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Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert region, 1893–2001

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Abstract

Precipitation varied substantially in the Mojave Desert through the 20th century in a manner broadly similar to the other warm North American deserts. Episodes of drought and prolonged dry conditions (1893–1904, ca. 1942–1975, and 1999-present) alternated with relatively wet periods (1905–ca. 1941 and ca. 1976–1998), probably because of global-scale climate fluctuations. These are the El Niño-Southern Oscillation that affects interannual climate and the Pacific Decadal Oscillation that evidently causes decadal-scale variability such as prolonged dry and wet episodes. Studies done in the late 20th century demonstrate that precipitation fluctuations affected populations of perennial vegetation, annuals, and small herbivores. Landscape rephotography reveals that several species, particularly creosote bush, increased in size and density during the ca. 1976–1998 wet period. A brief, intense drought from 1989 to 1991 and the ongoing drought caused widespread mortality of certain species; for example, chenopods and perennial grasses suffered up to 100% mortality. Drought pruning, the shedding of above-ground biomass to reduce carbon allocation, increased substantially during drought. Overall, drought had the greatest influence on the Mojave Desert ecosystem.

Keywords: Mojave desert; Precipitation variability; ENSO; PDO; Desert ecosystem

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1. Introduction

The Mojave Desert region has complex geology, diverse topography, and distinctive plant communities. The desert occupies 152 000 km^2 of the central Basin and Range province of southeastern California, southern Nevada, the southwestern corner of Utah, and northwestern Arizona (Fig. 1). The region is heavily used and disturbed by recreational activity, particularly off-highway vehicles, mining, grazing, and military operations (Lovich and Bainbridge, 1999). Climate variability affects the recovery and restoration of these disturbed lands as well as the productivity of relatively undisturbed vegetation. In this paper, we present evidence showing the seasonality and spatial coherence of precipitation, the multidecadal variability of precipitation caused by fluctuations of global climate, and the affects of drought and wet conditions on the plants and animals of the Mojave Desert ecosystem. Our motivation is that land management will benefit from knowledge of past climate variability, prognostications of future climate, and the response of the ecosystem to variable precipitation. In addition,

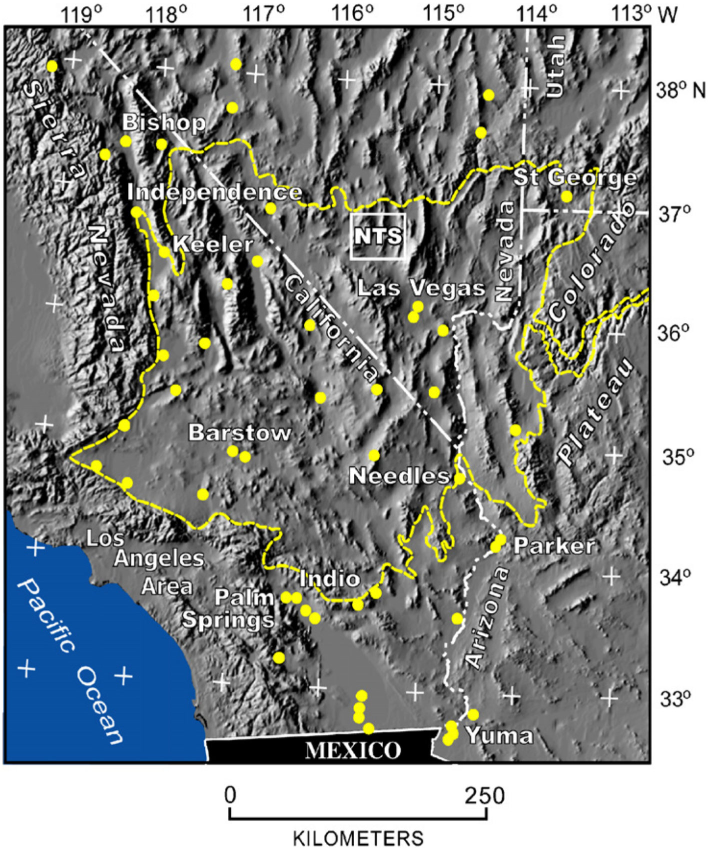

Fig. 1. Weather stations (circles) in the Mojave Desert region (dashed line) used in the precipitation analysis. Labeled stations have records beginning from 1893 to 1900. The desert boundary is close to but does not necessarily coincide with the Mojave Desert scrub formation of Brown and Lowe (1980). NTS = Nevada Test Site.

much of the scientific research on ecosystem processes in the Mojave Desert was done during a period of sustained above average precipitation.

The Mojave Desert is bounded on the west and southwest by the Sierra Nevada, San Gabriel, and San Bernardino Mountains. These imposing mountains alter the prevailing westerly winds, intercepting moisture derived from the Pacific Ocean, which produces a rain-shadow effect downwind. On the east, the Mojave is bounded by the mostly semiarid Colorado Plateau, a broad elevated region rising more than 1 km above the general elevation of the desert. The northern and southern boundaries of the Mojave are transitional; to the south, the Mojave Desert ecosystem grades into the Colorado Desert, the western extension of the Sonoran Desert; to the southeast, it grades into the Sonoran Desert; and to the north, it merges with the Great Basin Desert. Climate and topography are primary factors controlling the distribution and abundance of desert plant species in the Mojave Desert region (Rowlands, 1995; Rundel and Gibson, 1996).

1.1. *Previous studies of climate variability*

Twentieth-century precipitation variability in the Mojave Desert region has not been specifically addressed. Huning (1978) described the climate and meteorology of the Mojave within the context of land-management practices. Although he did not analyse temporal climate variability, he recognized an overall decline of precipitation between 1950 and the mid-1970s, a period now viewed as the mid-century dry period that ended around 1976.

Generally, climate variability in the Southwest is related with a modest degree of predictability to large-scale spatial and temporal changes in sea-level atmospheric pressure and sea-surface temperature (SST) that are indicative of global-scale climate forcing (Cayan et al., 1998). These forcing processes are the El Niño–Southern Oscillation (ENSO), which affects interannual climate variability (Cayan et al., 1999; McCabe and Dettinger, 1999), and the Pacific Decadal Oscillation (PDO), which modulates decadal variability (Mantua and Hare, 2002). The state of the Southern Oscillation (whether highly positive or negative) influences precipitation (Ropelewski and Halpert, 1986) in the Great Basin, although the effect has not been quantified for the Mojave Desert region. Broadly speaking, El Niño conditions, which are associated with increased SST in parts of the Pacific Ocean, result in wet winters in the Southwest and increased streamflow by southerly displacement of storm tracks, although normal or even drought conditions may also occur. Conversely, La Niña conditions and reduced SST typically result in dry winters.

