

Perennial plant mortality in the Sonoran and Mojave deserts in response to severe, multi-year drought

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ABSTRACT

Recent drought caused considerable shrub mortality in parts of the Sonoran and Mojave deserts (USA). The most severe impacts occurred in southern parts of the Mojave Desert and the adjacent Lower Colorado section of the Sonoran Desert in southernmost California and southwestern Arizona. In that region, mortality of the small, drought-deciduous shrubs *Ambrosia deltoidea* and *Ambrosia dumosa* was 100% or nearly so. The larger, drought-enduring evergreen *Larrea tridentata* fared much better, although nearly two-thirds of all *L. tridentata* plants succumbed at one location. Data on 21 additional perennial species showed that other species of small, drought-deciduous shrubs also sustained considerably higher mortality. The best predictor of plant responses was the Standard Precipitation Index (SPI) calculated for a 60-month time frame ending in March 2003, indicating the importance of the cumulative effect of successive drought years. Deficits of cool-season precipitation were more extreme than warm-season deficits and were probably the greatest contributor to plant mortality. Soil conditions, including differences in parent materials and texture, also influenced plant responses. Episodes of drought-induced, perennial plant mortality represent extensive, region-wide ecological disturbances and may be one of the most important processes affecting plant populations and community composition in deserts.

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1. Introduction

Arid and semi-arid regions across the American Southwest have experienced considerable decadal-scale variations in precipitation over the last century. Most recently, an interval of above-average precipitation from the mid 1970s to the late 1990s, especially winter precipitation associated with more frequent El Niño–Southern Oscillation (ENSO) conditions, was followed by protracted, severe drought. In many places, several years of below-average precipitation that began in late 1998 led up to a year with extreme precipitation deficits in 2002. This prolonged drought and an earlier, less severe one from 1989 to 1991 (Hereford et al., 2006) prompted several studies that documented the impacts of drought on perennial plants in the Sonoran and Mojave deserts. Hereford et al. (2006) and Webb et al. (2003) documented the nature of the precipitation shifts and associated responses of perennial plants in the northern Mojave Desert. Hamerlynck and McAuliffe (2008) showed that plant responses to drought varied considerably as

a function of soil types at a site in the east-central Mojave Desert. Miriti et al. (2007) documented mortality of perennials in permanent plots in a site near the transition of the Sonoran and Mojave deserts in southern California, and Bowers and Turner (2001) and Bowers (2005) documented mortality of various shrubs and the tree *Cercidium* [= *Parkinsonia*] *microphyllum* near the northeastern margin of the Sonoran Desert near Tucson, Arizona.

One general pattern from these studies emerged: adult, long-lived, drought-deciduous shrubs and long-lived, drought-enduring evergreen shrubs fared better than did shorter-lived, drought-deciduous shrubs. However, dissimilar results were obtained regarding relationships between mortality and plant size in individual species. In some species, larger plants exhibited greater mortality (Bowers and Turner, 2001; Hamerlynck and McAuliffe, 2008), whereas in others, smaller plants were more susceptible (Miriti et al., 2007).

These few studies do not provide a comprehensive picture of either region-wide or local variation in responses of desert plants to extreme drought. The primary purpose of this study is to document responses of perennial plants to extended, severe drought at sites across the Sonoran and Mojave deserts and to relate those responses to regional variation in drought intensity. The paper has five components: (1) analysis and summarization of regional

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variation in drought intensity, (2) documentation of regional variation in condition and mortality of dominant species (*Larrea tridentata*, *Ambrosia dumosa*, *Ambrosia deltoidea*), (3) analyses of statistical relationships between plant responses and drought intensity, (4) examination of how responses of dominant species to drought are related to soil conditions and plant size and (5) presentation of responses of other coexisting perennial plant species and evidence of a previous episode of drought-related perennial plant mortality.

2. Study sites and methods

Sites distributed throughout the Sonoran and Mojave Deserts in southwestern Arizona, southern California, and southern Nevada were examined and surveyed from March through May, 2003 (Appendix 1, electronic version only). A total of 22 transects were established at nine of the sites (Sites 1–9). Several sites (Sites 2, 6, 7, 15) were locations of previous published studies (Hamerlynck et al., 2002; McAuliffe, 1988, 1994; McAuliffe et al., 2007). The remaining locations were chosen to provide a wide geographic distribution of sites in order to investigate regional variation in plant responses. Most transects were located on alluvial fan deposits. When a site possessed alluvial deposits of different geological age (i.e., Pleistocene vs. Holocene deposits), separate transects were established on the different deposits in order to investigate plant responses on contrasting soils.

For each transect at Sites 1–8, a point of origin was arbitrarily chosen and marked with a steel stake driven into the soil, each marked with a labeled brass tag (Appendix 1, electronic version only). A 50 m-long measuring tape was extended from the origin to a second steel stake driven into the soil at the 50 m mark. The compass bearing of this transect was recorded, measured from the origin. Most transects were 50 m-long, but in some cases where plant density was extremely low, a second transect segment was established from the 50 m mark to a third stake at 100 m. One transect was limited to a single, 30 m segment because of topographic limitations of sampling area size. The transects were all positioned between flumes and did not intersect surface drainages. Locations of all stakes along the transects (0 m, 50 m, 100 m or other specific distances) were measured with a hand-held GPS unit. All metal stakes along transects were covered with small stone cairns approximately 25–35 cm tall.

2.1. Timing of surveys

Surveys in the Sonoran Desert (Sites 1–4, 9, 10) and one lower elevation site in the Mojave Desert (Site 8) were conducted in mid-March 2003 (Table 1), approximately 1 month after the entire region received rain in mid-February from a widespread Pacific frontal storm. Prior to that rain, drought-deciduous shrubs were dormant due to persistent drought. The time that had elapsed between the February, 2003 rains and the mid-March surveys ensured that surviving drought-deciduous plants that respond to cool-season precipitation (e.g., *A. deltoidea*, *A. dumosa*) had adequate time to produce new leaves and shoots.

The remainder of the sites in the Mojave Desert were also initially visited in mid-March, 2003. However, despite the earlier precipitation, plants at most of those sites remained dormant because of the cooler temperatures of the more northern locations and higher elevations. As a consequence, the higher elevation sites in the Mojave Desert were surveyed in early-mid May, 2003 in order that surviving plants be given sufficient time to initiate shoot and leaf development.

2.2. Sampling methods

Since *L. tridentata* and either *A. deltoidea* or *A. dumosa* were usually the dominant species, sampling was designed principally to ensure that adequate numbers of each were included in each surveyed area. Data were taken on all individuals of *Ambrosia* spp. and other small subshrub species located within a 4 m-wide belt centered on the axis of each transect. Larger sampling areas consisting of wider belts, generally 5 m on each side of the transect, were used in assessments of *L. tridentata* and other species that attained larger sizes but were present in lower densities. At a few sites where plant densities were extremely low, the belts were extended to 10 m on each side of the transect in order to ensure that adequate numbers of *L. tridentata* were included (usually a minimum of 20–25 plants).

Plants were visually examined and stems were considered living if they had initiated new leaf production and/or shoot development in response to the earlier rains of late winter 2003. Overall condition of each plant was determined visually and assigned a score on the following 6-point categorical scale. A score of 0 was assigned to plants that completely lacked living stems, but retained persistent, dried leaves on at least some of the branches that had been produced the previous year. Only the data on these most recently expired plants were included for analyses of recent mortality (i.e., within the year preceding the spring, 2003 sampling). Dead woody stems of desert shrubs can persist for decades (e.g., Ebert and Zedler, 1984). Consequently, the occurrence of persistent, dead and dehydrated leaves that had been produced in the previous year, but absence of any new shoot or leaf growth, despite adequate precipitation to foster such production, provided the best available field indicator that the plant had died within the past year.

