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COMPARATIVE FLOWERING PHENOLOGY OF PLANTS IN THE WESTERN MOJAVE DESERT

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ABSTRACT

Above-average precipitation fell on the western Mojave Desert in February and March 1991, which resulted in the flowering of most plant species that spring. This mass germination event occurred despite the almost total lack of rainfall between September and December 1990, a finding inconsistent with previous observations from the Mojave Desert. The 58+ annual species observed on the study site flowered in a sequential manner from early March to mid-June, 1991.

Climatic phenomena were similar the following year, as several winter storms produced large amounts of precipitation in February and March 1992. Consequently, at least 63 annual and 15 perennial plant species bloomed over spring 1992. Like the previous year, plants flowered sequentially from early March to late June. An analysis of flowering dates between years suggests that timing of flowering for these species is highly consistent from year to year. Some phylogenetic biases in flowering dates were evident among some of the locally-dominant taxa. Species in the families Brassicaceae and Boraginaceae flowered in early spring, whereas species in the Fabaceae, Asteraceae, and Polygonaceae, bloomed from mid- to late-spring. However, Polemoniaceous species flowered throughout spring.

The Mojave Desert has a remarkably diverse ephemeral plant flora consisting of over 250 species and varieties (Shreve and Wiggins 1964). As a result, this region has long attracted biologists interested in germination and flowering phenomena of desert plants (Went 1948, 1949; Juhren et al. 1956; Tevis 1958a, b; Beatley 1967, 1969, 1974; Johnson et al. 1978). These studies from various localities in the Mojave Desert have reached similar conclusions as to environmental requirements for successful germination and community-wide flowering phenology.

Germination of Mojave Desert winter annuals may be a straightforward consequence to particular environmental conditions with regards to the quantity and timing of precipitation. In general, it is thought that a minimum of 20–25 mm of rain is required for successful germination of winter annuals (Went 1948; Juhren et al. 1956; Tevis 1958a; Beatley 1967, 1969, 1974). Seasonal timing of precipitation may also be a critical factor, as Beatley (1974) concluded that successful germination of winter annuals in the Mojave Desert is contingent upon a “critical autumn rain.”

Another common finding among previous studies is the observation that different plant species flower in a temporal sequence during the spring growing season. Beatley (1974), who extensively studied plants at the Nevada Test Site in the eastern Mojave Desert (Fig. 1), defined this phenomenon as follows: “flowering and fruiting are phenomena of April and May, with the precise time of anthesis, fruiting, and death varying among the species, and with the elevation and the season, but in any case proceeding in an orderly overlapping species sequence once in progress.” Tevis (1958b) also noted sequence-like flowering times for plants growing at

a Colorado Desert site. The “Colorado Desert” represents a subdivision of the Sonoran Desert biogeographic province located in southeastern California and is bounded by the Mojave Desert, Little San Bernardino Mountains, Peninsula Ranges, and Colorado River (Turner and Brown, 1982; Fig. 1). At another Colorado Desert site, Burk (1982) also documented interspecific variation in flowering phenology among 18 ephemeral species within and between the spring and summer growing seasons. Yet another example comes from the southern Atacama Desert of southern Chile where Vidiella et al. (1999) described the sequential flowering of 25 annual and perennial species during the spring season. Thus although deserts are defined by their scant and unpredictable precipitation, the within-season timing of flowering may be a more predictable occurrence.

In early 1991 and again in 1992 an El Niño/Southern Oscillation (ENSO) event produced large amounts of precipitation across the California deserts. This afforded the author an opportunity to study flowering phenologies of plants found in the western Mojave Desert. Here, I describe the flowering phenologies for the majority of annual and perennial species coexisting on a single site during spring 1991 and 1992. I also show that the temporal sequence of flowering within a single growing season is predictable.

MATERIALS AND METHODS

This study was conducted at the Desert Tortoise Natural Area (DTNA) in eastern Kern County, California. This 100 km² nature preserve, which is located along the western edge of the Mojave Desert (Fig. 1), contains a variety of vegetation communities including creosote bush scrub, Joshua tree