1.2. *Climate variability and ecosystem processes*

As reviewed by Rowlands (1995) and Rundel and Gibson (1996), much is known or has been speculated about the relation between average climate and the attributes and processes of the Mojave Desert ecosystem. Turner et al. (2003), for example, relate many landscape-scale ecological effects to 20th-century climate fluctuations. These range from general increases in woody plants and cacti because of increased winter rainfall to decreases in specific species (e.g., Mexican blue oak at its lower elevation limit) because of drought. Few studies, however, address the affects of climate variability on the Mojave Desert ecosystem. Using an elaborate precursor to a state-transition model, Beatley (1974) discussed the influence of rainfall timing and amount on growth and flowering of Mojave Desert annuals and shrubs. Because rodent populations are dependent on winter annuals, they too are affected by climate variability (Beatley, 1969a, 1976a). Moreover, the physiology of the desert tortoise (*Gopherus agassizii*), a threatened species, is strongly affected by ENSO-related precipitation variability (Henen et al., 1998).

Perennial shrubs also respond to climate variability. Beatley (1980) measured changes in 56 plant associations using permanent plots at the Nevada Test Site (NTS, Fig. 1) between 1963 and 1975. She reported large turnover in the shrub populations and measured increases in shrub cover related to precipitation fluctuations. At Rock Valley on the NTS, Rundel and Gibson (1996) found significant correlation between net above ground primary production and September to August precipitation during 1966–1976. Natural recovery of perennial vegetation (Webb et al., 1988) can be strongly affected by climate variability through germination and establishment of new individuals during wet periods and death of short-lived species during drought.

2. Materials and methods

2.1. Data sources

Records of daily precipitation were assembled from 52 weather stations in the Mojave Desert region. Digital data are typically available from only 1948 to the present. To develop long-term time series of daily precipitation, archival records (available on microfiche from National Oceanographic and Atmospheric Administration, Asheville, North Carolina) were used to backfill records of the longest running stations. Ten of these (labeled in Fig. 1) have records beginning from 1893 to 1900. Indices of the Southern Oscillation (SOI) were obtained from the Climate Prediction Center (2001) website. El Niño and La Niña events were identified using the chronologies of Trenberth (1997), Ropelewski (1999), and the Climate Prediction Center. Indices of the PDO were obtained from the PDO website. The term "20th century," as used here, refers to the broader period 1893–2003.

Phytoecological data on perennial vegetation species were collected from abandoned townsites in the Death Valley region (Webb et al., 1988) and the NTS. The NTS data were collected from permanent vegetation plots established by Beatley (1980) and remeasured using her techniques. The raw data from these plots are given in Webb et al. (2003).

2.2. Analyses

Software written in FORTRAN was used to process the daily precipitation data. These programs tabulate total precipitation, maximum and minimum daily values, and days without precipitation for any desired accounting period (e.g., calendar year, cool season, or warm season). During settlement of the desert in the early to mid-20th century, the number of reporting weather stations was 10 in 1900, 16 in 1914, 25 in 1945, and 47 in 1959. Aside from this gradual increase, the number of stations entering the calculations varies from year-to-year due to abandonment of the station or missing observations. For a particular station and accounting period, total precipitation was assigned a missing value if more than 10% of the daily entries of the period were missing. Where appropriate, several of the precipitation time series were expressed as the Standardized Anomaly Index (SAI; $\mu = 0$, $\sigma = 1$) using the methods described by Katz and Glantz (1986).

Statistical analyses were done with the Statistica version 6.1 (StatSoft, Inc.) software package. We used *k*-means cluster analysis (Davis, 1986) with the number of clusters set at 2 to identify seasonal patterns in the annual precipitation cycle. The coherence of precipitation among the weather stations (Fig. 1) was evaluated using the distance and statistical correlation (Pearson correlation coefficient, *r*) between all pairs of weather stations. The approximate periodicities of irregular oscillations in the calendar-year precipitation time series were estimated with spectral analysis (Shumway and Stoffer, 2000). Before tests of statistical significance were performed, prewhitening (Storch, 1999) of the global climate indices, and pre-whitening and transformation of the precipitation data were done to remove serial correlation and skew, respectively. Finally, differences in average precipitation between dry and wet episodes were tested with analysis of variance (ANOVA) and multiple-planned pairwise comparisons using Fisher's least significant difference (LSD) test procedure. Three pairwise comparisons are sufficient for the tests; therefore, adjustment of the type I error rate (α) is not required (Sheskin, 2000).

3. Results and discussion

3.1. The precipitation cycle and spatial coherence of precipitation

The precipitation cycle is the average monthly contribution (in percent) to total annual precipitation (Fig. 2). The cycle has 2 distinctive patterns that approximately divide the region along the 117° W meridian, which bisects the desert near Barstow, California (Fig. 1). A biseasonal pattern prevails in 90% of the stations lying east of 117° W, whereas winter-dominant precipitation is typical of 70% of the stations west of this longitude. In both cases, May through June is consistently dry accounting for less than 5% of annual rainfall. October through April precipitation of the winter dominant pattern accounts for 82% of the annual total and 66% of the biseasonal pattern total. During the warm months of July through September, 13% and 29% of the total falls in the winter and biseasonal patterns, respectively. Two precipitation seasons were defined using this monthly

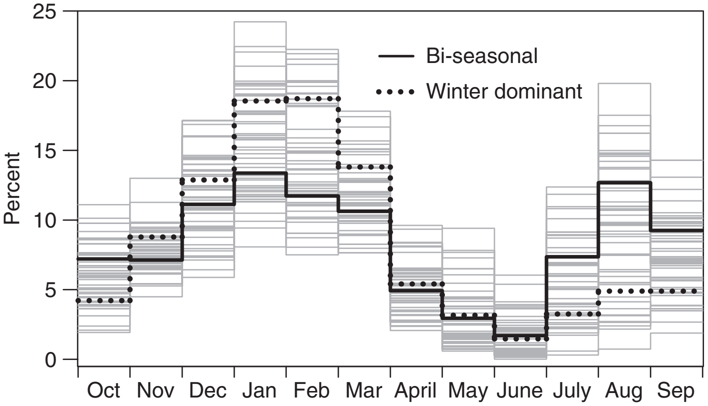

Fig. 2. Annual precipitation cycle by month of 51 weather stations for their periods of record. Gray lines are individual stations and the 2 heavy lines show the dominant precipitation patterns identified with *k*-means cluster analysis.

information and plots of the precipitation cycle based on average daily precipitation. These are the cool season (October 15–April 15), warm season (July 4–October 14), and the derivative cool and warm-season precipitation (October 15–October 14 excluding April 16–July 3), referred to as cool + warm-season precipitation.

Cool-season precipitation results largely from extratropical cyclones of the North Pacific Ocean that occur in conjunction with large synoptic and planetary scale tropospheric depressions and with the polar and subtropical jet streams. This pattern develops in fall and winter during the southward shift of the prevailing Pacific cyclone track and expansion of the semi-permanent Aleutian-low pressure center (Pyke, 1972). Rainfall in the desert is widespread and of relatively long duration during the cool season. Cool-season precipitation is the most important and dependable source of rainfall for most of the vascular plants in the Mojave Desert region because they use the C3 photosynthetic pathway (Johnson, 1976).