The remaining scores (1–5) were assigned to surviving plants: 1 = less than 1/8 of the entire canopy was alive, as indicated by presence of new leaves; 2 = 1/8–1/4 alive; 3 = 1/4–1/2 alive; 4 = 1/2–3/4 alive, and class 5 = more than 3/4 of canopy alive. For each *L. tridentata*, position along each transect, perpendicular distance from the transect, and side of transect (compass direction) was recorded so that individual plants could be relocated in the future. Because the data on plant condition were recorded on an ordinal scale, Kruskal–Wallis one-way nonparametric analysis of variance by ranks and subsequent pair-wise comparisons were used to statistically compare distributions of plant condition classes among various transects (Kruskal–Wallis One-Way AOV, Statistix v.8.0, Tallahassee FL).

At one site (Site 4A) there was an unusual abundance of large, dead *L. tridentata* plants, the remains of which exhibited considerable weathering and decay (complete loss of bark and fine twigs and stems; decomposition and splitting of wood of larger stems; lack of any sign of more recent resprouting), indicating the plants had died a long time ago. Data were taken on these dead individuals (basal diameters and locations) but these data were not included in analyses of recent mortality.

Next to the origin of each transect, the soil was examined from the vertical side of a small pit excavated to variable depths, depending on the presence of relatively impenetrable, cemented calcic horizons (“caliche”) or rock. A soil profile was described and included identification and thicknesses of soil horizons, Munsell soil color, and field determination of textural class. Slope inclination was measured with a clinometer and aspect was measured with a compass. The regional pattern of plant responses to climatic drought per se was evaluated by comparing plants occupying young (Holocene) alluvial or eolian deposits that lacked strong soil horizon development. Those substrates allow maximal surface infiltration of precipitation due to the permeable nature of the sandy to gravelly soils.

Table 1

Condition of *Larrea tridentata* and *Ambrosia* spp.; data taken in spring, 2003. Data on *Ambrosia* spp. refer to *A. dumosa* unless marked with and asterisk (*). Percentage data are rounded to the nearest whole number.

Site name	Initial survey date	Transect number & substrate type	<i>Ambrosia</i> spp.							<i>Larrea tridentata</i>							Survey width (m)
			Percentage of plants in each condition class							Percentage of plants in each condition class							
			Condition classes							Condition classes							
			N	0	1	2	3	4	5	N	0	1	2	3	4	5	
1. Organ Pipe	11–12 Mar	1A. Rocky hillslope	*66	100	0	0	0	0	0	49	35	35	10	6	12	2	10
		1B. Holocene fan	*21	100	0	0	0	0	0	32	3	3	3	19	22	50	10
		1C. Pleistocene fan	1	100	0	0	0	0	0	52	15	21	6	15	21	21	10
2. Dateland AZ	14 Mar	2A. Eolian sand	56	57	7	18	7	7	4	23	0	0	0	4	26	70	10
3. Mohawk Mts	14 Mar	3A. Rocky hillslope	(absent)							13	0	8	8	38	23	20	
4. Ocotillo CA	15 Mar	4A. Holocene fan	66	94	2	2	2	0	2	23	0	0	0	39	35	26	20
		4B. Pleistocene fan	63	98	0	2	0	0	0	25	16	12	32	12	24	4	10
5. Joshua Tree	6 May	5A. Late Holocene fan	1	100	0	0	0	0	0	27	22	59	4	4	7	4	20
		5B. Late Holocene terrace	(Absent)							15	0	20	0	7	40	33	20
	7 May	5C. Holocene fan	167	100	0	0	0	0	0	31	39	45	13	3	0	0	10
6. Johnson Valley	9 May	5D. Pleistocene fan	36	97	3	0	0	0	0	22	0	0	0	18	23	59	20
		6A. Late Holocene fan ¹	47	89	6	4	0	0	0	26	4	0	0	8	35	54	20
		6B. Mid Holocene fan ²	81	80	15	3	3	0	0	31	0	0	0	0	10	90	20
		6C. Pleistocene fan ³	99	99	1	0	0	0	0	37	3	0	0	3	35	60	20
7. Providence Mts.	7 May	7A. Holocene fan ⁴	68	28	43	22	4	3	0	17	0	0	0	12	18	71	8
		7B. Late Pleistocene fan ⁵	158	14	13	20	27	22	4	13	0	0	0	0	8	92	8
		7C. Mid Pleistocene fan ⁶	134	0	3	6	27	39	25	24	0	0	0	0	0	100	8
		7D. Late Pleist. Pavement ⁷	1	0	0	0	0	100	0	22	0	0	0	0	23	77	8
		7E. Late Pleist. limestone fan	1	0	100	0	0	0	0	28	7	4	7	21	46	14	8
8. Mormon Mesa	19 March	8A. Pleistocene dune deposits	74	37	20	8	10	8	18	15	0	0	0	0	100	20	
9. Buckskin Mts.	21 March	9A. Pleist. fan remnant ridge	3	100	0	0	0	0	0	43	7	33	12	12	26	12	10
		9B. Pleist. fan remnant slope	33	21	31	15	9	21	3	15	7	7	0	0	20	67	10
10. Cactus Plain	21 March	10A. Dune slope	28	7	14	18	18	18	25	(Absent)							
		10B. Holocene alluvium	33	18	24	12	9	18	18	16	0	0	0	0	0	100	10
11. Usery Mts	1 April	10A. Runoff producing slope	*50	34	34	16	6	8	2	(Absent)							
		10B. Runoff producing slope	*50	38	36	22	4	0	0	(Absent)							
		11C. Runoff receiving footslope	*34	3	0	6	9	35	47	(Absent)							
		11D. Holocene alluvial fan	*50	8	28	22	18	16	8	14	0	0	0	0	29	71	
12. Desert Botanical	3 April	12A. Pediment	*25	72	20	4	4	0	0	(Not recorded)							
13. Florence (south)	15 April	13A. Pleistocene fan remnant	50	12	12	6	28	34	8	50	2	0	0	0	6	92	
14. Florence (southeast)	15 April	14A. Holocene fan	*50	36	12	8	14	18	12	50	0	0	0	0	6	94	
		14B. Holocene fan depression	*50	0	0	0	4	6	90	(Not recorded)							
15. Silverbell	15 April	15A. Mid Pleistocene fan	*50	6	8	8	8	34	36	(Absent)							
		15B. Late Pleistocene fan	*50	24	22	8	12	22	12	50	0	0	0	0	0	100	
		15C. Late Pleistocene fan	*50	24	14	10	18	24	10	(Not recorded)							
		15D. Holocene fan	*50	16	10	14	34	20	6	50	0	0	0	0	0	100	

¹ Site Y-1 in McAuliffe et al. (2007).

² Site I-1 in McAuliffe et al. (2007).

³ Site O-1 in McAuliffe et al. (2007).

⁴ Young Alluvial site in Hamerlynck et al. (2002).

⁵ Intermediate Alluvial site in Hamerlynck et al. (2002).

⁶ Old Alluvial site in Hamerlynck et al. (2002).

⁷ Pavement site in Hamerlynck et al. (2002).

Transects at Organ Pipe Cactus National Monument, Ocotillo CA, Joshua Tree National Park, and Johnson Valley (Sites 1, 4, 5 and 6) were revisited in March–May 2004 and 2005 and in late April 2009 (only Site 5) and plants contained within the original sampling belts along the transects were re-examined. All individual plants of *L. tridentata* were relocated and their condition scored using the same 6-point categorical scale described above. Condition of all subshrubs, including *Ambrosia* spp. in the 2-m wide belts along each side of a transect was examined and scored. These subsequent surveys allowed us to detect whether or not any of the plants originally classified as dead in 2003 may have actually survived and eventually resprouted, and provided the means of evaluating the accuracy of the original 2003 mortality estimates.