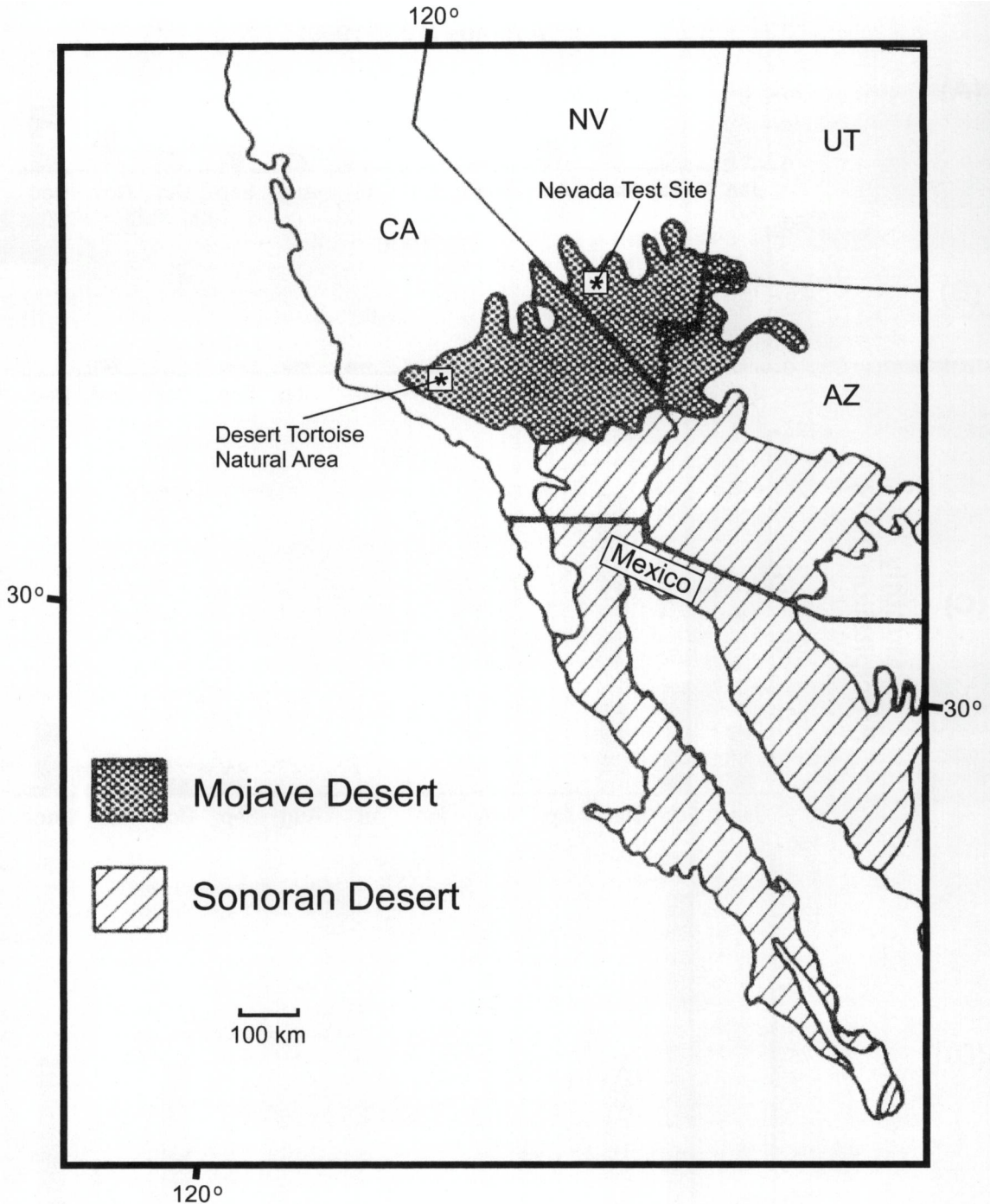


FIG. 1. Map showing the Mojave and Sonoran Deserts in the southwestern United States and adjacent Mexico (after MacMahon, 1988). The locations of the Desert Tortoise Natural Area (Kern County, California) and Nevada Test Site (Nye County, Nevada) are also shown.

woodland, saltbush scrub, and sandy wash. The flora of the DTNA is rich by Mojave Desert standards, as it is comprised of at least 126 annual and 57 perennial species.

Flowering phenologies of annuals and perennials

were studied in the northwestern corner of the DTNA (elevation ~900 m) between 1 March–12 June 1991 and 1 March–21 June 1992. Local topography consisted of flat sandy areas interspersed by sandy washes and low rolling, rocky, hills.