Broadly speaking, warm-season precipitation is the northwesterly extension of the Mexican monsoon into southeastern California. The monsoon is a seasonal reversal of atmospheric circulation that transports maritime tropical moisture into the desert region from the Gulf of Mexico and (or) the Gulf of California (Douglas et al., 1993). Because of intervening mountainous terrain and the prevailing westerly winds, this low-level moisture does not regularly penetrate the western Mojave Desert, resulting in the weakly developed warm-season precipitation pattern west of approximately 117° W. Rainfall results largely from convective precipitation in the form of isolated or organized thunderstorms. Although rather infrequent, the most dramatic precipitation source is tropical cyclones and hurricanes (referred to as chubascos) that develop off the coast of Baja California (Eidemiller, 1978; Smith, 1986). These storms rarely make landfall, instead they dissipate offshore while moisture is advected over the continent either in weak circulation patterns or in combination with cutoff low-pressure systems (Smith, 1986; Webb and Betancourt, 1992). Chubascos typically occur late in the warm season and are accompanied by widespread and severe flash flooding (Huning, 1978).

The distribution of certain desert vegetation is strongly influenced by the extent and magnitude of warm-season rainfall. Many species of cacti, yuccas, agaves, and agave-like plants increase in number where warm-season rainfall is relatively abundant (Rowlands, 1995), particularly east of approximately 117° W. Leguminous trees, such as palo verde (*Cercidium microphyllum*), are dependent on reliable summer rainfall and are present only in the southeastern Mojave Desert. Other yuccas, such as the Joshua tree (*Yucca brevifolia*), are somewhat more abundant in areas dominated by winter precipitation.

Spatial coherence is the consistency of precipitation among the weather stations and across the desert region. The distances and correlations among 50 stations were calculated for the period 1950–2000, yielding 1225 interstation distances and correlation coefficients. The median distance between stations is 250 km and the interquartile range is 150–350 km. Regarding calendar year, cool season, and warm-season precipitation, respectively, 91%, 92%, and 80% of the between-station correlations are significant ($\alpha < 0.05$). In the cases lacking significant correlation, the number of data of the particular stations entering the calculation is small. The median interstation correlation of the calendar year, cool season, and warm-season precipitation is $r = 0.65$, 0.72, and 0.45 with interquartile ranges of 0.4–0.8, 0.6–0.8, and 0.3–0.6, respectively. As expected, the interstation correlation decreases with distance. In the case of calendar-year precipitation, the distance-decay function indicates that on average the interstation correlations decline from $r \approx 0.8$ at

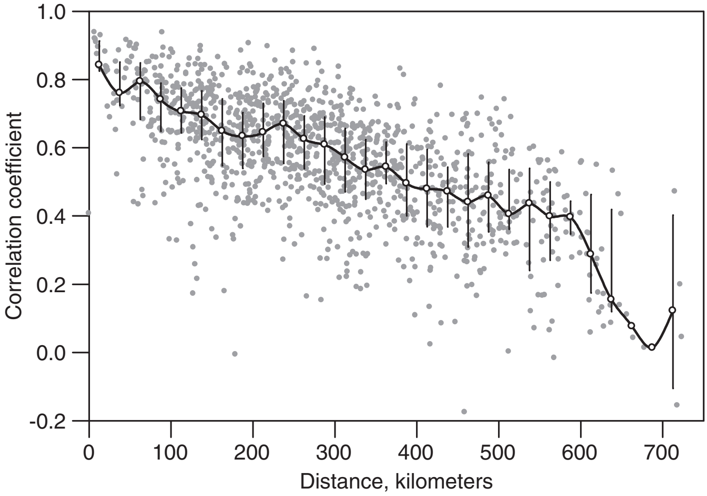

Fig. 3. Distance decay function of calendar-year precipitation showing the decline of correlation coefficient with distance ($n = 1225$). The open circles and vertical lines are the median and quartile range, respectively, of 30 windows with length 25 km.

50 km to $r \approx 0.4$ at 600 km (Fig. 3). Generally, these results suggest that precipitation is spatially consistent across the desert for the calendar year as well as the cool and warm seasons.

3.2. *Interannual and multidecadal precipitation variability*

In this section, we examine the temporal variability of calendar year, cool season, and warm-season precipitation. Calendar-year precipitation in the Mojave Desert region calculated from the 52 stations averages 137 mm yr^{-1} and ranges from 34 to 310 mm yr^{-1}. The driest year was 1953, whereas 1941 and 1983 were the wettest (Fig. 4). Calendar-year precipitation has varied in 5 episodes: 1893–1904 (drought): 1905–1941 (above average), 1942–1975 (mid-century dry period), 1976–1998 (above average), and 1999–2003 (drought). The droughts and dry spells are characterized by the low percentage of stations reporting precipitation more than 1 standard deviation above the station average. Regarding the current drought, the post-1998 climate of the Mojave Desert region and Southwest USA is characterized by a sustained drought that continues into the present (NOAA, September 2003).

The choice of limiting dates for the mid-century dry period is somewhat subjective and varies by one or more years depending on the accounting period. Regardless of the exact dates, the middle of the 20th century was clearly dry and was sandwiched between 2 wetter episodes. Although precipitation during the mid-century increased somewhat after 1953, it did not reach the levels of the late 20th century. For the calendar year, the period from 1976 to 1998 was the wettest since the 1940s, if not the 20th century, although the largest shift to wet conditions occurred in 1978. This wet period was broken only by the relatively brief, intense drought of 1989–1991 that was caused by La Niña conditions.

Spectral analysis, which partitions the variance of a time series among its harmonic frequencies, suggests the calendar-year precipitation time series differs from a purely

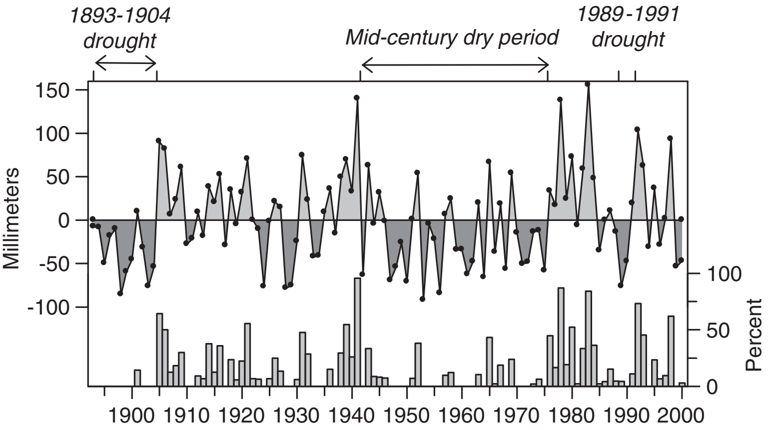

Fig. 4. (upper) Calendar-year precipitation displayed as the average deviation from the mean of the reporting stations and (lower) percent of stations having precipitation more than one standard deviation above average.

