering annuals in packrat middens from eight Sonoran Desert sites dropped steeply after about 8,000 years before the present (B.P.) (Fig. 6). Paleoenvironmental records indicate that ENSO did not operate until 5,000 to 6,000 yr BP (Markgraf and Diaz 2000, Andrus et al. 2002). After 3,000 years BP, by which time ENSO was well established, there was an increase in diversity of spring-flowering annuals in the macrofossil record (Fig. 6). The resurgence might have been stimulated in part by the appearance of ENSO and its abundant cool-season moisture.

Axelrod (1979) suggested that many spring-flowering annuals in the Sonoran Desert, especially those with affinities to the California flora, are relicts of the Wisconsin. Others have argued that spring-flowering annuals, especially in large

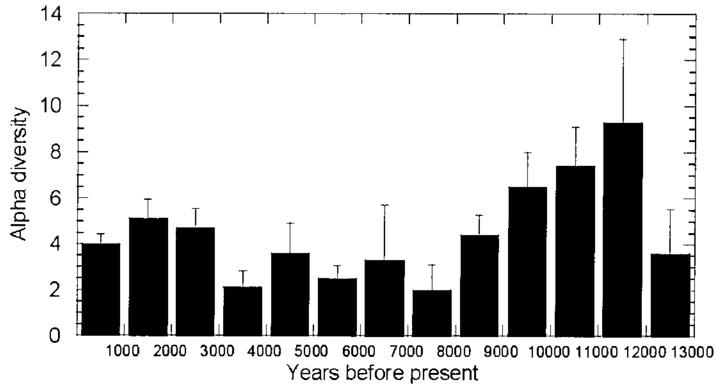

FIG. 6. Alpha diversity (± SE) of spring-flowering annuals (forbs and grasses) represented in packrat middens from eight Sonoran Desert sites. The number of species present in 1000-year increments was summed across all sites then divided by the number of samples. Not all sites were represented in each 1000-year period. Data are from Cole (1986), Van Devender (1987), Van Devender et al. (1990, 1991, 1994), Anderson and Van Devender (1991), Van Devender and Wiens (1993), and McAuliffe and Van Devender (1998).

genera such as *Cryptantha*, *Camissonia*, *Phacelia*, *Gilia*, and *Chorizanthe*, might have evolved much more recently than the early Holocene, perhaps even in the past 2,000 to 3,000 years (McLaughlin 1986, Thorne 1986), that is, after ENSO became established. Either way, an argument could be made that many spring-flowering annuals are present today only because of ENSO. In the first case, El Niño episodes effectively recreate the cool, moist conditions of the latest Pleistocene. In the second case, recurrent El Niños simply continue the conditions under which species might have evolved.

Indirect evidence in favor of these ideas is that spring-flowering annuals do not appear to be especially well-adapted to arid conditions (Forseth et al. 1984). Their high rates of transpiration and photosynthesis depend upon ample soil moisture, for example (Forseth et al. 1984). The rosette growth-form allows leaf develop-