Additional surveys in 2003 restricted to assessments of condition of *Ambrosia* spp. and *L. tridentata* were conducted at 5 sites in the eastern-most Sonoran Desert (Sites 11–15). Substantially less mortality occurred at those sites and permanent transects were not established at them. At each area, different sites with contrasting soil conditions were examined and 50 plants of each species (*L. tridentata* and either *A. dumosa* or *A. deltoidea*) were selected using the wandering quarter technique (Krebs, 1989). Plant condition was scored on the 6-point categorical scale and GPS coordinates of site locations were recorded.

2.3. Precipitation records and analyses

We used the Standardized Precipitation Index (SPI) to assess variation in drought intensity across the Sonoran and Mojave Desert regions of the southwestern United States. Computation of SPI for a location requires at least 30 years of continuous monthly precipitation data, and renders a normalized index in which precipitation periods can be directly compared among localities from highly different climate regimes (McKee et al., 1993). SPI is ideal for comparing variation in drought across the Mojave and Sonoran deserts, which have distinctly different annual distributions of cool- and warm-season precipitation. For any given time period, an SPI of 0 indicates normal precipitation, -1 to -1.99 severely dry and ≤ -2.0 indicate extreme dry conditions compared to all other similar time periods in the data set (McKee et al., 1993, 1995). Monthly precipitation data was obtained from the Western Regional Climate Center (<http://www.wrcc.dri.edu/summary/Climsmaz.html>) for sixty-seven National Weather Service cooperative stations at elevations below 1525 m ASL and having continuous monthly precipitation totals for the 30 year periods of 1974–2004 or 1975–2005. Cumulative SPI indices for 6, 12, 24, 36, 48 and 60-month periods ending in March, 2003 for each station were generated (SPI SL 6.exe; available at http://www.drought.unl.edu/monitor/spi/program/spi_program.htm). Six-month SPI for cool season (October–March) and warm season (April–September) were also generated for 1998–2003. Latitude and longitude provided in the metadata for each NWS station was used to generate contour plots of March 60-month SPI generated by ordinary kriging with a search radius of 4.0, and based on hyperbolic semivariograms having a nugget of 0.1, a sill of 0.80 and range of 4.0 (Systat v8.0, SPSS Chicago, IL). Estimated SPI values for the study sites were obtained through arithmetic interpolation using values of adjacent SPI isolines.

Split-plot repeated-measures analysis of variance (RM-ANOVA; Statistix v.8.0, Tallahassee FL) was used to compare 6-month SPI for National Weather Service stations from the Mojave ($n = 28$) and Sonoran ($n = 28$) deserts for cool season (Oct–March) and warm season (April–September) from 1998 to 2003. Main (whole-plot) effect was desert region (Mojave vs. Sonoran), using the region-by-replicate interaction as the whole-plot error term. Sub-plot (within-region) effects were year (1998–2003) and season (warm

vs. cool), and all higher order interactions, using the region-by-year-by-season-by-replicate interaction as the sub-plot *F*-test error term. The region-by-year interaction was of specific interest, since a significant *F*-test result here would indicate regional differences in year-to-year variation in drought intensity.

3. Results

3.1. Drought severity

In the Sonoran and Mojave deserts, drought conditions began in 1999 and prevailed for several years. Six-month SPI values for 56 precipitation recording stations within the Sonoran and Mojave deserts provide a comparison of drought severity in the two regions and the magnitude of cool- vs. warm-season precipitation anomalies (Fig. 1). For the 1998 through 2003 period, the Mojave desert stations had significantly higher SPI than Sonoran desert stations pooled across the entire five years ($F_{1,54} = 5.64$; $p = 0.021$), while cool-season precipitation (Oct–March) 6-month SPI was significantly lower than warm-season SPI (April–September; $F_{1,594} = 48.52$; $p \leq 0.001$). In 2000, average deficits of cool-season precipitation were significantly less severe in the Mojave Desert than in the Sonoran due to near-normal conditions in the northern part of the Mojave Desert for the period October 1999 through March 2000 (Fig. 1); driving a significant desert-by-year interaction ($F_{5, 594} = 4.19$; $p \leq 0.001$). Extreme deficits of both summer and winter precipitation occurred in 2002; the two consecutive 6-month periods ending in late 2002 (October 2001–March 2002 and April–September 2002) immediately preceded the timing of the plant mortality surveys conducted in spring 2003.

3.2. Plant mortality

3.2.1. 2003 Surveys

Data were taken from a total of 1225 individuals of *Ambrosia* spp. and 566 *L. tridentata* in March through May, 2003. Compared to *L. tridentata*, *Ambrosia* spp. exhibited considerably higher mortality and poorer condition of survivors (Table 1, Fig. 2). At locations where mortality of *L. tridentata* was only a few percent, mortality of *Ambrosia* sp. was typically 90% or more (Fig. 3). Mortality rates of 90% or higher in *Ambrosia* spp. occurred at several

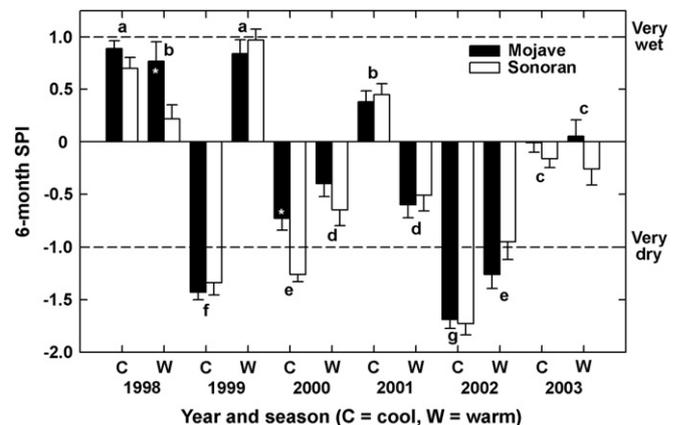


Fig. 1. Six-month SPI values for 56 precipitation recording stations within the Sonoran and Mojave Deserts classified by location (Sonoran vs. Mojave) and cool- vs. warm-season precipitation (October–March; April–September, respectively). The SPI values for each season reflect the 6-month time frame leading up to the end of each season. The letters above or below histogram bars indicate significant differences pooled across both desert regions within a season; asterisks indicate significant differences between deserts pooled across both seasons within a year.