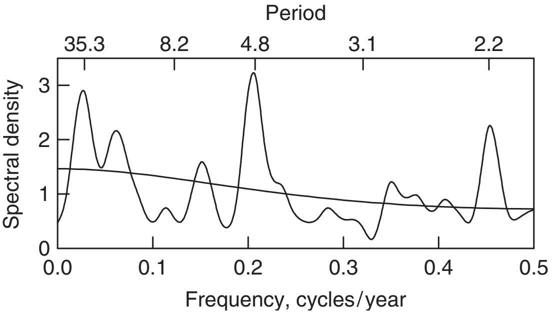

Fig. 5. Spectral density function of calendar-year precipitation smoothed with the Bartlett window (bandwidth = 5). The subhorizontal line is the theoretical spectrum of a red-noise process with the same lag-1 autocorrelation coefficient as the precipitation time series.

random series of events. The spectral density function has peaks corresponding to periodicities of about 35, 5, and 2.2 yr (Fig. 5). The 95% confidence interval of these peaks is larger than the baseline of the spectrum, which is assumed to be autocorrelated noise. As discussed below, the irregular oscillations of approximately 35 and 5 yr correspond with the oscillations of the PDO and ENSO, respectively.

These long-term variations of calendar-year precipitation are largely contemporaneous with well-known drought or drought-like episodes elsewhere in the Southwest USA, specifically an 11-yr drought from 1893 to 1904 and a mid-century drought from 1942 to 1956. This drought is recognized throughout the Southwest (Gatewood, 1962, 1963) and was perhaps the most severe drought in the past 400 yr in New Mexico (Swetnam and Betancourt, 1998).

Precipitation variability on the adjoining southern Colorado Plateau (Fig. 1), at approximately the same latitude as the Mojave Desert, mirrors that of the desert region. Hereford and Webb (1992) and Hereford et al. (2002) found that the 20th century began with a severe drought lasting until about 1905 that was followed by a wet period ending after the 1940–1942 El Niño. This early wet episode was followed by a prolonged drought and dry spell during the mid-century that lasted until ca. 1977. The mid-century drought and dry period gave way to a second wet period lasting until about 1998.

Several studies of the Sonoran Desert also identified discrete wet-and-dry periods in the 20th century that are broadly coincident with those of the Mojave Desert and Colorado Plateau. Turner et al. (2003) report an extreme drought at the start of the 20th century, a wet period from about 1905 through the early 1930s, a mid-century dry period from the early 1940s through the late 1960s, and a highly variable, generally wet period from the late 1970s through the mid-1990s. These precipitation episodes broadly correspond to fluctuations in the PDO as well as to changes in flood-frequency (Webb and Betancourt, 1992; Schmidt and Webb, 2001).

Precipitation of the cool season averages 95 mm yr^{-1} with a range of 27–249 mm yr^{-1}. The driest years were 1904, 1934, 1951, 1972, and 1990, and the wettest were 1941, 1978, 1983, 1992, and 1993 (Fig. 6a). These wet and dry (except 1934) episodes coincide with El Niña and La Niña conditions, respectively. The mid-century dry period is well defined in the cool-season precipitation time series from 1945 to 1977. The period 1978–1998 was unusually wet and was distinctive in having 8 wet years with more than 50% of the stations recording precipitation more than 1 standard deviation above normal.

Warm-season precipitation averages 35 mm yr^{-1} and ranges from 1 to 125 mm yr^{-1}. The driest years were 1928 and 1944, although several others were nearly as dry (Fig. 6b). The wettest were 1939, 1976, 1983, and 1984. Although the early 20th century drought and

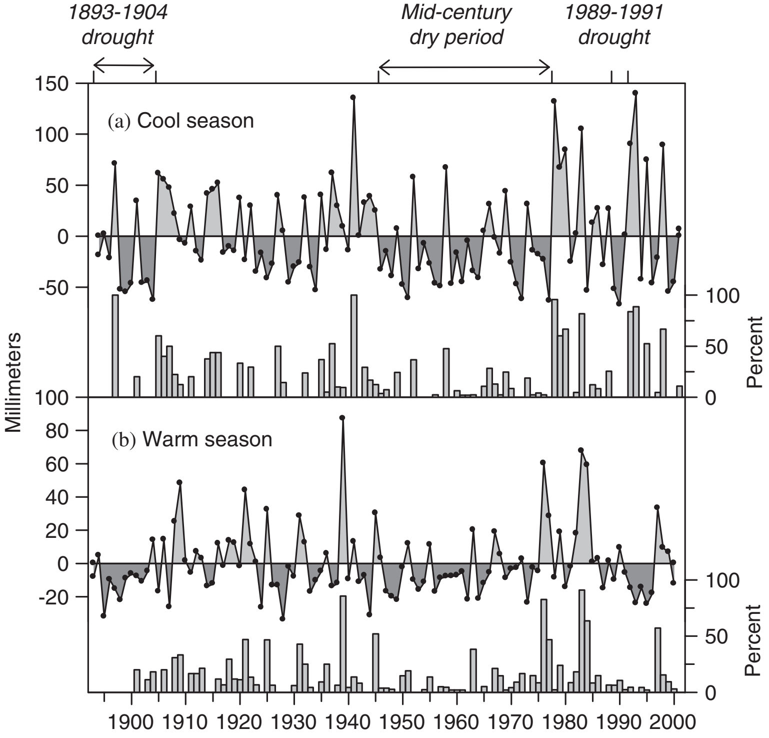

Fig. 6. Cool (a) and warm-season precipitation (b) displayed the same as Fig. 4.

the mid-century dry period are visibly evident in the time series, the average precipitation of the 4 periods discussed above is not significantly different ($\alpha = 0.05$). Nevertheless, the post-1975 period is notable for having 3 unusually wet seasons (1976, 1983, and 1984) with more than 50% of the stations reporting rainfall more than 1 standard deviation above normal. The average annual total of the cool + warm-season precipitation is 128 mm yr^{-1} with a range of 44–309 mm yr^{-1}. These figures and the time series of cool + warm-season precipitation are similar to those of calendar-year precipitation.

Analysis shows that the average precipitation deviation during the early drought and mid-century dry period is not significantly different. However, precipitation during the wet periods differs significantly from the dry periods for the calendar year, cool season, and cool + warm season accounting periods (Table 1). This suggests that precipitation in the Mojave Desert region was nonstationary during the 20th century, with at least a time-variant mean and possibly variance. The long-term precipitation patterns, therefore, consist of multidecadal wet and dry periods.

3.3. *Mojave Desert precipitation and global climate*

3.3.1. *ENSO and interannual variability*

One of the main indices of ENSO is the SOI, which is the standardized difference in sea-level atmospheric pressure between Darwin, Australia and Tahiti (Rasmussen, 1984). Warm SST in the eastern equatorial Pacific Ocean and sustained negative SOI indicate El Niño conditions. In contrast, cool SST and sustained positive SOI indicate La Niña conditions. The term El Niño was originally applied to the weak, seasonal (usually late December), warm, and south-flowing current off the coast of Peru (Trenberth, 1997).