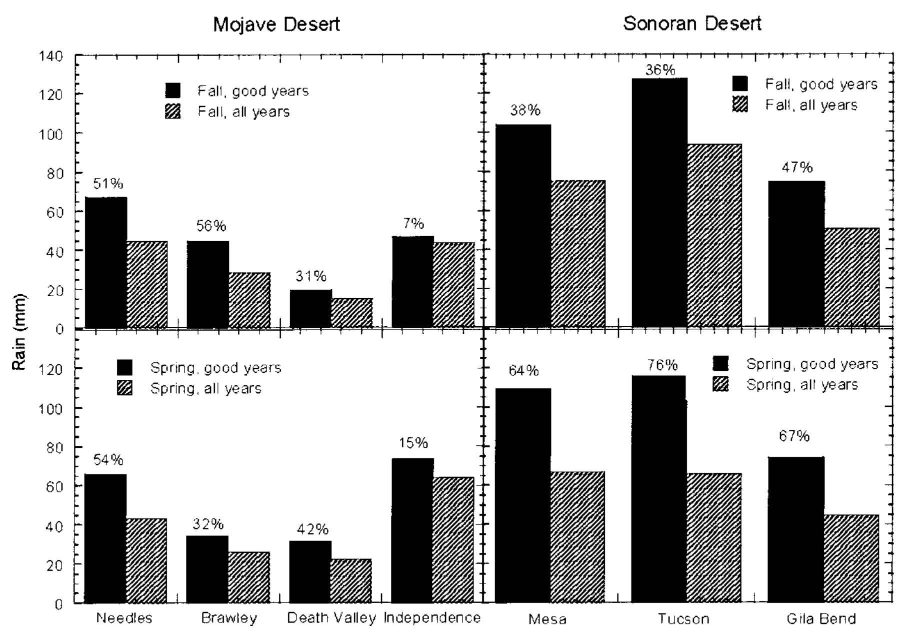

FIG. 7. Seasonal rain (mm) at stations in the Mojave and Sonoran deserts. Dark bars show average of all good years; long-term means are represented by light bars. Values above bars show percent difference from long-term means.

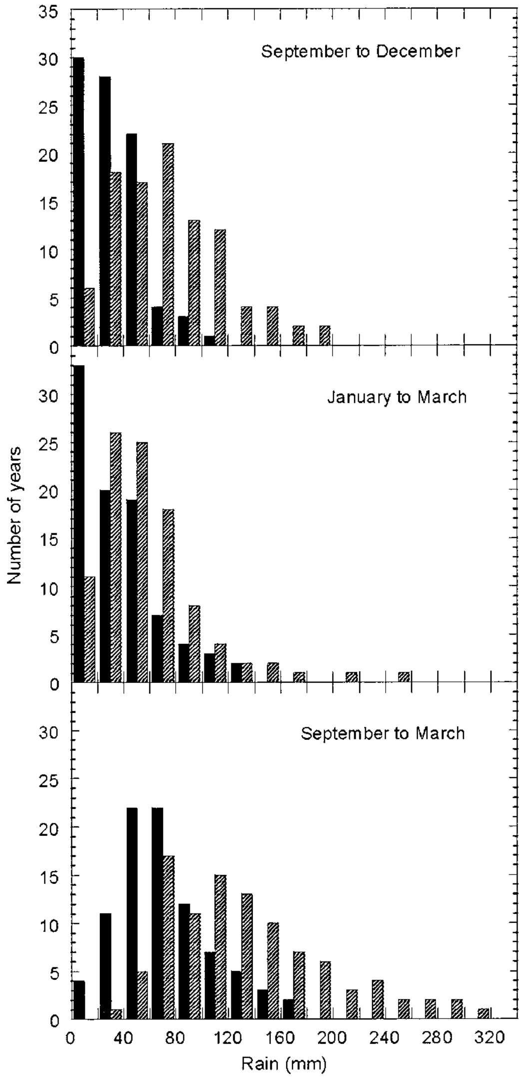

FIG. 8. Frequency distribution of seasonal rains in the Mojave (black bars) and Sonoran (gray bars) deserts. Seasonal rain in each year was averaged across four (Mojave Desert) or three (Sonoran Desert) stations.

ment during winter when temperatures are cold (Mulroy and Rundel 1977), suggesting adaptation to a relatively cool climate. The annual cycle of seed dormancy in at least one species is typical of annuals found in predictably moist environments (Baskin et al. 1993). For those species that predate the formation of deserts in the Holocene, occasional El Niño episodes are now the most reliable source of cool-season moisture available.

RAINFALL REQUIREMENTS FOR GOOD WILDFLOWER YEARS. Although anecdotal evidence suggests how much rain is required for germination (Tevis 1958a, b; Beatley 1974, Clauss and Venable 2000), few studies have addressed the total amount needed for spring-flowering annuals to be diverse, robust and abundant over a broad area. At three Sonoran Desert stations, long-term averages for September to December and for January to March were 73.4 mm and 58.9 mm, respectively (N = 99 years). In good wildflower years, September to December rain exceeded the long-term mean by 36 to 47%, January to March rain by 64 to 76% (Fig. 7). Long-term average rain at four Mojave Desert stations was 33.0 mm from September to December, 37.8 mm from January to March (N = 86 years). At these stations, too, seasonal rain during good wildflower years exceeded the long-term average, although to a lesser degree (Fig. 7). The frequency distribution of seasonal rains in both deserts was left-skewed, indicating that very wet seasons were rare, dry seasons common, but less so for the Sonoran than for the Mojave desert stations (Fig. 8).