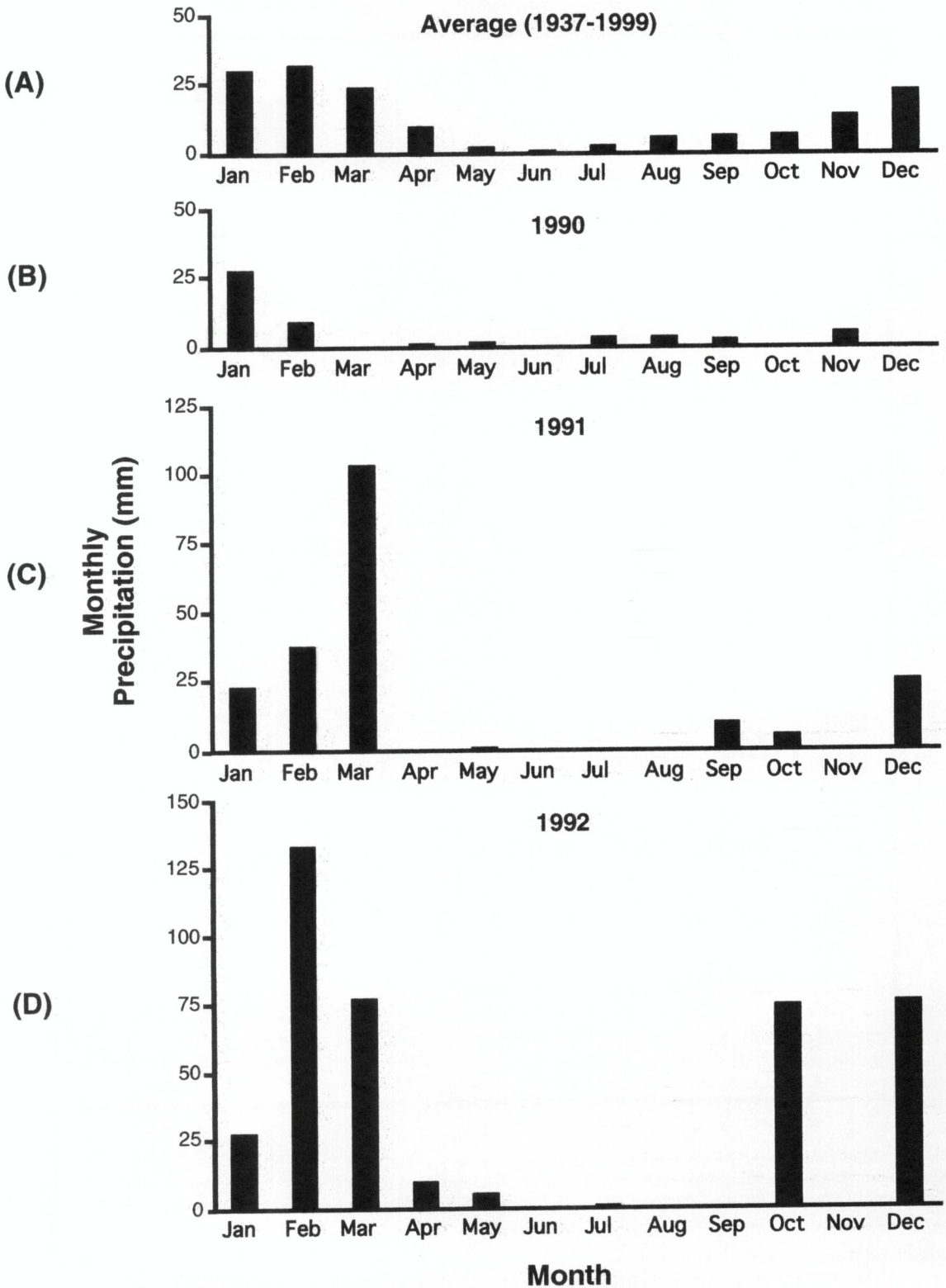


FIG. 2. Monthly precipitation in the western Mojave Desert measured at Randsburg, California 1937–1999: (A) average monthly precipitation for years 1937–1999, (B) total monthly precipitation during 1990, (C) total monthly precipitation during 1991, (D) total monthly precipitation during 1992 (data from NCDC 2000).

SPECIES	FAMILY	MARCH	APRIL	MAY	JUNE
<i>Tropidocarpum gracile</i>	Brassicaceae	●			
<i>Erodium cicutarium</i>	Geraniaceae	●			
<i>Gilia minor</i>	Polemoniaceae	●			
<i>Phacelia fremontii</i>	Hydrophyllaceae	●			
<i>Lasthenia californica</i>	Asteraceae	●			
<i>Lepidium flavum</i>	Brassicaceae	●			
<i>Guillenia lasiophylla</i>	Brassicaceae	●			
<i>Amsinckia tessellata</i>	Boraginaceae	●			
<i>Linanthus dichotomus</i>	Polemoniaceae	●			
<i>Pectocarya</i> spp.	Boraginaceae	●			
<i>Phacelia tanacetifolia</i>	Hydrophyllaceae	●			
<i>Coreopsis bigelovii</i>	Asteraceae	●			
<i>Cryptantha angustifolia</i>	Boraginaceae	●			
<i>Pholistoma membranaceum</i>	Hydrophyllaceae	●			
<i>Cryptantha nevadensis</i>	Boraginaceae	●			
<i>Eschscholzia minutiflora</i>	Papaveraceae	●			
<i>Mentzelia eremophila</i>	Loasaceae	●			
<i>Caulanthus inflatus</i>	Brassicaceae		●		
<i>Oxytheca perfoliata</i>	Polygonaceae		●		
<i>Chorizanthe watsonii</i>	Polygonaceae		●		
<i>Chorizanthe brevicornu</i>	Polygonaceae		●		
<i>Mentzelia</i> spp.	Loasaceae		●		
<i>Gilia latiflora</i>	Polemoniaceae		●		
<i>Syntrichopappus fremontii</i>	Asteraceae		●		
<i>Caulanthus cooperi</i>	Brassicaceae		●		
<i>Camissonia palmeri</i>	Onagraceae		●		
<i>Cryptantha pterocarya</i>	Boraginaceae		●		
<i>Lupinus odoratus</i>	Fabaceae		●		
<i>Descurainia pinnata</i>	Brassicaceae		●		
<i>Camissonia campestris</i>	Onagraceae		●		
<i>Eriogonum pusillum</i>	Polygonaceae		●		
<i>Salvia columbariae</i>	Lamiaceae		●		
<i>Plantago ovata</i>	Plantaginaceae		●		
<i>Salvia carduacea</i>	Lamiaceae		●		
<i>Chaenactis fremontii</i>	Asteraceae		●		
<i>Calycosœris parryi</i>	Asteraceae		●		
<i>Cryptantha circumcissa</i>	Boraginaceae		●		
<i>Malacothrix glabrata</i>	Asteraceae		●		
<i>Nama demissum</i>	Hydrophyllaceae		●		
<i>Lotus humistratus</i>	Fabaceae		●		
<i>Centrostegia thurberi</i>	Polygonaceae		●		
<i>Malacothrix coulteri</i>	Asteraceae		●		
<i>Eriophyllum pringlei</i>	Asteraceae		●		
<i>Eriogonum gracillimum</i>	Polygonaceae		●		
<i>Astragalus didymocarpus</i>	Fabaceae		●		
<i>Linanthus parryae</i>	Polemoniaceae		●		
<i>Glyptopleura marginata</i>	Asteraceae		●		
<i>Chaenactis carphoclinia</i>	Asteraceae		●		
<i>Loeseliastrum schottii</i>	Polemoniaceae		●		
<i>Eriogonum nidularium</i>	Polygonaceae		●		
<i>Nemacladus</i> spp.	Campanulaceae		●		
<i>Langloisia setosissima</i> ssp. <i>punctata</i>	Polemoniaceae		●		
<i>Camissonia boothii</i>	Onagraceae		●		
<i>Chorizanthe rigida</i>	Polygonaceae		●		
<i>Prenanthes exiguua</i>	Asteraceae		●		
<i>Eriastrum eremicum</i>	Polemoniaceae		●		
<i>Eriogonum angulosum</i>	Polygonaceae		●		
<i>Eremocarpus setigerus</i>	Euphorbiaceae		●		●