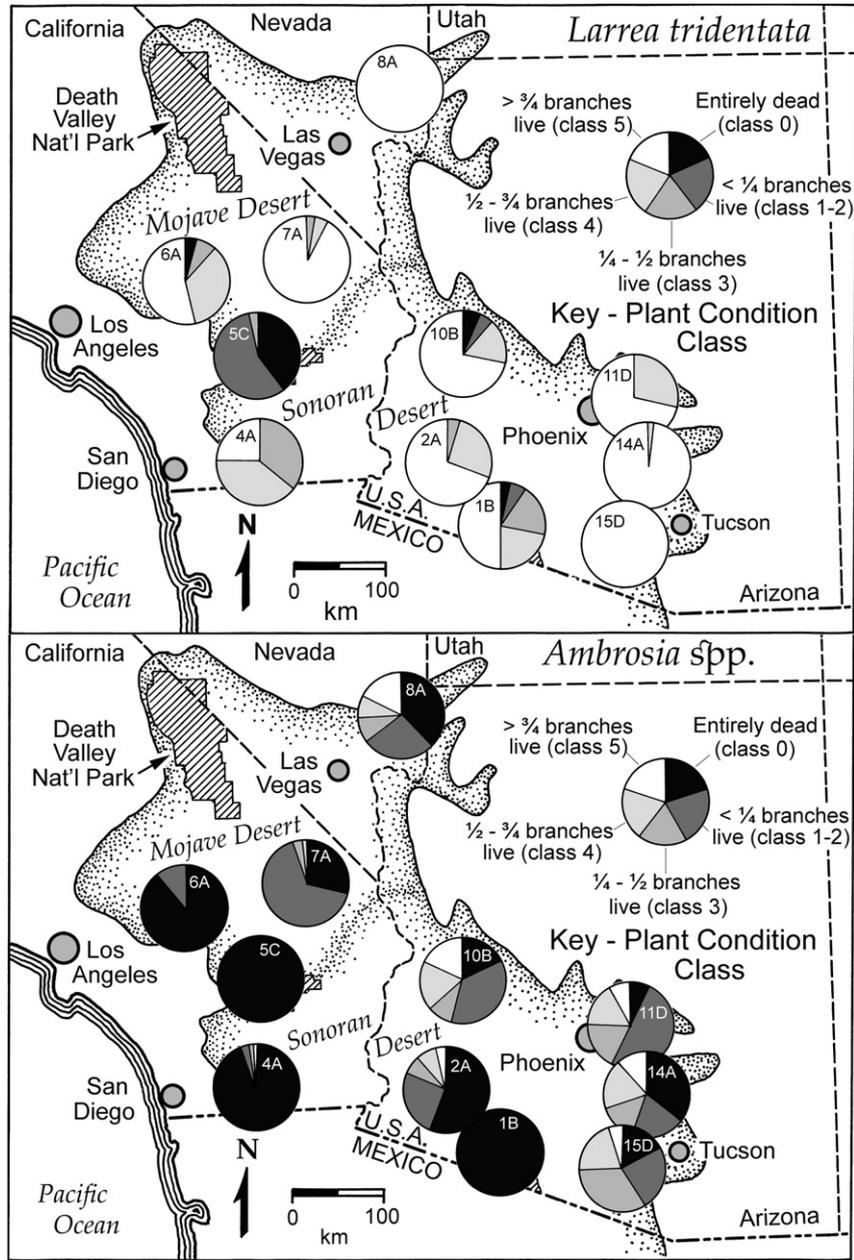


Fig. 2. Responses of *Larrea tridentata* (upper panel) and *Ambrosia* spp. (lower panel) at selected sites throughout the study region. Transect identification numbers are superimposed on individual pie diagrams.

locations in Organ Pipe Cactus National Monument, Ocotillo CA, and Joshua Tree National Park (Fig. 2; Sites 1B, 4A, 5C). In contrast, mortality of *L. tridentata* exceeded 10% at only a few places. The greatest mortality in *L. tridentata* recorded in 2003 was at Joshua Tree National Park, where 39% of the plants were classified as dead at Transect 5C (Table 1, Fig. 2).

3.2.2. Changes in subsequent years

At the two transects in Joshua Tree National Park where considerable mortality of *L. tridentata* occurred, two of 5 plants at transect 5A and one of 12 at 5C that were recorded as dead (condition class 0) in May 2003 had sprouted a few, very small living shoots at the base of the plants by April 2004. However, all plants recorded as dead in 2004 showed no recovery in 2005 or 2009. In 2009 bark of all stems of plants classified as dead in 2004 had begun to exfoliate, clearly indicating the plants were dead.

Furthermore, the 2004, 2005, and 2009 surveys of those two transects showed additional mortality of some plants that were recorded as alive in 2003. At transect 5A, the percentage of plants classified as dead was 22% from 2003 to 2005, but increased to 26% in 2009 due to one additional death. At transect 5C, percentage mortality increased from 39% (2003) to 52% (2004) and finally 65% (2005) and remained at that level, with no additional deaths or recoveries through 2009.

Repeated surveys in 2004 and 2005 were conducted at four transects to check on condition of *A. deltoidea* and *A. dumosa*. At two sites where 100% mortality was recorded in 2003 (Transects 1B, 5C; Appendix 2, electronic version only), the subsequent surveys showed that these plants were dead; none had resprouted or recovered. At Transects 4A, 4B, and 5D, several plants that were classified as dead and placed in condition class 0 in 2003 had recovered and exhibited new, but very limited shoot growth

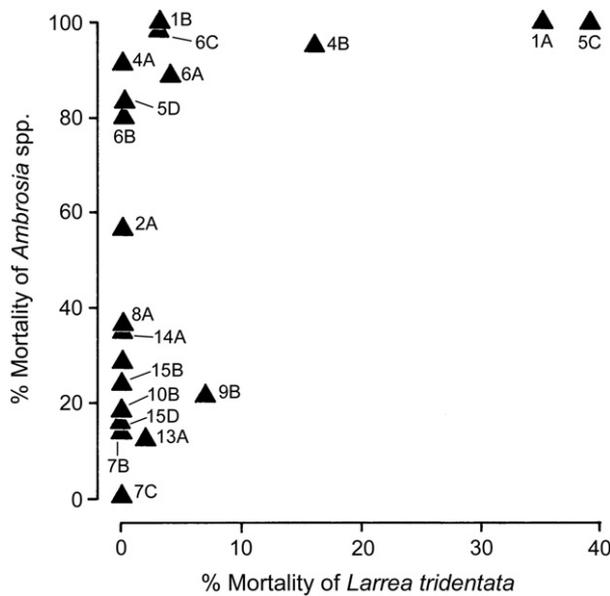


Fig. 3. Comparison of mortality of *Ambrosia* spp. and *L. tridentata* at 20 sampling locations where they co-occurred.

(Appendix 2, electronic version only). However, the reduction of estimated mortality at those sites due to the recovery of those plants was typically only a few percentage points. Although our initial surveys slightly overestimated mortality at those sites, the error was minimal. At three other locations (Transects 6A, 6B, 6C), the number of dead plants actually increased from 2003 to 2005 indicating additional mortality since the original survey (Appendix 2, electronic version only).

3.2.3. Regional variation

The highest plant mortality occurred in southwestern Arizona and southernmost California in the Sonoran Desert to just north of the transition between Sonoran and Mojave deserts in the region of Joshua Tree National Park (Site 5C, Fig. 2). Plant condition markedly improved further to the north. For example, all *L. tridentata* at the northern-most site at Mormon Mesa (Site 8A; Fig. 2) were in the highest condition class 5; similarly the distribution of condition classes for *A. dumosa* was also among the highest. Although quantitative surveys were not conducted in Death Valley National Park, reconnaissance in March 2003 showed no widespread plant mortality in this area near the northwestern limit of the Mojave Desert. Similarly, sites near the eastern margin of the Sonoran Desert south and east of Phoenix, Arizona and in the vicinity of Tucson exhibited little or no mortality of *L. tridentata* and relatively high values for condition scores of *A. deltoidea* (Sites 11D, 14A, 15D; Fig. 2).

Within this general geographic pattern, plant responses were frequently variable over the scale of kilometers to several tens of

kilometers. Within the southwestern portion of the area where high mortality occurred, local sites were occasionally encountered where plants were in markedly better condition. Conversely, to the north and east, local sites could be found where plant condition was poorer than was generally the case for the area. In addition, all plant survey transects were located between flumes and drainages. At all sites, including those where substantial mortality was recorded, plants fared better along ephemeral drainages.

SPI calculated for the 76 regional recording stations for six time scales preceding March 2003 (6, 12, 24, 36, 48 and 60 months) allow comparison of geographic variation in the severity of short-term drought (precipitation deficits during the most recent 6 months) vs. longer term drought (cumulative effects of increasing intervals of up to 5 years duration). Although SPI values generally declined from the 6–60-month time scales (Table 2), the geographic position of peaks and troughs in SPI shifted (Fig. 4), reflecting regional changes in precipitation deficits during different time intervals. Additionally, the absolute range of low to high values of SPI increased with increasing time scale (Table 2, Fig. 4), indicating greater spatial variation in drought intensity measured at longer time scales.