Between September and March, Sonoran Desert stations averaged twice as much rain as Mojave Desert stations, both during good wildflower years and over the long term. From the Mojave Desert stations, it would appear that at least 100 mm of rain between September and March is required for a good wildflower display; from the Sonoran Desert stations, a minimum of 200 mm would seem necessary (Fig. 7). The difference is likely real rather than a matter of which stations were selected for analysis. Average September to March rain at the three Sonoran Desert stations frequently exceeded 100 mm; if that amount were enough for a good wildflower year in the Sonoran Desert, there would have been 80 such between 1900 and 1999. Similarly, if 200 mm of rain were necessary for good displays of spring-flowering annuals in the Mojave Desert, there would have been none between 1900 and 1999. Apparently spring-flowering annuals in the Mojave Desert have less stringent moisture requirements for germination. Differences among sites in effective precipitation might account at least in part for divergent germination requirements. Because the Mojave Desert is generally colder in winter than the Sonoran Desert, evapotranspiration is reduced; as a result, smaller amounts of rain might be needed to trigger germination. Various workers have reported clinal variation in the amount of water required to germinate annuals, with seeds from xeric locations needing less than those from wetter sites (e.g., Cruden 1974, Clauss and Venable 2000). From these findings, it appears that genotypic differences within species might also influence how much moisture is needed for good wildflower years in the Mojave and Sonoran deserts.

Literature Cited

Anderson, R. S. and T. R. Van Devender. 1991. Comparison of pollen and macrofossils in packrat (*Neotoma*) middens: a chronological sequence from the Waterman Mountains of southern Arizona, U.S.A. Review of Palaeobotany and Palynology 68: 1–28.

Andrade, E. R., Jr.and W. D. Sellers. 1988. El Niño and its effect on precipitation in Arizona and western New Mexico. J. Climatol. 8: 403–410.

Andrus, C. F. T., D. E. Crowe, D. H. Sandweiss, E. J. Reitz and C. S. Romanek. 2002. Otolith δ^{18}O record of mid-Holocene sea surface temperatures in Peru. Science 295: 1508–1511.

Arizona-Sonora Desert Museum. 2000. Arizona-Sonora Desert Museum home page. <http://www.desertmuseum.org>. Accessed December 10, 2001.

Axelrod, D. I. 1979. Age and origin of Sonoran Desert vegetation. Occasional Papers of the California Academy of Science, no. 132. San Francisco, CA. 74 p.

Baskin, C. C., P. L. Chesson, and J. M. Baskin. 1993. Annual seed dormancy cycles in two desert winter annuals. J. Ecol. 81: 551–556.

Beatley, J. C. 1967. Survival of winter annuals in the northern Mojave Desert. Ecology 48: 745–750.

Beatley, J. C. 1969. Dependence of desert rodents on winter annuals and precipitation. Ecology 50: 721–724.

Beatley, J. C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55: 856–863.

Betancourt, J. L., E. A. Pierson, K. A. Rylander, J. A. Fairchild-Parks, and J. S. Dean. 1993. Influence of history and climate on New Mexico piñon-juniper woodlands, p. 42–62. USDA Forest Service General Technical Report RM-23. Fort Collins, CO.

Betancourt, J. L., K. A. Rylander, C. Peñalba, and J. L. McVickar. 2001. Late Quaternary vegetation history of Rough Canyon, south-central New Mexico, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 165: 71–95.

Bowers, M. A. 1987. Precipitation and the relative abundances of desert winter annuals: a 6-year study in the northern Mojave Desert. J. Arid Environ. 12: 141–149.

Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979. Granivory in desert ecosystems. Ann. Rev. Ecol. Syst. 10: 201–227.

Burk, J. H. 1982. Phenology, germination, and survival of desert ephemerals in Deep Canyon, Riverside County, California. Madroño 29: 154–163.

Cayan, D. R., M. D. Dettinger, H. F. Diaz, and N. E. Graham. 1998. Decadal variability of precipitation over western North America. J. Climate 11: 3148–3166.

Cayan, D. R., K. T. Redmond, and L. G. Riddle. 1999. ENSO and hydrologic extremes in the western United States. J. Climate 12: 2881–2893.

Clauss, M. J. and D. L. Venable. 2000. Seed germination in desert annuals: an empirical test of adaptive bet hedging. Am. Nat. 155: 168–186.

Climatic Research Unit. 2003. Climate Research Unit home page. <http://www.cru.uea.ac.uk>. Accessed January 21, 2004.

Cole, K. L. 1986. The lower Colorado River Valley: a Pleistocene desert. Quat. Res. 25: 392–400.