FIG. 3. Dates of first flowering for 58+ species of annual plants at the Desert Tortoise Natural Area, eastern Kern County, California during spring 1991.

SPECIES	FAMILY	MARCH	APRIL	MAY	JUNE
<i>Lepidium lasiocarpum</i>	Brassicaceae	█	█		
<i>Tropidocarpum gracile</i>	Brassicaceae	█	█		
<i>Pholistoma membranaceum</i>	Hydrophyllaceae	█	█		
<i>Pectocarya</i> spp.	Boraginaceae	█	█		
<i>Erodium cicutarium</i>	Geraniaceae	█	█	█	█
<i>Gilia minor</i>	Polemoniaceae	█	█		
<i>Cryptantha nevadensis</i>	Boraginaceae	█	█		
<i>Guillenia lasiophylla</i>	Brassicaceae	█	█		
<i>Cryptantha pterocarya</i>	Boraginaceae	█	█		
<i>Mentzelia</i> spp.	Loasaceae	█	█		
<i>Amsinckia tessellata</i>	Boraginaceae	█	█		
<i>Eschscholzia minutiflora</i>	Papaveraceae	█	█	█	█
<i>Lepidium flavum</i>	Brassicaceae	█	█		
<i>Lasthenia californica</i>	Asteraceae	█	█		
<i>Phacelia tanacetifolia</i>	Hydrophyllaceae	█	█		
<i>Phacelia fremontii</i>	Hydrophyllaceae	█	█		
<i>Caulanthus inflatus</i>	Brassicaceae	█	█		
<i>Caulanthus cooperi</i>	Brassicaceae	█	█		
<i>Linanthus dichotomus</i>	Polemoniaceae	█	█		
<i>Uropappus lindleyi</i>	Asteraceae	█	█		
<i>Astragalus acutirostris</i>	Fabaceae	█	█		
<i>Mentzelia eremophila</i>	Loasaceae	█	█		
<i>Malacothrix coulteri</i>	Asteraceae	█	█		
<i>Descurainia pinnata</i>	Brassicaceae	█	█		
<i>Syntrichopappus fremontii</i>	Asteraceae	█	█		
<i>Cryptantha circumscissa</i>	Boraginaceae	█	█		
<i>Camissonia campestris</i>	Onagraceae	█	█		
<i>Coreopsis bigelovii</i>	Asteraceae	█	█		
<i>Camissonia palmeri</i>	Onagraceae	█	█		
<i>Gilia latiflora</i>	Polemoniaceae	█	█		
<i>Linanthus parryae</i>	Polemoniaceae	█	█		
<i>Lupinus odoratus</i>	Fabaceae	█	█		
<i>Monoptilon bellioides</i>	Asteraceae	█	█		
<i>Centrostegia thurberi</i>	Polygonaceae	█	█		
<i>Eriogonum pusillum</i>	Polygonaceae	█	█		
<i>Astragalus didymocarpus</i>	Fabaceae	█	█		
<i>Oxytheca perfoliata</i>	Polygonaceae	█	█		
<i>Cryptantha angustifolia</i>	Boraginaceae	█	█		
<i>Eriophyllum pringlei</i>	Asteraceae	█	█		
<i>Malacothrix glabrata</i>	Asteraceae	█	█		
<i>Salvia carduacea</i>	Lamiaceae	█	█		
<i>Chaenactis fremontii</i>	Asteraceae	█	█		
<i>Nama demissum</i>	Hydrophyllaceae	█	█		
<i>Nemacladus</i> spp.	Campanulaceae	█	█		
<i>Calycoseris parryi</i>	Asteraceae	█	█		
<i>Plantago ovata</i>	Plantaginaceae	█	█		
<i>Chorizanthe watsonii</i>	Polygonaceae	█	█		
<i>Lotus humistratus</i>	Fabaceae	█	█		
<i>Glyptopleura marginata</i>	Asteraceae	█	█		
<i>Mucronea perfoliata</i>	Polygonaceae	█	█		
<i>Loeseliastrum schottii</i>	Polemoniaceae	█	█		
<i>Chaenactis carphoclinia</i>	Asteraceae	█	█		
<i>Salvia columbariae</i>	Lamiaceae	█	█		
<i>Chorizanthe brevicornu</i>	Polygonaceae	█	█		
<i>Eriogonum nidularium</i>	Polygonaceae	█	█		
<i>Eriogonum gracillimum</i>	Polygonaceae	█	█		
<i>Prenanthes exiguua</i>	Asteraceae	█	█		
<i>Camissonia boothii</i>	Onagraceae	█	█		
<i>Chorizanthe rigida</i>	Polygonaceae	█	█		
<i>Eriastrum eremicum</i>	Polemoniaceae	█	█		
<i>Langloisia setosissima</i> ssp. <i>punctata</i>	Polemoniaceae	█	█		
<i>Eriogonum angulosum</i>	Polygonaceae	█	█		
<i>Eremocarpus setigerus</i>	Euphorbiaceae	█	█		