Measures of plant responses recorded in spring 2003 were significantly positively correlated with 60-month scale SPI values (e.g., higher survival and better plant condition scores with higher SPI values; Fig. 5). The geographic area in which plant mortality was highest and condition of survivors poorest corresponds closely with the lighter shaded zones (indicating the most severe drought conditions) on the 60-month SPI contour map (cf. Figs. 2 and 4). No such correspondence occurs between plant condition and the 12-month SPI contour map. There were no other significant positive correlations between plant responses and SPI values for any other time scale (2). However, for *Ambrosia* spp., there were three significant negative correlations at the 6 and 12 month scales (e.g., relationships indicating better plant condition associated with more severe drought; Table 2). Those positive correlations indicate the unsuitability of relying only on information about relatively short-term precipitation deficits to predict condition of these shrubs. For example, the lowest relative 12-month SPI values were located in northern and eastern parts of the study area (Sites 8, 11, 14, and 15; Fig. 4), but *A. deltoidea* plants were in relatively good condition at those sites (Fig. 2) due to less extreme drought conditions over the longer term.

3.3. Influences of soil characteristics

Five sites (Sites 1, 4, 5, 6, and 7) offered comparisons of plant responses in contrasting soils formed in non-calcareous deposits of Holocene vs. Pleistocene alluvium. Soils in sandy to gravelly Holocene deposits show minimal horizon development. In contrast, soils that have formed in the older, stony Pleistocene deposits are strongly developed and contain clay-enriched B horizons and underlying calcic horizons [see McAuliffe, 1994, 1999a,b for general information about these soil differences]. Plants at the sites

Table 2
Variation in SPI for 6- to 60-month time frames preceding March, 2003 and associated correlation coefficients (r) of SPI with mean plant condition and percent survival of *Ambrosia* spp. and *Larrea tridentata*. Significant correlation coefficients are in bold, asterisk indicate * $p < 0.05$ and ** $p < 0.01$, respectively.

Time scale (mo)	Mean SPI	SPI range (low to high)	<i>Ambrosia</i> condition	<i>Ambrosia</i> % survival	<i>Larrea</i> condition	<i>Larrea</i> % survival
6	-0.15	-0.80 to 0.20	-0.60*	-0.54*	-0.21	-0.18
12	-0.65	-1.2 to -0.15	-0.53*	-0.45	-0.19	-0.17
24	-1.54	-2.04 to -0.96	0.13	-0.11	-0.08	-0.09
36	-1.17	-1.60 to -0.15	0.38	-0.23	0.22	0.15
48	-1.14	-1.50 to -0.15	0.46	0.39	0.41	0.34
60	-1.47	-1.80 to -0.15	0.79**	0.68**	0.74**	0.61**

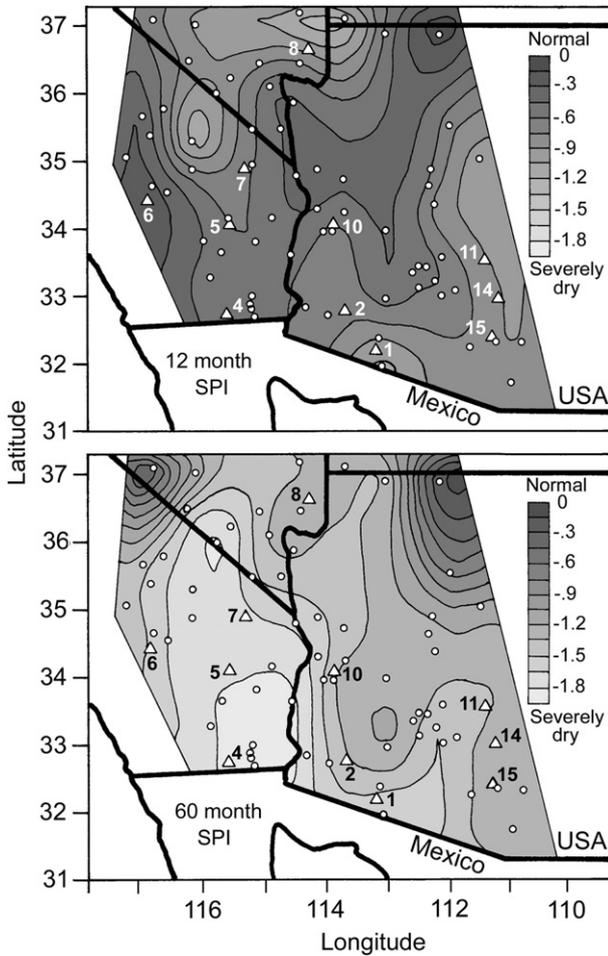


Fig. 4. SPI contour maps for time scales of 12 months (upper panel) and 60 months (lower panel) preceding the end of March, 2003. Small open circles represent locations of precipitation recording station data used in calculation of SPI; open triangles and accompanying numbers are study site locations and numbers.

exhibited three different kinds of responses in relation to soil characteristics and site elevation (Fig. 6). Group 1 includes two sites (Site 1: 435 m, Site 2: 200 m), both lower in elevation and more arid than sites in the other groups, where plants growing on Holocene alluvial deposits were in markedly better condition than those growing on Pleistocene deposits. Group 2 contained a single site (Site 6: 920 m) where plant responses on Holocene and Pleistocene deposits were not statistically different. Group 3 includes two sites (Site 5: 1050 m, Site 7: 910 m) where plants usually fared better on the well-developed soils of Pleistocene deposits (e.g., *L. tridentata* at sites 5A and 5C vs. 5D; *A. dumosa* at site 7A vs. sites 7B and 7C). The Pleistocene fan deposits at both sites 5A, 7B, and 7C are composed of coarse, cobbly to bouldery materials and pronounced argillic horizons have developed within these substrates [see Hamerlynck et al., 2002 for soils information]. Examination of subsurface soil layers at Site 5 in May 2003 indicated the presence of substantially more moisture in the soils of the Pleistocene surface (site 5D) than soils of the fine gravelly-sandy Holocene surfaces (Sites 5A, 5C). The relatively large stones on the surface and within the Pleistocene deposit impede the evaporative loss of soil water; the fine-grained Holocene deposits lack this kind of evaporative barrier.

In addition to the contrasts between Holocene and Pleistocene fan deposits of non-calcareous alluvium, three sites contained soil environments formed in other kinds of geological settings and soil parent materials. Site 1A, where *L. tridentata* exhibited the poorest

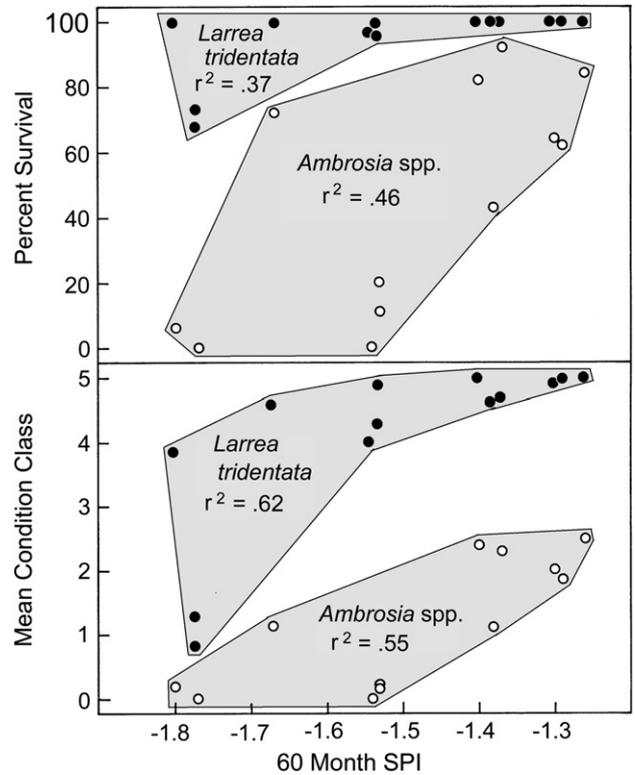


Fig. 5. Survival and condition in *Larrea tridentata* and *Ambrosia* spp. as a function of the 60-month time frame SPI values for each site. Correlation coefficients (r) for all four relationships are significant at $P < 0.05$.

condition among the sites at Organ Pipe Cactus National Monument (Fig. 6, Group 1), was located on a hillslope with a thin mantle of sandy-loam textured soil, generally 20 cm or less in thickness, over extremely hard, little-weathered metamorphic bedrock. Site 5B in Joshua Tree National Park was located on a low terrace next to a large ephemeral stream. Although the terrace was composed of fine-grained sandy to gravelly Holocene alluvium, *L. tridentata* plants at that location were substantially taller and in better condition than those on the other Holocene surfaces, indicating a substantial augmentation of soil moisture by occasional flows from the wash (Fig. 6, Group 3). Transect 7E (Fig. 6, Group 3) is a Pleistocene fan deposit composed of coarse gravelly to fine cobbly limestone alluvium with a very small fine soil fraction and a corresponding small capacity to store water within the rooting zone.