Cruden, R. W. 1974. The adaptive nature of seed germination in *Nemophila menziesii* Aggr. Ecology 55: 1295–1305

Davis, O. K. and D. S. Shafer. 1992. A Holocene climatic record for the Sonoran Desert from pollen analysis of Montezuma Well, Arizona. Palaeogeogr. Palaeoclimatol. Palaeoecol. 92: 107–119.

Forseth, I. N., J. R. Ehleringer, K. S. Werk, and C. S. Cook. 1984. Field water relations of Sonoran Desert annuals. Ecology 65: 1436–1444.

French, N. R., B. G. Maza, H. O. Hill, A. P. Aschwanden, and H. W. Kaaz. 1974. A population study of irradiated desert rodents. Ecol. Monogr. 44: 45–72.

Gershunov, A., T. P. Barnett, and D. R. Cayan. 1999. North Pacific interdecadal oscillation seen as factor in ENSO-related North American climate anomalies. EOS, Transactions, American Geophysical Union 80: 1– 2, 29–31.

Juhren, M, F. W. Went, and E. Phillips. 1956. Ecology of desert plants: IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. Ecology 37: 318–330.

Kearney, T. H. and R. H. Peebles. 1960. Arizona flora, 2nd ed. Univ. California Press, Berkeley, CA. 1085 p.

Kiladis, G. N. and H. F. Diaz. 1989. Global climatic anomalies associated with extremes in the Southern Oscillation. J. Climate 2: 1069–1090.

Markgraf, V. and H. F. Diaz. 2000. The past ENSO record: a synthesis, p. 465–488. *In* H. F. Diaz and V. Markgraf [eds.]. El Niño and the Southern Oscillation: multiscale variability and global and regional impacts. Cambridge Univ. Press, Cambridge, UK.

McAuliffe, J. R. and T. R. Van Devender. 1998. A 22,000-year record of vegetation change in the north-central Sonoran Desert. Palaeogeogr. Palaeoclimatol. Palaeoecol. 141: 253–275.

McCabe, G. J. and M. D. Dettinger. 1999. Decadal variations in the strength of ENSO teleconnections with precipitation in the western United States. International J. Climatol. 19: 1399–1410.

McLaughlin, S. P. 1986. Floristic analysis of the southwestern United States. Great Basin Nat. 46: 46–65.

Morgan Ernest, S. K., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88: 470–482.

Mulroy, T. W. and P. W. Rundel. 1977. Annual plants: adaptations to desert environments. BioScience 27: 109–114.

Nabhan, G. P. and J. Cole [tech. eds.]. 1988. Arizona Highways presents desert wildflowers. Arizona Department of Transportation, Phoenix, AZ.

NELSON, J. F. AND R. M. CHEW. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. Am. Midl. Nat. 97: 300–320.

PHILANDER, S. G. 1990. El Niño, La Niña, and the Southern Oscillation. Academic Press, San Diego, California. 293 p.

PHILIPPI, T. 1993. Bet-hedging germination of desert annuals: variation among populations and maternal effects in *Lepidium lasiocarpum*. Am. Nat. 142: 488–507.

QUINN, W. H., V. T. NEAL, AND S. E. ANTUNEZ DE MAYOLO. 1987. El Niño occurrences over the past four and a half centuries. J. Geophys. Res. 92: 14449–14461.

RAVEN, P. H. AND D. I. AXELROD. 1978. Origin and relationships of the California flora. University of California Publications in Botany no. 72.

REDMOND, K. T. AND R. W. KOCH. 1991. Surface climate and streamflow variability in the western United States and their relationship to large-scale circulation indices. Water Resour. Res. 27: 2381–2399.

REDMOND, K. T. 1998. Western Regional Climate Center home page. <http://www.wrcc.dri.edu>. Accessed January 28, 2004.

ROPELEWSKI, C. F. AND M. S. HALPERT. 1986. North American precipitation and temperature patterns associated with the El Niño/Southern Oscillation (ENSO). Monthly Weather Rev. 114: 2352–2362.

RUNDEL, P. W. AND A. C. GIBSON. 1996. Ecological communities and processes in a Mojave Desert ecosystem, Rock Valley, Nevada. Cambridge Univ. Press, Cambridge, UK. 369 p.

SHREVE, F. 1942. The desert vegetation of North America. Bot. Rev. 8: 195–246.

SHREVE, F. 1951. Vegetation of the Sonoran Desert. Carnegie Institution of Washington Publication no. 591. Washington, D.C.