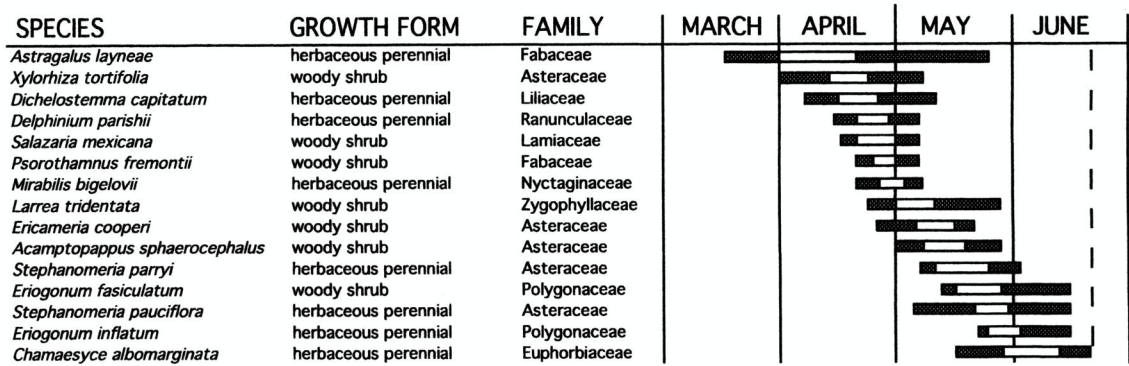


FIG. 5. Flowering phenologies for 15 species of perennial plants at the Desert Tortoise Natural Area, eastern Kern County, California during spring 1992. Horizontal bars illustrate the flowering phenology of each species as follows: shaded bar to left of white bar = “first flowering” stage, white bar = “peak flowering” stage; and shaded bar to right of white bar = “past-peak flowering” stage. Vertical dashed line shows the final day of observations, June 21, 1992.

Dominant species of shrubs in this area were *Larrea tridentata* (DC.) Cov., *Ambrosia dumosa* (A. Gray) Payne, and *Acamptopappus sphaerocephalus* A. Gray. Daily and monthly precipitation data were obtained from climatic records of Randsburg, California (22 airline km away), a NOAA station since 1937 (National Climatic Data Center [NCDC], 2000).

Observations were generally made several times per week throughout the study period. However, as this study was in a pilot stage during 1991, phenological data for that year only consists of dates of first flowering for each species, whereas the 1992 data set contains additional phenological data (see below) for each species. Field identification of species of *Nemacladus*, *Pectocarya*, and *Mentzelia* (except for *M. eremophila* (Jepson) H. J. Thompson & Joyce Roberts) proved difficult therefore I only considered these taxa at the level of genus and family in all analyses. Nomenclature follows Hickman (1993). Flowering phenology of each species was subjectively partitioned into four stages: “first flowering”: minority of individuals in flower; “peak flowering”: most individuals in flower; “past-peak flowering”: majority of individuals still succulent but few still in flower; and “dried”: majority of individuals in dried state or, in the case of shrubs, are completely in seed.

I analyzed seasonal variation in flowering dates by comparing the 1991 and 1992 first flowering dates for each annual species. Concordance of relative flowering dates would suggest that species’ flowering times are predictable.

RESULTS

Following 1990, a period of well-below normal precipitation, winter storms across the western Mojave Desert produced well-above average precipitation during February and March 1991 and again during the same period in 1992 (Fig. 2A–D; NCDC, 2000). Not only were climatic conditions nearly duplicated both years, but the diversity of plants that underwent flowering was also quite similar.

Annuals in 1991 flowered between early March and middle June (Fig. 3). Observations ended in middle June 1991 so it is unknown if any plants bloomed over summer. However, it is doubtful that many could have flowered because few annuals were even succulent in June. An examination of first flowering dates for 58+ annual species in 1991 reveals substantial temporal variation in flowering with some species beginning to flower in early March, while others didn’t start blooming until April, May, or even June (Fig. 3).

Complete flowering-phenology data were obtained for 63+ annual and 15 perennial species during spring 1992. Like 1991, much seasonal variation in flowering was apparent, as annuals and perennials apparently flowered in a sequential manner throughout spring (Fig. 4, 5). It remains unknown if any plants bloomed over summer 1992 but, again, few annuals were even green by June so it is doubtful the flowering season extended much further. Most annuals remained in their peak flowering stage for only 1–2 weeks but some main-

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FIG. 4. Flowering phenologies for 63+ species of annual plants at the Desert Tortoise Natural Area, eastern Kern County, California during spring 1992. Horizontal bars illustrate the flowering phenology of each species as follows: shaded bar to left of white bar = “first flowering” stage, white bar = “peak flowering” stage; and shaded bar to right of white bar = “past-peak flowering” stage. Vertical dashed lines shows the final day of observations, June 21, 1992.

tained this stage for up to a month (Fig. 4). Following the peak flowering stage very few annuals remained in flower beyond a month (Fig. 4). While some annuals began flowering in early March, no perennials bloomed until April (Fig. 5). However, like the annuals the perennials displayed considerable temporal variation in flowering (Fig. 5).