3.4. Effects of plant size

Comparisons of the sizes of plants that were recorded as dead (condition class 0) in 2003 vs. those that survived (classes 1–5, combined) were made for transects containing a minimum of 10 plants in either category (live vs. dead) for *A. dumosa* and a minimum of 5 plants in either category for *L. tridentata*. There were no significant differences in basal diameter of live and dead *L. tridentata* at the four locations examined (1A, 1B, 5A, 5C; two-sample t -tests, $P > 0.05$). However, the mean canopy diameter of *A. dumosa* plants that had died was significantly less than those that had survived at four of five locations (Fig. 7).

3.5. Responses of other species

Although *L. tridentata* and *Ambrosia* spp. were the dominant species at most sites, 21 other species were sampled. Although

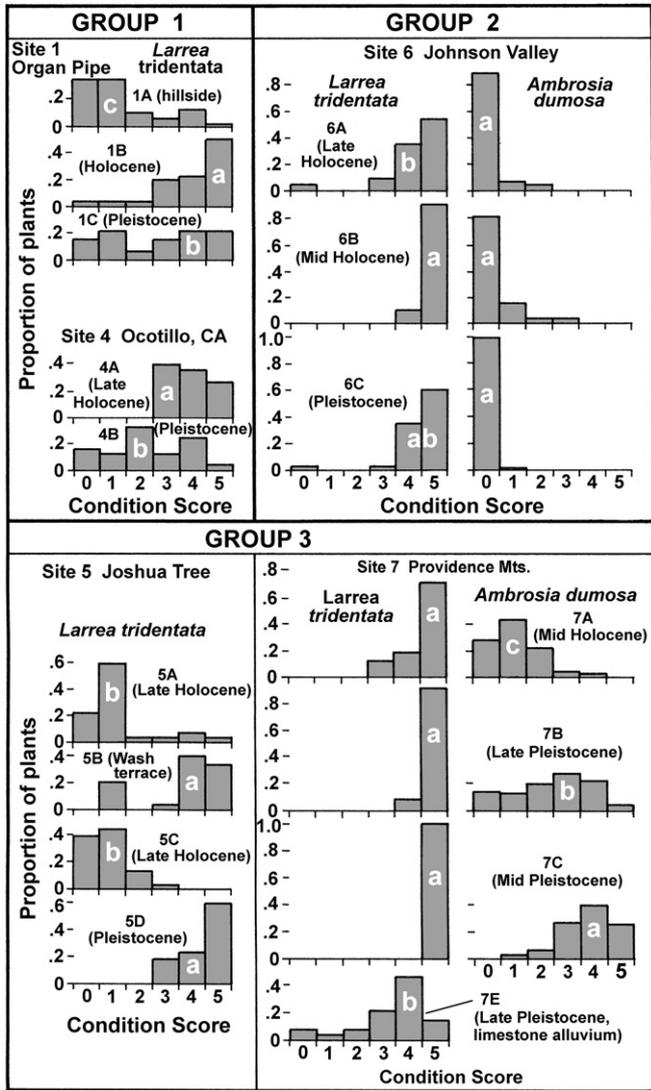


Fig. 6. Plant condition scores (horizontal scales) for *L. tridentata* and *A. dumosa* on different substrates and associated soils at four different study sites. White miniscule letters superimposed on histograms represent designations of significantly different distributions (Kruskal–Wallis ANOVA and subsequent multiple comparisons, $P < 0.05$).

relatively few individuals of those other species were typically located within individual surveyed areas, they collectively showed clear responses among different groups of species and across sites from different geographic areas. Fig. 8 presents those responses in a site-by-species visual matrix of the incidence of mortality. Data for a species were included only if at least two individuals of that species were recorded along a particular sampling transect. Four groups are shown in the figure. Group 1 contains the dominant species, *L. tridentata* and *Ambrosia* spp., included for visual comparison with other species' responses. Group 2 contains shrubs that exhibited considerable mortality at many sites. Group 3 contains shrubs and a small tree (*C. microphyllum*), all of which exhibited little or no mortality. Group 4 contains succulents (*Opuntia* spp., *Yucca* spp.).

Several species in Group 2 sustained mortality as high as *A. dumosa*, with 100% mortality at some sites. Geographically, the highest mortality within members of this group was at sites 1 through 6, the same set of sites that exhibited highest mortality for *Ambrosia* spp. and highest mortality and poorest condition for *L. tridentata*. At sites in Joshua Tree National Park (Sites 5A–D), 100% mortality of *Cassia* (= *Senna*) *armata*, *Psoralea* *fremontii*, *Hymenoclea* *salsola*, *Lycium* *andersonii*, *Menodora* *spinescens*, *Salazaria* *mexicana*, and *Thamnosma* *montana* yielded vegetation assemblages in which virtually all drought-deciduous shrubs had died within the sampled areas. *Ephedra nevadensis*, *Krameria erecta*, and *Krameria grayi* had somewhat better survival. Collectively, the responses of *E. nevadensis*, *Krameria* spp., and *Lycium andersonii* showed relatively high mortality at the more southerly sites 1–6 but little or no mortality at sites 7–10 to the north.

Group 3 (Fig. 8) contains three Sonoran Desert species whose growth responses are strongly linked to warm-season precipitation inputs (*C. microphyllum*, *Fouquieria splendens*, *Jatropha cuneata*) (Bobich and Huxman, 2009; J. McAuliffe, pers. obs). Mortality was extremely low for these species at the few sites where they occurred, even where *Ambrosia* spp. and species in Group 2 experienced considerable mortality (e.g., Sites 1A, 4A).

Succulent plants in Group 4 exhibited responses similar to those in Group 3. These succulents, especially the *Opuntia* spp., strongly depend on warm-season precipitation as do the woody plants in Group 3. At sites 4, 5, and 6, many *Opuntia* spp. and *Yucca* spp. exhibited extremely dehydrated stems and leaves, but most plants survived through 2005. However, approximately half of the *Opuntia echinocarpa* died at two sites (5B, 5D) in Joshua Tree National Park.

3.6. Evidence for a previous episode of plant mortality

At one site (Site 4A, Ocotillo, CA), we observed abundant remains of large (up to 100 cm basal diameter) dead individuals of *L. tridentata* that were spatially interspersed among living plants. Based on the marked decay of those plants, they had been dead for a considerable length of time. The 100 × 20 m sampling area centered on the transect contained 11 of these long-dead plants and 23 living plants. The extent of decay in all of the long-dead plants was similar, with all traces of bark and terminal twigs absent. Only the largest, main stems remained and those stems were split and extremely weathered, indicating entire plants had died long ago. Visual comparison with living plants of similar basal diameters indicated that at least half, if not more, of the original volume of woody material had disappeared since the plants died. Ebert and Zedler (1984) measured the decomposition of woody stems of *Fouquieria splendens* in the same region and estimated that 20–30 years was required for 50% dry mass loss in this extremely dry environment. Decay rates of the harder, denser wood of *L. tridentata* are probably considerably lower; therefore it is likely that the plants died many decades ago.