SPAULDING, W. G. 1995. Environmental change, ecosystem responses, and the late Quaternary development of the Mojave Desert, p. 139–164. *In* D. W. Steadman and J. I. Mead [eds.]. Late Quaternary environment and deep history: a tribute to Paul S. Martin. The Mammoth Site of Hot Springs Inc., Hot Springs, South Dakota.

SYSTAT. 1998. Statistics. SPSS, Inc., Chicago, IL. 1086 p.

TEVIS, L., JR. 1958a. Germination and growth of ephemerals induced by sprinkling a sandy desert. Ecology 39: 681–688.

TEVIS, L., JR. 1958b. A population of desert ephemerals germinated by less than one inch of rain. Ecology 39: 688–695.

THORNE, R. F. 1986. A historical sketch of the vegetation of the Mojave and Colorado deserts of the American Southwest. Ann. Mo. Bot. Gard. 73: 642–651.

TRENBERTH, K. E. 1997. The definition of El Niño. Bull. Am. Meteorol. Soc. 78: 2771–2777.

TURNAGE, W. V. AND T. D. MALLERY. 1941. An analysis of rainfall in the Sonoran Desert and adjacent territory. Carnegie Institution of Washington Publication no. 529. Washington, DC.

TURNER, R. M. 1994. Mojave desertscrub, p. 157–168. *In* D. E. Brown (ed.). Biotic communities: southwestern United States and northwestern Mexico. Univ. Utah Press, Salt Lake City, UT.

TURNER, R. M. AND D. E. BROWN. 1994. Sonoran desertscrub, p. 181–221. *In* D. E. Brown [ed.]. Biotic communities: southwestern United States and northwestern Mexico. Univ. Utah Press, Salt Lake City, UT.

UNIVERSITY OF CALIFORNIA. 2001. University and Jepson herbaria home page. <http://www.ucjeps.berkeley.edu>. Accessed December 8, 2001.

VAN DEVENDER, T. R. 1987. Holocene vegetation and climate in the Puerto Blanco Mountains, southwestern Arizona. Quat. Res. 27: 51–72.

VAN DEVENDER, T. R., T. L. BURGESS, R. S. FELGER AND R. M. TURNER. 1990. Holocene vegetation of the Hornaday Mountains of northwestern Sonora, Mexico. Proc. S. Diego Soc. Nat. Hist. 2: 1–19.

VAN DEVENDER, T. R., T. L. BURGESS, J. C. PIPER AND R. M. TURNER. 1994. Paleoclimatic implications of Holocene plant remains from the Sierra Bacha, Sonora, Mexico. Quat. Res. 41: 99–108.

VAN DEVENDER, T. R., J. I. MEAD AND A. M. REA. 1991. Late Quaternary plants and vertebrates from Picacho Peak, Arizona. Southwest. Nat. 36: 302–314.

VAN DEVENDER, T. R. AND W. G. SPAULDING. 1979. Development of vegetation and climate in the southwestern United States. Science 204: 701–710.

VAN DEVENDER, T. R. AND J. F. WIENS. 1993. Holocene changes in the flora of Ragged Top, south-central Arizona. Madroño 40: 246–264.

VENABLE, D. L. AND C. E. PAKE. 1999. Population ecology of Sonoran Desert annual plants, p. 115–142. *In* R. H. Robichaux [ed.]. Ecology of Sonoran Desert plants and plant communities. Univ. Arizona Press, Tucson, AZ.

WEBB, R. H. AND J. L. BETANCOURT. 1992. Climatic variability and flood frequency of the Santa Cruz River, Pima County, Arizona. U.S. Geological Survey Water-Supply Paper 2379. U.S. Government Printing Office, Washington, DC.

WENT, F. W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. Ecology 29: 242–253.

WENT, F. W. 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. Ecology 30: 1–13.

WENT, F. W. AND M. WESTERGAARD. 1949. Ecology of desert plants. III. Development of plants in the Death Valley National Monument, California. Ecology 30: 26–38.

WILCOTT, J. C. 1974. A seed demography model for finding optimal strategies for desert annuals. Ph.D. dissertation, Utah State University, Logan, UT.

ZABRISKIE, J. G. 1979. Plants of Deep Canyon and the central Coachella Valley, California. Philip L. Boyd Deep Canyon Desert Research Center, Univ. California, Riverside, CA. 175 p.