A comparison of first flowering dates for over 58 annual species between 1991 and 1992 indicates that between year flowering dates were remarkably similar (Fig. 6). This suggests that the observed temporal variation in flowering is mostly sequential and predictable. Furthermore, this sequence in flowering times occurred irrespective of growth form, as species of annuals, herbaceous perennials, and woody shrubs flowered throughout spring (Fig. 3–5).

An examination of the phenological sequence from the level of plant family suggests a possible phylogenetic connection, as species within the families Brassicaceae and Boraginaceae bloomed early in the growing season while the Fabaceae, Asteraceae, and Polygonaceae flowered relatively late (Fig. 7). However, not all families displayed seasonal specificity in flowering, as members of the Polemoniaceae flowered throughout spring (Fig. 7).

DISCUSSION

The variable nature of desert rainfall was evident in the western Mojave Desert during the early 1990s. Little rain fell in 1990 while relatively large amounts fell in early 1991 and again in 1992. These substantial rainfall events promoted the flowering of nearly every plant species known from the study site each year. The duration of the flowering season as well as the general flowering sequence of species was also strikingly similar both years.

Beatley (1967, 1969, 1974) hypothesized that successful germination of Mojave Desert winter annuals is contingent upon a >25 mm rainfall event occurring sometime between late September and mid-December. Yet apparently most winter annuals at the DTNA flowered throughout spring 1991 even though almost no rain fell in the area the previous autumn and early winter period. Therefore, germination of DTNA annuals must have occurred in response to ENSO-driven rains falling in early 1991. The first winter storm of 1991 passed through the area between January 3–5 leaving an accumulation of 19 mm of precipitation (Table 1). While some plants may have flowered in response to this minor rainfall event (see Went 1948; Beatley 1974), it seems much more likely that the storm(s) of February 28 through March 5 caused the massive flowering of plants, as over 67 mm of rain fell during this brief period (Table 1). Another series of storms passed through the area between March 19–28 resulting in a total of 73 mm of precipitation (Table 1).

Climatic and flowering phenomena during early

1992 were extraordinarily similar to the same period the year before. The autumn and early winter period of 1991 was very dry with only 22.5 mm of precipitation from five different rainfall events (Table 1). Flowering in early 1992 must have been triggered by the 47.1-mm rainfall event of late December to early January or the 134.5-mm event in early February (Table 1). Two additional storms passed through the area in early and late March leaving accumulations of 23.7 and 64 mm of rain respectively (Table 1).

These results are noteworthy because Beatley (1967, p. 746) noted that native winter annuals at the Nevada Test Site never germinated during the months January–September regardless of rainfall during this period. Why then did native winter annuals in the western Mojave Desert respond to late winter rainfall and in such dramatic fashion? The annual plant floras in the eastern and western regions of the Mojave Desert are roughly similar, especially at the level of family (Beatley 1967, 1974). This raises the possibility that winter annuals in the eastern Mojave Desert have different germination requirements than their relatives in the western Mojave Desert.

Indeed, geographic variation in climate may help explain this paradox. The eastern Mojave Desert experiences substantial rainfall events during summer and autumn (Beatley 1974; Turner 1982). Winter annuals in this region must have restrictive germination requirements otherwise a heavy downpour in the middle of summer could trigger germination, which might be maladaptive for these C_3 annuals (Mulroy and Rundel 1977). On the other hand, winter annuals in the western Mojave Desert are not faced with this problem owing to the lack of summer rainfall (Turner 1982) so more flexible germination requirements may be a more advantageous strategy. Cool and moist conditions during the late winter-spring period of 1991 and 1992 in the western Mojave Desert seemed to be ideal for winter annual growth and reproduction. Perhaps these plants would have “missed out” had they not responded to late winter precipitation. Thus, geographical differences in climate may select for region-specific germination strategies but more research is needed to precisely determine what environmental variables other than rainfall influence germination in these plants.

Sequential flowering of desert plants seems to be a general phenomenon and involving species of various growth forms and phylogenetic lineages (Beatley 1974; Tevis 1958b; Vidiella et al. 1999; this study; also see Poole and Rathcke 1979; Stiles 1979; Cole 1981; Rathcke 1984). While Beatley (1974) suggested that species' flowering times are predictable, to my knowledge there has been no multi-year comparison of flowering dates for any Mojave Desert community to corroborate this hypothesis. In the present study, I have demonstrated that first flowering dates for a winter annual com-