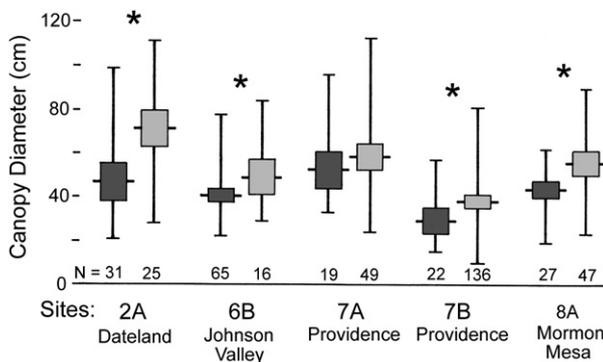


Fig. 7. Comparison of canopy diameters of dead vs. live (dark vs. light shaded error boxes, respectively) *Ambrosia dumosa* at five sampling locations. Vertical lines represent the ranges, error boxes are means ± 2 standard errors, horizontal lines centered in error boxes are arithmetic means. Asterisks represent significant differences, 2-sample *t*-tests, $P < 0.05$.

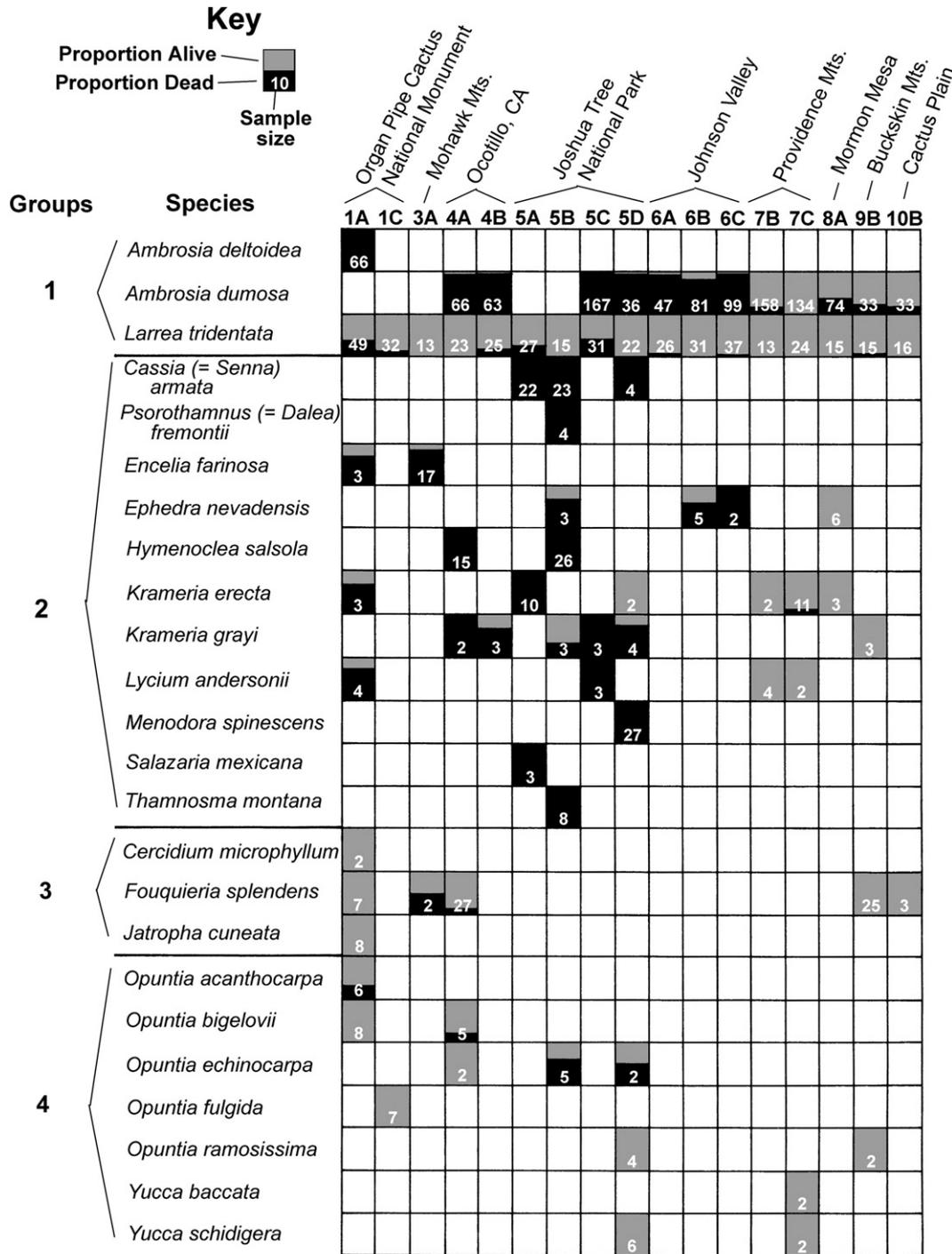


Fig. 8. Matrix of sites (columns) and species (rows) showing the distribution of mortality among sites and groups of species.

In addition to the advanced state of decay, another line of evidence indicated that the plants had died decades ago. Large, fully-developed individuals of the subshrub *H. salsola* were commonly found clustered next to the dead *L. tridentata*. Nine of the 11 dead *L. tridentata* had *H. salsola* present within a 1 m-radius circle centered on the dead plant, but only 2 of 13 living *L. tridentata* had *H. salsola* associated with them ($X^2 = 10.6, P < 0.01$). As many as six *H. salsola* plants were associated with individual, dead *L. tridentata*. Although the *H. salsola* had all recently succumbed to the current drought, most were large, fully formed, mature plants. *H. salsola* is more typically found in sandy soils along nearby

washes and disturbed areas along roadways. Its occurrence within the study area, especially closely associated with dead *L. tridentata*, is interpreted as the combined response of the local elimination of intense competition following the death of the *L. tridentata* and the provision of greater soil fertility and at least partial shade by remaining branches of the dead plant. The general lack of association of *H. salsola* with living *L. tridentata* indicates that most *H. salsola* associated with remains of dead *L. tridentata* established after the latter had died.

The nearest long-term precipitation record (Brawley 2SW), located 65 km east-northeast of site 4, provided information on

a past episode of severe, extended drought that was probably responsible for mortality of *L. tridentata* several decades ago. An 11-year period from 1952 through 1963 was the longest period on record of below-average total annual precipitation at that site for both the cool season (October–March) and warm season (April–September). Because 70% of the average total rainfall occurs during the cool season at this site, the greatest absolute contribution to annual precipitation deficits was the below-average cool-season precipitation. For the Brawley 2SW station, SPI calculated for the 60-month period preceding 1957 yielded a value of -2.03 , the lowest score until the 2003 value of -2.31 .

4. Discussion

Responses of plants to severe drought varied among species; the greatest mortality clearly occurred in *Ambrosia* spp. and other relatively small, drought-deciduous shrubs that rely on cool-season precipitation (Figs. 2, 3 and 8). Mortality of shrubs was nearly 100% even at sites where the drought-enduring evergreen *L. tridentata* experienced less than 10% mortality (Figs. 2 and 8). This is in agreement with other studies of single locations in Joshua Tree National Park (Miriti, 2006, 2007), the Providence Mountains (Hamerlynck and McAuliffe, 2008), and remote sensing-based regional studies that charted lower mortality of *L. tridentata* across the northeastern Mojave Desert (Hereford et al., 2006). The strongest predictor of plant condition and survival in both *L. tridentata* and *Ambrosia* spp. was the 5-year cumulative measure of drought severity (60-month SPI) calculated for March 2003 (Table 2, Fig. 5). SPI values calculated for shorter antecedent time periods were not good predictors of the relationship between drought intensity and plant responses. A 60-month SPI of -1.5 was a threshold at which significant mortality occurred in *Ambrosia* spp. and SPI of -1.7 was associated with dramatic increases in mortality of *Ambrosia* spp. and significant canopy die-back and mortality of *L. tridentata* (Fig. 5).