Table 1
Results of analysis of variance (ANOVA) and planned pairwise group comparisons

ANOVA[a]	Calendar year $F(3, 102) = \mathbf{7.36}$	Cool season $F(3, 101) = \mathbf{4.44}$	Warm season $F(3, 102) = 0.448$	Cool + warm $F(3, 101) = \mathbf{6.11}$
Group comparisons	Average precipitation deviation (mm) of the period and α[b]			
1893[1894][c]–04 (dry)	−36.5	−21.9	−2.3	−31.54
1942–1977 (dry)	−17.8	−13.5	−0.85	−16.2
	1	0.589	0.418	0.347
1942–1977 (dry)	−17.8	−13.5	−0.85	−16.2
1978–1998 (wet)	27.8	24.3	0.74	27.7
	0.0008	**0.003**	0.288	**0.006**
1942–1977 (dry)	−17.8	−13.5	−0.85	−16.2
1905–1941 (wet)	14.0	8.7	0.87	11.7
	0.006	**0.038**	0.077	**0.0089**

ANOVA was applied to 4 precipitation periods (1893[1894]–1904 dry, 1905–1941 wet, 1942–1977 dry, and 1978–1998 wet) of the calendar year, cool, warm, and cool + warm season accounting periods (columns 2–5). Three *t*-test group comparisons (column 1) of the dry/dry and dry/wet periods applied to the 4 accounting periods.

[a] Single factor ANOVA between the four precipitation periods. Highlighted omnibus *F* values are significant at the $\alpha = 0.05$ level.

[b] Unadjusted type-I error rate. Highlighted values are groups with significantly different average precipitation.

[c] [1894] is the first year of the cool and cool + warm season accounting periods.

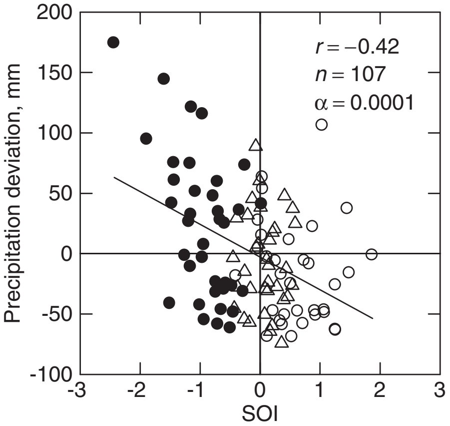

Fig. 7. Average annual deviation of cool + warm-season precipitation as a function of the average June to May Southern Oscillation Index (SOI) with precipitation classified by type of ENSO activity: solid circles are El Niño, open circles are La Niña, and open triangles are non-ENSO.

In the Mojave Desert region, cool + warm-season precipitation is inversely correlated with the SOI when averaged from the June preceding to May of the seasonal precipitation. This inverse correlation is shown (Fig. 7) with precipitation expressed as average deviation and coded by the type of ENSO activity (El Niño, La Niña, and non-ENSO climate). Although the strength of the correlation is relatively weak, it is large enough to infer that SOI and precipitation are not independent, which is consistent with the low probability of no association. In an analysis of precipitation variability in the Sonoran Desert of Baja California, Bullock (2003) also found a negative, statistically significant correlation with the SOI. In the Mojave Desert region, La Niña conditions produced above normal cool + warm-season precipitation in only 27% of years, whereas El Niño conditions produced above normal precipitation in 55% of years and the precipitation amounts were substantially larger than the precipitation associated with La Niña. Although the correlation is modest, precipitation tracks the SOI in time reasonably well, which is plotted as negative SOI in Fig. 8. Although several El Niño events occurred in the 1950s to early 1970s, they increased cool + warm season precipitation only slightly. As suggested by the spectral density (Fig. 5), the ENSO signal produces an irregular oscillation of about 5-yr duration in Mojave Desert precipitation.

3.3.2. PDO and multidecadal variability

The PDO is related to SST and atmospheric pressure of the North Pacific Ocean (Mantua and Hare, 2002). Changes in SST and atmospheric pressure evidently trigger sharp transitions from one climate regime to another, altering the climate of North America for periods of 2–3 decades (Zhang et al., 1997). Phase shifts of the PDO evidently affect the spatial connection between ENSO and precipitation in the western United States (McCabe and Dettinger, 1999). During the warm (positive) PDO phase, the SST off the west coast of North America is relatively warm, whereas it is relatively cool during the negative phase. The PDO is thought to explain certain aspects of Mojave Desert climate because of its relation to 20th century climate variability elsewhere in the Southwest (Hereford et al., 2002).

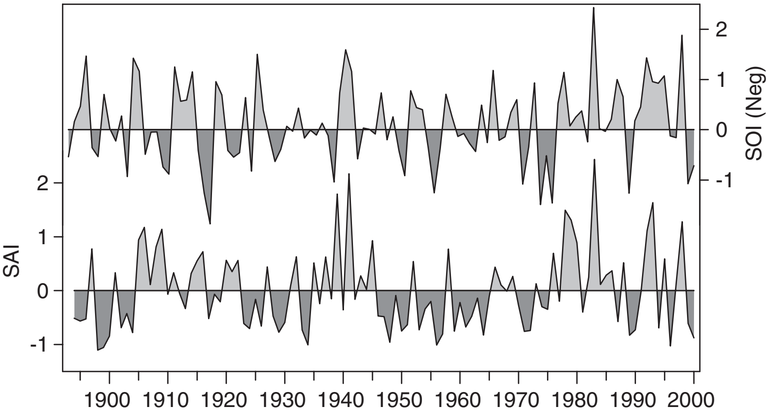

Fig. 8. (upper) Average negative June to May Southern Oscillation Index (SOI; El Niño-like conditions have positive values) and (lower) Standardized Anomaly Index (SAI) of cool + warm-season precipitation.

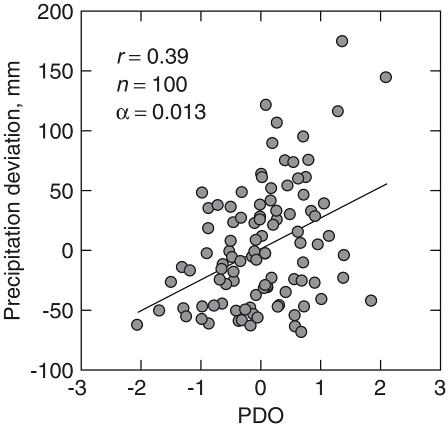

Fig. 9. Standardized Anomaly Index (SAI) of cool + warm-season precipitation as a function of average October to September Pacific Decadal Oscillation (PDO), 1901–2000.

Precipitation in the Mojave Desert region is modestly but significantly correlated with the PDO (Fig. 9). The 3 regime shifts of the PDO (Gedalof and Smith, 2001) at about 1942, 1977, and 1999 are largely in-phase with the calendar year and cool + warm-season precipitation time series, particularly since the mid-1940s (Fig. 10). The mid-century dry period shows this in-phase relation, which corresponds to a period of low indices and a prolonged cool phase of the PDO. The strong warm phase of the PDO beginning around 1977 is readily associated with the wet cool-season climate beginning in 1978 (Fig. 6a). Of particular interest is the downward regime shift in the PDO beginning in 1999 along with decreased precipitation that has continued through the winter of 2002 with only slight increase in the winter of 2003. These multidecadal swings in SST that modulate precipitation of the Mojave Desert region also affect important Pacific Ocean fisheries, causing decades long changes in landings of sardines, anchovies, and salmon (Chavez et al., 2003).