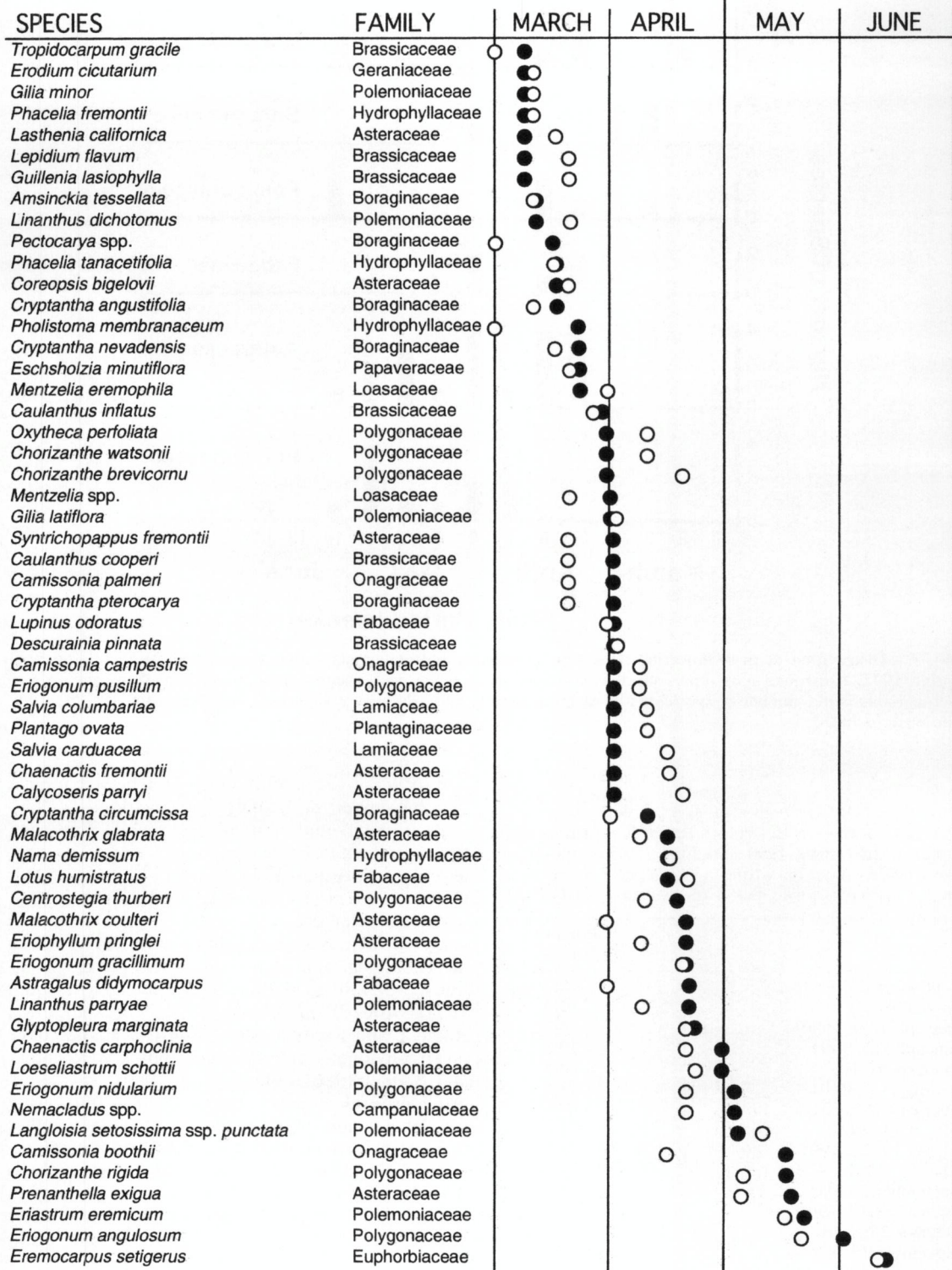


FIG. 6. First flowering dates for 58+ species of annual plants in 1991 (black circles) and 1992 (white circles) at the Desert Tortoise Natural Area, eastern Kern County, California.

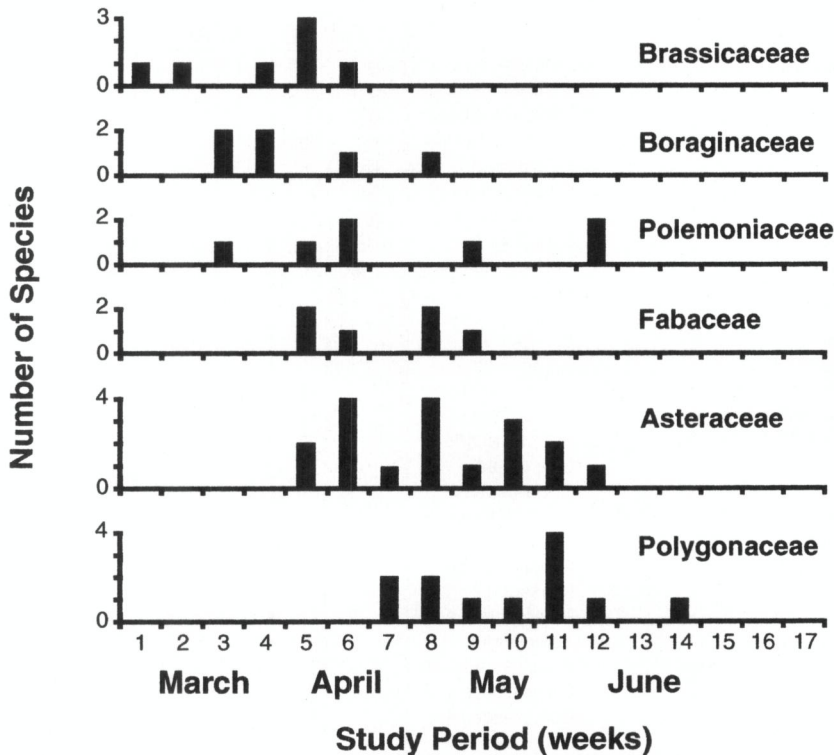


FIG. 7. Distribution of peak flowering dates among annuals and perennials within six selected families throughout spring 1992. Horizontal axis represents the particular week when each species entered its "peak-flowering" stage. Vertical axis is the number of species within a given family. Only families with at least six species found at the study site were included.