4.1. Long-term ecological consequences

Drought-induced mass mortality of long-lived perennial plants is probably one of the most important processes shaping the demographic structure of populations and composition of communities in deserts. The death of nearly all drought-deciduous shrubs at some of the sites certainly will affect the demography of those species' populations and community composition well into the future. The most seriously affected locations in Joshua Tree National Park, where all *A. dumosa* were dead in 2003 and nearly two-thirds of all *L. tridentata* died by 2005, were nearly unoccupied by any living individuals of long-lived perennials. Additionally, by 2005 the surviving *L. tridentata* at that site incurred extensive stem mortality and in most of those plants less than one-quarter of the stems remained alive. This extensive mortality coupled with the substantial reduction of leaf surface area (and corresponding water use) of survivors should greatly affect soil water availability. In a Chihuahuan Desert ecosystem dominated by *L. tridentata*, Schlesinger et al. (1987) demonstrated that the amount of water lost from the soil through plant transpiration exceeded that lost by evaporation. Substantial reductions in transpiration in the aftermath of extensive perennial plant mortality could greatly affect subsequent patterns of recruitment at the site. Considerable mortality of *L. tridentata* may have a particularly great impact because this species is capable of photosynthesis (and transpiration) at extremely low water potentials and consequently, is capable of drawing down soil moisture reserves far more than can other plants (Oechel et al., 1972). As long as a locale remains substantially "underpopulated" by *L. tridentata*, more soil water

will be available for other plants, including ephemerals and shorter-lived shrubs. Furthermore, the deaths or considerable reduction of canopy volumes of *L. tridentata* could substantially lessen the intensity of root exudate-mediated interactions with other plants that inhibit root elongation in those plants (Mahall and Callaway, 1991, 1992). Elimination or lessening of this kind of competitive interference could enhance the establishment, growth, and survival of other plant species for a considerable duration. For example, at site 4A where there was apparently an episode of considerable mortality of *L. tridentata* many decades ago, the current anomalous abundance of *H. salsola* may be due to this kind of competitive release.

Death of shrubs in these desert ecosystems can impact facilitative as well as competitive interactions. Various factors limit establishment of many perennial species, including succulents and woody plants, to locations beneath nurse plant canopies, especially the dense, compact canopies of certain shrubs (McAuliffe, 1986, 1988). For example, at three sites in the Sonoran Desert, McAuliffe (1986) found that 61, 70, and 76% of all successful recruitment of saplings of the tree *C. microphyllum* occurred beneath canopies of *Ambrosia* spp. that covered only 7, 11, and 22%, respectively, of the ground surface. Concealment within the dense shrub canopies protected tree seedlings from consumption by lagomorphs, the principal cause of seedling mortality. Another study showed that most recruitment of young *L. tridentata* occurred beneath canopies of *A. dumosa* (McAuliffe, 1988). The extremely high mortality of *Ambrosia* spp. documented in the present study at some of the sites could significantly reduce the recruitment of other perennial plants until substantial recovery of the *Ambrosia* populations occurs.

4.2. Impacts of drought contingent on soil characteristics

Responses of plants to drought depend on soil characteristics (Fig. 6). Soil hydrological behavior, including depth of storage and temporal persistence of soil moisture, is influenced by various characteristics of parent materials, soil horizon development, and elevation (McAuliffe, 2003). In the most arid sites at lower elevations, plant condition was poorer on older (Pleistocene) landforms containing soils with stronger horizon and surface pavement development. In those settings, the high silt and clay content of the subsurface A_v horizon significantly impedes the infiltration of water (Hamerlynck et al., 2002; McDonald et al., 1996), and likely contributed to the poorer condition of plants in those locations. At the higher elevation, less arid sites, plant responses as a function of landform age reversed, probably because of increased infiltration capacity associated with weaker A_v horizon development in soils of older landforms in less arid settings. Furthermore, large stones distributed on the surface and throughout the soil of those older alluvial deposits slow the evaporative losses of water. This kind of reversal of plant responses in relation to a single variable (e.g., elevation, a proxy for average precipitation) likely represents a complex, probably nonlinear interaction among multiple soil characteristics. Such complexity represents a significant challenge to modeling of plant responses to any kind of climate change or perturbation and meaningful and useful modeling efforts will include the influences of relevant features of landforms and soils.

4.3. Plant size and mortality

Size-related plant mortality was only noted in *A. dumosa* at four sites, and did not follow any clear trend in soil characteristics, and was not confined to one desert region or the other (Fig. 7). This stands somewhat in contrast with Miriti (2006) and Miriti et al. (2007), who showed that under these severe drought conditions, mortality was greater among young plants closely associated with

adult “nurse plants”, suggesting a switch from a facilitative to competitive effect of the nurse plant. It is possible that the earlier phase of the drought in 1999 and 2000 may have caused higher mortality in juveniles (e.g., Bowers and Turner, 2001), but that the subsequent, more extreme drought conditions of 2002 (Fig. 1) caused additional mortality among older plants. By the time we sampled in 2003, mortality may have become distributed fairly evenly across different demographic groups of these populations.

5. Conclusions

Instrumental records dating to the 1890s show that the duration and intensity of this most recent drought was similar to two others that have affected the region within the last century: the late 1890s to early 1900s drought, and the “1950s drought,” an extended period of below-average precipitation from the 1940s through the 1960s. Furthermore, dendroclimatological reconstructions for the last 1400 years indicate that the drought that began in the late 1990s is comparable to the most severe droughts experienced in the region during the last 1400 years (Salzer and Kipfmüller, 2005). The recent episode of mass mortality of long-lived perennials at some locales undoubtedly represents only one of many such episodes that have occurred in response to extreme droughts of the past.

Episodic recruitment of perennial plants during infrequent intervals of above-average precipitation has long been recognized as an important process in these desert ecosystems but the other side of the demographic ledger – plant mortality – has until recently received far less research attention (Bowers and Turner, 2001; Bowers, 2005; Hereford et al., 2006; Miriti et al., 2007; Webb et al., 2003). At sites where considerable mortality of dominant perennial plants is caused by episodic drought, the demographic structure of populations and possibly the composition of communities may never be at a long-term equilibrium. Models of the population and community dynamics of desert plant communities that implicitly assume constant (but slow) rates of recruitment and mortality (e.g., McAuliffe, 1988) do not provide a sound basis for understanding these systems. Data from Site 2A (Dateland, Arizona) in the present study were collected within the same study plots used by McAuliffe (1988), in which data collected in 1985 on densities of dead individuals of *L. tridentata* and *A. dumosa* were used to calculate average annual mortality rates for each. Similarly, data on densities and estimated ages of small, young plants was used to calculate average annual recruitment rates. These and other data on spatial patterns of establishment were used in a Markov chain model of site occupancy and equilibrium community structure for that site. Yet if the same kind of data on either dead plants or newly recruited plants were taken 18 years later (in 2003, the year of mortality surveys reported here), completely different results would have been derived, especially mortality rates for *A. dumosa*, since slightly over half of all plants had died within the previous year. Clearly, modeling the long-term dynamics of this community using constant mortality and recruitment rates is extremely unrealistic; at least one component of the dynamics of populations and community structure at this site – mortality of *A. dumosa* – is incontrovertibly episodic.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the on-line version, doi:10.1016/j.jaridenv.2010.01.001.

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