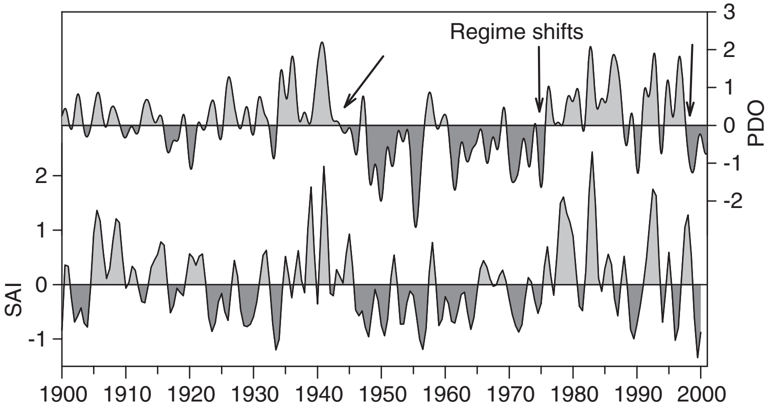

Fig. 10. (upper) Average monthly Pacific Decadal Oscillation (PDO; smoothed to retain 63% of the original variability), and (lower) Standardized Anomaly Index (SAI) of cool + warm-season precipitation. The 3 arrows indicate regime shifts of the PDO recognized by Gedalof and Smith (2001).

Globally, this unusually dry climate in the Mojave Desert region since 1998 is associated with a nearly continuous belt of high pressure in the northern mid-latitudes that produced drought conditions elsewhere in parts of the United States, the Mediterranean region, southern Europe, and central Asia. This global-scale drying is quite likely related to unusually cool and persistent SST in the eastern Pacific Ocean (Hoerling and Kumar, 2003).

The weather, SST, and surface-pressure patterns of the past several years suggest that a transition to another PDO regime is presently underway (Gedalof and Smith, 2001), suggesting the dry conditions since 1998 in the desert region may continue for some time. Although understanding of the PDO has developed rapidly, its usefulness in climate prediction is not fully resolved (Gedalof et al., 2002; Bond et al., 2003). Specifically, the time scale of the 20th century regime shifts may not be typical, the influence of the PDO on North American climate evidently varies in time, and the PDO incompletely specifies the present climate of the North Pacific Ocean.

3.4. Ecosystem responses to climate variation

Interannual and multidecadal climate variation affects Mojave Desert plant and animal associations in several ways. Annual plant populations, a major food source for reptiles and mammals, closely respond to the amount of cool-season precipitation (Beatley, 1969b). Most perennial plants in the Mojave use the C3 photosynthetic pathway (Johnson, 1976), and increased cool-season precipitation would influence germination, establishment, and increases in the biomass of existing plants. Conversely, cool-season drought may substantially increase mortality, particularly of short-lived species. Warm-season drought, on the other hand, probably has little or no affect on these plant associations. A wet warm season, however, may increase the probability of establishment of some species such as creosote bush (*Larrea tridentata*) that germinate under warm conditions (Kay et al., 1977). In the case of the desert tortoise, studies show that heavy winter rain during the 1982–1983 and 1992–1993 El Niño events (Fig. 8) increased metabolic rate and reproductive output, probably because of high annual plant production. In contrast, drought conditions that are typically associated with La Niña activity substantially reduced activity and reproductive output (Henen et al., 1998).

3.4.1. Climate, production of annuals, and small animal populations

Here, we use examples from the Death Valley region and the NTS (northern Mojave Desert) to illustrate some ecosystem responses to the climate fluctuations of the late 20th century (Figs. 4, 6a). Generally, primary production of annuals in the Mojave Desert is largest during wet periods. Beatley (1969b, 1976a) developed a conceptual model to predict growth of annual plants in response to cool-season precipitation at the NTS. She documented substantial germination following rainfall events $\geqslant$ 25 mm that occurred between late September and early December. Turner et al. (1982) irrigated seasonally to verify Beatley's model, applying 50 mm of water (2 treatments of 25 mm each) in both the fall of 1969 and the fall of 1971. Annual production increased from 8 g/m^2 compared with 0.5 g/m^2 in the control plot in 1970 and 5 g/m^2 compared with 0.1 g/m^2 in 1972. Rundel and Gibson (1996) summarized annual plant-production data from Turner and Randall (1989) at Rock Valley in the southwestern NTS. These data indicate that increased annual production and changes in species composition are directly related to precipitation.

Growth of annuals, therefore, should be greatest during wet periods, particularly during El Niño conditions. Bowers (2005) examined historical records of wildflower displays in the Mojave and Sonoran deserts and found that only a little more than half occurred during El Niño conditions. However, if El Niño conditions are redefined to include winter rainfall, good displays of wildflowers are 3.6 times more likely under El Niño conditions than during La Niña or non-ENSO climate. Nonetheless, predictive models of annual plant production with El Niño as the only independent variable will require a much better linkage to regional precipitation than is presently known (Figs. 7 and 8).

Given the strong influence of climate on the production of annuals, herbivores are expected to have short- and long-term population fluctuations in response to decadal climatic variability. However, the change in animal numbers may be lagged by 1–2 yr as reproductive successes propagate through the population. Generally, high winter precipitation increases annual biomass and insect populations, improving resource availability for lizards (Turner et al., 1982).

3.4.2. Plant growth during wet periods, 1978–1998

As shown previously, precipitation during the cool seasons of 1978–1998 was mostly above average throughout the Mojave Desert region, interrupted only by the drought of 1989–1991. Between 1963 and 2003, an index of biomass was measured on 57 permanent vegetation plots at the NTS through the elevational range of the Mojave Desert into pinyon-juniper woodlands (Webb et al., 2003). These plots range in species composition from low-elevation assemblages dominated by saltbush to high elevation plots dominated by sagebrush (*Artemisia tridentata)*. Most of them have various combinations of creosote bush–white bursage (*Ambrosia dumosa*). Of the 57 plots, 40 increased in biomass index by 59%, whereas, the remaining 17 plots decreased by 18%. This decrease was caused by the ongoing drought and the 1989–1991 drought, which affected many plant associations.

Landscape rephotography (Fig. 11) shows that some species such as creosote bush increased substantially in size and cover in the northeastern Mojave Desert during this overall wet period, despite periodic drought. Other plants responded differently during this period. Some long-lived species gained biomass without establishing new individuals, some