TABLE 1. RAINFALL EVENTS AT RANDSBURG, CALIFORNIA BETWEEN SEPTEMBER 1990 AND JUNE 1992. RAINFALL ON CONSECUTIVE DAYS OR WITHIN A 3-DAY PERIOD IS CONSIDERED A SINGLE RAINFALL EVENT (DATA FROM NCDC 2000).

	Rainfall (mm)
September 20, 1990	2.5
November 19, 1990	5.3
December 20, 1990	0.3
January 3–5, 1991	19.0
January 10, 1991	4.5
February 17, 1991	1.8
February 28–March 5, 1991	67.0
March 14, 1991	1.0
March 19–28, 1991	73.1
May 21, 1991	1.0
September 5, 1991	6.0
September 22, 1991	3.8
October 26, 1991	5.3
November 14, 1991	0.5
December 8–11, 1991	7.0
December 28–January 8, 1992	47.1
February 6–16, 1992	134.5
March 1–7, 1992	23.8
March 21–April 2, 1992	64.8
May 7, 1992	5.8

munity were remarkably consistent between years thereby supporting Beatley's observations.

As to the evolution of species' specific flowering times, this could be driven either by ecological interactions (Mosquin 1971; Stiles 1977; Waser 1978; Gleeson 1981; Rathcke and Lacey 1985) or by phylogenetic relatedness (Vidiella et al. 1999; this study). Previous investigations have largely taken the ecological approach such as looking at the influence of limited pollinator availability (Mosquin 1971; Stiles 1977; Waser 1978; Gleeson 1981; Rathcke and Lacey 1985), while few studies have taken phylogeny into account (but see Kochmer and Handel 1986; Vidiella et al. 1999). This study provides weak evidence that the timing of flowering for some plants may be due to phylogeny rather than solely to ecological factors. Additional research should be undertaken in an effort to elucidate the relative roles of ecology and phylogeny in arranging the temporal aspect of plant community structure.

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LITERATURE CITED

- BEATLEY, J. C. 1967. Survival of winter annuals in the northern Mojave Desert. *Ecology* 48:745-750.
- . 1969. Biomass of desert winter annual plant populations in southern Nevada. *Oikos* 20:261-273.
- . 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55:856-863.
- BURK, J. H. 1982. Phenology, germination, and survival of desert ephemerals in Deep Canyon, Riverside County, California. *Madroño* 29:154-163.
- COLE, B. J. 1981. Overlap, regularity, and flowering phenologies. *American Naturalist* 117:993-997.
- GLEESON, S. K. 1981. Character displacement in flowering phenologies. *Oecologia* 51:294-295.
- HICKMAN, J. C. 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley.
- JOHNSON, H. B., F. C. VASEK, AND T. YONKERS. 1978. Residual effects of summer irrigation on Mojave Desert annuals. *Bulletin Southern California Academy of Science* 77:95-108.
- 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.
- KOCHMER, J. P. AND S. N. HANDEL. 1986. Constraints and competition in the evolution of flowering phenology. *Ecological Monographs* 56:303-325.
- MACMAHON, J. A. 1988. Warm deserts. Pp. 231-264 in M. G. Barbour and W. D. Billings (eds.), *North American terrestrial vegetation*, 1st ed. Cambridge University Press, NY.
- MOSQUIN, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* 22:398-402.
- MULROY, T. W. AND P. W. RUNDEL. 1977. Annual plants: adaptations to desert environments. *Bioscience* 27:109-114.
- NATIONAL CLIMATIC DATA CENTER. 2000. Monthly precipitation data (Randsburg Station, California 1937-99). NOAA, U.S. Department of Commerce, Asheville, NC.
- POOLE, R. W. AND B. RATHCKE. 1979. Regularity, randomness, and aggregation in flowering phenologies. *Science* 203:470-471.
- RATHCKE, B. 1984. Patterns of flowering phenologies: testability and causal inference using a random model. Pp. 383-393 in D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle (eds.), *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton.
- AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16:179-214.
- SHREVE, F. AND I. L. WIGGINS. 1964. *Vegetation and flora of the Sonoran Desert*. Stanford University Press, Stanford.
- STILES, F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* 198:1177-1178.
- . 1979. Response to Poole and Rathcke. *Science* 203:471.
- Tevis, L., Jr. 1958a. Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology* 39:681-688.
- . 1958b. A population of desert ephemerals germinated by less than one inch of rain. *Ecology* 39:688-695.
- TURNER, R. M. 1982. 153.1 Mohave desert scrub. Pp. 157-168 in D. E. Brown (ed.), *Biotic communities of the American southwest—United States and Mexico*. University of Arizona Press, Tucson.
- AND D. E. BROWN. 1982. 154.1 Sonoran desert scrub. Pp. 181-221 in D. E. Brown (ed.), *Biotic communities of the American southwest—United States and Mexico*. University of Arizona Press, Tucson.
- VIDIELLA, P. E., J. J. ARMESTO, AND J. R. GUTIERREZ. 1999. Vegetation changes and sequential flowering after rain in the southern Atacama Desert. *Journal of Arid Environments* 43:449-458.
- WASER, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* 59:934-944.
- WENT, F. W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. *Ecology* 29:242-253.
- . 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. *Ecology* 30:1-13.