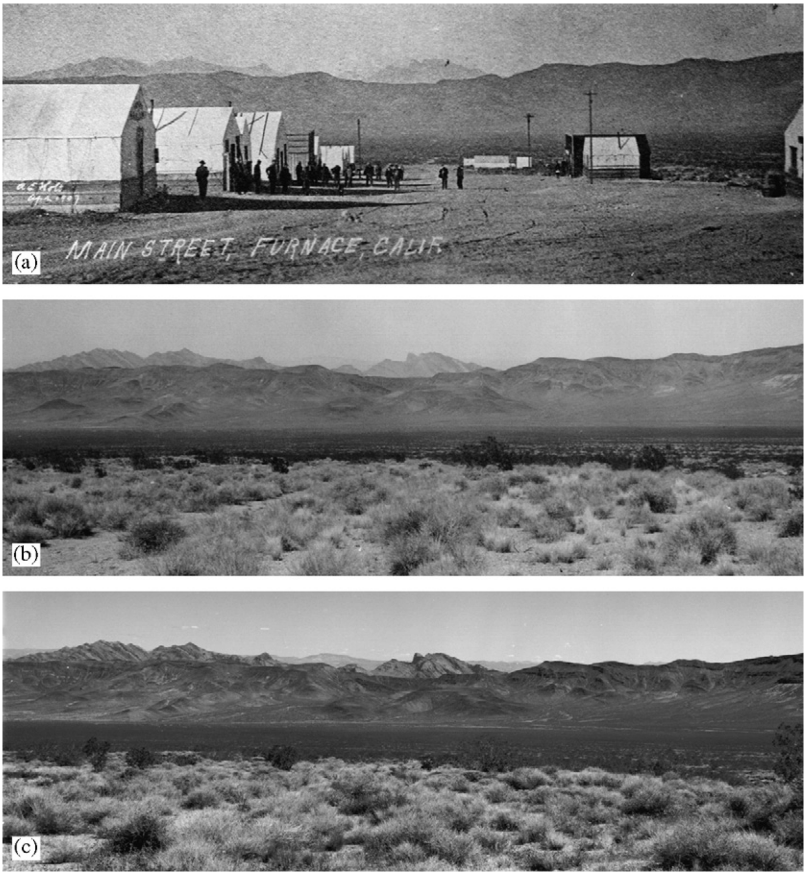

Fig. 11. (a) (1907). Founded in mid-1906 and abandoned in 1908, Furnace, California, was a boom town built to support speculative copper mining in the Greenwater Mining District of the eastern Death Valley region. Along main street, most of the buildings were tent frames over a wooden base (photographer unknown, courtesy of the Sidney Norman Weight Collection, number 8). (b) (1984). The townsite was difficult to detect through the recovering vegetation. Most of the vegetation in this view is cheesebush (*Hymenoclea salsola*), desert needlegrass (*Achnotherum speciosum*), scattered Mormon tea (*Ephedra nevadensis*), and scattered creosote bush (*Larrea tridentata*) in the background (Raymond M. Turner, Desert Laboratory Collection, Stake 1139). (c) (1998). Many of the plants apparent in the 1984 view were still alive and much larger, particularly the creosote bush in the background. Many of the cheesebush and most of the desert needlegrass were dead, probably from the 1989–1991 drought (Dominic Oldershaw, Desert Laboratory Collection, Stake 1139).

species established new individuals and gained biomass over existing ones, while other species had modest gains in size while establishing only a few new individuals. Still other species decreased in size, or died, probably the result of drought. These changes are also documented in plant transect data from undisturbed sites in the region (Table 2), where the cover of perennial species increased significantly.

3.4.3. *Plant mortality during the drought of 1989–1991*

The drought of 1989–1991, which was extreme in the northeastern Mojave Desert (Flint and Davies, 1997), caused widespread mortality of certain species. In the Death Valley

Table 2
Cover of perennial vegetation in undisturbed area adjacent to Furnace townsite, Death Valley National Park, California (Fig. 11)

Species	Cover (%)	
	1981	1998
Larrea tridentata	4.8	10.4
Menodora spinescens	8.1	6.6
Lycium andersoni	4.4	5.4
Grayia spinosa	1.8	1.9
Ericaneria cooperi	1.1	1.8
Hymenoclea salsola	0.0	0.5
Salazaria mexicana	0.4	0.5
Thamnosma montana	0.2	0.4
Achnatherum speciosum	0.5	0.4
Tetradymia spinosa	0.2	0.3
Ephedra nevadensis	0.9	0.1
Ambrosia dumosa	0.0	0.1
Total live cover	22.4	28.2
Dead	1.6	3.0
Total cover	24.0	31.2

Data from Webb et al. (1988) was remeasured in 1998 (Webb et al., unpublished data).

region and NTS, species within the Chenopodiaceae and perennial grasses suffered population mortalities up to 100%. In particular, spiny hopsage (*Grayia spinosa*) decreased significantly on the NTS. On 30 permanent plots totaling 929 m^2 with 5 or more individuals present, both average coverage and biomass index decreased by 77.3 ($\sigma = 18.9$) and 75.5 ($\sigma = 20.3$) percent, respectively, from 1975 to 2002. Most of this decrease is attributed to mortality during the 1989–1991 drought.

In her descriptions of plant communities on the NTS, Beatley (1976b) defined 16 vegetation associations in the Mojave and Transition deserts. Of these, 8 named spiny hopsage as a dominant species. Ostler et al. (2000) defined 10 vegetation associations for Mojave and Transition deserts in classification work done after the 1989–1991 drought; only one post-drought association had spiny hopsage as the dominant species. In plot remeasurements done from 1999 to 2002, spiny hopsage did not dominate any of Beatley's plots. Furthermore, only 3 of 28 plots had enough spiny hopsage to justify including it in the association description (Webb et al., 2003). Although Beatley's plots were measured in 1975 and again in 2000–2003, changes could be related to specific climatic events in that period, notably the drought of 1989–1991 and the current drought. Other measurements made through this period (e.g., Hunter, 1994) indicate that the drought had major short- and long-term effects on perennial plants. The drought had its largest influence on plant associations dominated by sagebrush (*A. tridentata* and *A. nova*) and those with a large percentage of chenopods, particularly spiny hopsage.

Perennial grasses also suffered widespread mortality during the 1989–1991 drought (Hunter, 1994). This mortality was magnified because the perennial grasses increased substantially after 1960 (Webb et al., 2003), particularly during the wet period of the 1980s. Fluffgrass (*Erioneuron pulchellum*) was not measured from 1963 to 1975, yet it contributed 1.2% total cover in 2000 (Webb et al., 2003). Because of the current drought (1999–2003), no live fluffgrass was measured in 2003. Schultz and Ostler (1995a) measured substantial mortality related to the 1989–1991 drought in southern Nevada. They found widespread death of perennial grasses and C4 chenopod species and extensive drought pruning of other species. The cover of species affected by drought, however, increased during the wet 1993 El Niño (Figs. 4 and 6a; Schultz and Ostler, 1995b).

3.4.4. Drought pruning, 1989–1991 and 1999–2002

During drought, living plants shed branches to reduce above-ground carbon allocation and increase water-use efficiency. This process, known as drought pruning, leaves dead above-ground biomass that forms a significant component of total ground cover when combined with the preexisting coverage of dead shrubs. The combination of the 1989–1991 drought and the ongoing drought caused significant drought pruning on surviving individuals at the NTS (Appendix A). Comparing the average change from 1963 up to at least 2003, the total coverage of dead plant parts increased nearly 700%, with most of the increase (433%) occurring between 1975 and 2003, presumably during the 2 droughts. Total death of above-ground parts occurs, and some species—most notably creosote bush—can resprout from subterranean root stock.

Much of this dead biomass remains standing and unavailable for nutrient cycling, particularly dead branches not in contact with soil. Our observations at the NTS indicate that decomposition rates of dead plants are species-specific; some root crowns, particularly of creosote bush, remain long after the plant dies, whereas the root crowns of other species, particularly spiny hopsage, disintegrate relatively quickly. The large amount of standing dead biomass, coupled with increases in non-native annual plants, could conceivably increase fuel loadings and the potential for fire in the Mojave Desert ecosystem.

4. Summary and conclusions

Precipitation in the Mojave Desert region can occur, depending largely on location, in either the cool season (October–April) or biseasonally in the cool and warm (July–September) seasons during an annual cycle that runs from October through September. The cool-season pattern prevails west of approximately 117°W and the biseasonal pattern is typical of the region east of the 117th meridian. The cool-season pattern develops in fall and early winter while the biseasonal pattern can peak in January and again in August. Cool-season precipitation results primarily from extratropical cyclones of the North Pacific Ocean, whereas, the warm-season pattern is the northwesterly extension of the Mexican monsoon, which transports maritime tropical moisture into the desert region. Precipitation is spatially coherent across the desert, as suggested by the predominantly positive, significant correlations among weather stations.

Precipitation in the desert region varied on interannual and multidecadal time scales during the 20th century. Interannual variability produced irregular oscillations of about 5-yr duration in the precipitation time series. This variability is partly related to ENSO, a phenomenon of the tropical Pacific Ocean, whereby El Niño conditions may increase moisture and La Niña conditions typically decrease moisture. Multidecadal variability is expressed by 3 drought or dry periods and 2 periods of relatively wet conditions. For the calendar year, these periods are 1893–1904 (drought), ca. 1905–1941 (wet), 1942–1975 (mid-century dry period), 1976–1998 (wet), and 1999-present (September 2003, drought). These precipitation periods are similar to those identified in the adjoining Colorado Plateau and Sonoran Desert. This multidecadal variability, since at least the early 1940s, was coincident with and probably resulted from alternating cool (dry) and warm (wet) phases of the PDO, an index of the SST and sea-level atmospheric pressure of the North Pacific Ocean. The ongoing drought evidently results from a cool phase of the PDO that began in 1999. If past relations between the PDO and climate are repeated, the desert region may remain dry for 2–3 decades.

Field observations and measurements show that late 20th century climate variability affected Mojave Desert plant and animal populations. Although no studies directly address multidecadal variability of plant or animal communities, studies conducted since the late 1960s indicate that annuals and perennials responded to the generally favorable moisture conditions of the mid-1970s to late 1990s. Primary production of annuals is largest during periods of increased cool-season precipitation. This increase in biomass improves resource availability for small herbivores, enhancing reproduction of small mammals and certain reptiles. Perennials were also affected by the moist conditions. Landscape rephotography and transect data show that creosote bush increased substantially in size and cover, and other long-lived species established new individuals and gained biomass over existing ones.

Perhaps the most striking changes in plant communities since the late 1960s occurred during the drought of 1989–1991 and the current drought of 1999–2003. During the early drought, chenopod species and certain perennial grasses underwent population mortalities up to 100%. In 1976, spiny hopsage was a dominant species in 8 of 16 vegetation associations defined in the Mojave Desert. In classification work done shortly after the early drought, 10 associations were recognized, but only one had spiny hopsage as a dominant species. Death of perennial grasses was widespread during this drought and was intensified because the grass cover increased during the earlier wet period. Moreover, drought pruning, the shedding of above-ground biomass, increased significantly on individuals that survived the droughts.

Finally, precipitation variability modifies ecosystem processes, which in turn has implications for land management. Precipitation, along with other climate variables, affects plant and animal communities and modulates the recovery rates from natural and human disturbances. Our work suggests that precipitation variability in the Mojave Desert was sufficient to change the ecosystem at least during the late 20th century, the period for which ecological data are available.

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Appendix A

Drought pruning, as measured by total ground cover of dead plant parts on 55 permanent plots on the NTS (adapted from Webb et al., 2003; Webb, unpublished data) (see Table A.1).

Table A.1
Drought pruning, as measured by total ground cover of dead plant parts on 55 permanent plots on the NTS (adapted from Webb et al., 2003; Webb, unpublished data)

Plots	Cover of dead plants (%)			Percent change		
	1963	1975	2000–2002	1963–1975	1975–2000	1963–2000
1	1.75	0.11	3.20	−93	2686	82
2	5.28	4.85	10.39	−8	114	97
3	5.55	3.15	5.25	−43	67	−5
4	2.05	3.32	10.18	62	207	398
5	1.15	1.50	1.46	30	−2	27
6	5.16	1.01	2.46	−80	144	−52
7	1.81	2.22	11.94	23	438	560
8	0.89	1.55	6.32	74	306	609
9	2.28	1.94	13.06	−15	575	473
10	0.15	1.41	7.45	812	428	4718
11	1.45	2.90	3.09	99	7	113
12	6.76	0.46	5.25	−93	1031	−22
13	2.65	2.82	8.64	6	206	225
14	2.93	1.45	9.85	−50	577	236
15	1.46	0.06	3.73	−96	5757	155
16	2.00	0.43	3.41	−79	698	70
17	1.72	4.22	5.48	146	30	219
18	0.10	0.85	2.23	745	164	2131
20	2.24	2.13	3.35	−5	57	50
21	0.74	0.53	0.31	−28	−41	−57
22	3.29	2.15	7.68	−35	258	133
23	2.41	0.77	4.89	−68	533	103
24	3.83	1.57	6.14	−59	290	60
25	3.15	3.10	8.61	−1	178	174
26	2.74	3.03	6.95	11	129	154
27	2.55	1.92	5.55	−25	190	117
28	2.74	2.04	11.54	−26	467	322
29	6.05	2.92	7.72	−52	164	27
30	0.52	0.25	2.10	−53	757	306
31	2.48	0.98	7.26	−60	640	193
32	2.88	1.60	5.67	−44	255	97
33	1.25	1.00	2.59	−20	159	108
34	0.00	0.09	6.19	.	6710	.
35	0.77	0.75	8.97	−4	1104	1061
36	0.30	0.59	6.21	97	951	1970
37	0.00	0.47	8.21	.	1637	.
38	0.34	1.13	5.75	235	410	1608
39	3.76	1.31	10.58	−65	708	181
41	2.50	0.84	5.00	−67	498	100
43	2.77	2.20	9.09	−21	313	228

Table A.1 (*continued*)

Plots	Cover of dead plants (%)			Percent change		
	1963	1975	2000–2002	1963–1975	1975–2000	1963–2000
44	4.28	1.11	6.34	−74	471	48
45	3.51	1.63	9.94	−54	511	183
46	3.46	1.40	13.42	−60	858	287
47	6.45	3.57	13.76	−45	285	113
49	2.32	1.55	8.18	−33	426	253
50	1.15	0.99	18.59	−13	1776	1523
51	2.85	1.35	14.61	−52	979	413
56	2.67	0.43	8.90	−84	1983	233
60	1.09	1.45	8.39	33	477	669
61	6.51	2.23	8.12	−66	264	25
62	3.98	4.42	12.91	11	192	224
63	10.50	1.84	6.93	−83	277	−34
65	0.25	1.74	3.05	607	76	1144
66	1.94	5.00	13.44	158	169	594
68	13.24	12.17	12.80	−8	5	−3
Average	2.85	1.94	7.51	27	694	433

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