# EPISODIC DEATH ACROSS SPECIES OF DESERT SHRUBS

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*Abstract.* Extreme events shape population and community trajectories. We report episodic mortality across common species of thousands of long-lived perennials individually tagged and monitored for 20 years in the Colorado Desert of California following severe regional drought. Demographic records from 1984 to 2004 show 15 years of virtual stasis in populations of adult shrubs and cacti, punctuated by a 55–100% die-off of six of the seven most common perennial species. In this episode, adults that experienced reduced growth in a lesser drought during 1984–1989 failed to survive the drought of 2002. The significance of this event is potentially profound because population dynamics of long-lived plants can be far more strongly affected by deaths of adults, which in deserts potentially live for centuries, than by seedling births or deaths. Differential mortality and rates of recovery during and after extreme climatic events quite likely determine the species composition of plant and associated animal communities for at least decades. The die-off recorded in this closely monitored community provides a unique window into the mechanics of this process of species decline and replacement.

*Key words: Ambrosia dumosa; drought; episodic mortality; Larrea tridentate; Tetracoccus hallii.*

## INTRODUCTION

Desert vegetation beguiles an observer into simplistic uniformitarianism: observations over a few years appear to reflect processes over much longer periods of time. Two factors that contribute to this "invisible present" (Magnuson 1990) are potentially extreme longevity among adults of conspicuous species (Vasek 1980, Miriti 1999) coupled with rarely observed adult mortality that arguably drives desert plant dynamics (Miriti et al. 2001). Initial opportunities for seedling recruitment during periods of high precipitation (Went 1949, Beatley 1974) or when nurse plants facilitate establishment of seedlings (Callaway and Walker 1997, Michalet et al. 2003) may not predict long-term changes in community composition because seedlings facilitated by adults early in life frequently become unsuccessful competitors against much larger "nurses" with time (Miriti 2006). Demographic analyses of desert plants show that, as with long-lived species in more mesic systems, the probability of mortality decreases as plants reach reproductive size (Miriti 1999). A general consequence is that population trajectories are sensitive to changes in adult persistence (Silvertown et al. 1993, Miriti et al. 2001). In the absence of adult mortality, the potential of seedling recruitment pulses to change community composition of long-lived perennials is slight, due to the relative unimportance of wide swings in seedling

numbers (Pfister 1998). If adult death is episodic, formative events that shift the composition of desert perennial communities are rarely observed.

Longevity and rare climatic extremes complicate observation of demography and its interpretation (Silvertown et al. 1996, Drechsler et al. 1999). For some shrubs, like *Ambrosia dumosa*, demographic projections based on as few as 10 years of observation are informative because 10 years capture substantial birth and death (Wright and Howe 1987, Miriti et al. 1998, 2001). If 10 years were as representative for *Larrea tridentata* (Zygophyllaceae) or the regional endemic *Tetracoccus hallii* (Euphorbiaceae), no adults of which died in the first years of our study, these plants would appear to live for millennia (Miriti 1999). The illusion of "immortality" disappears when climatic events cause episodic mortality of adults, thereby resetting demographic dynamics, and underscoring the importance of adult mortality from unusual extreme events.

Here we report an extensive die-off of adult perennials following extensive drought that places apparent community stasis into a context of critical episodes of birth, growth, and death (Fig. 1, Table 1), where adults are plants of sufficient size to have flowered at least once. Droughts of at least comparable severity occur irregularly every few decades to centuries in western North America (Cook et al. 2004, Breshears et al. 2005, Jackson et al. 2005). Studies of paleoclimate indicate that shifts in climate drive shifts in plant communities, but paleoecology alone does not offer the resolution necessary to understand how dynamics of facilitation, competition, birth, and death determine the relative abundance of
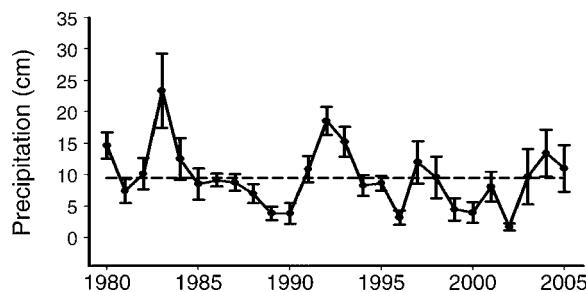
Fig. 1. Average monthly rainfall from 1980 to 2004 using 13 stations located within 81 km from the Eagle Mountain meteorological station near Joshua Tree National Park. The dotted line indicates the multi-annual average (9.47 cm); error bars indicate 95% confidence intervals for the mean. Information on the location of these stations is provided in Table 2. (Data are from NOAA [1980–2005].)

species. With global climate change projected to increase the frequency and severity of regional drought (Swetnam and Betancourt 1998, Easterling et al. 2000), understanding processes of episodic adult mortality and juvenile recruitment may become even more important with time.

Here we report a window into the dynamics of shifting community composition brought about by drought that culminated in a massive die-off of most of the common perennial species in a desert community. In general, episodic mortality of adult plants has consequences for community composition through interactions and replacements of species that operate on clearly different demographic rhythms (Miriti et al. 1998, Miriti 1999). Severe drought between 2000 and 2004 in the Colorado Desert of Joshua Tree National Park offers a unique insight into demographic mechanics of death and replacement of perennial shrubs and cacti. Here we ask: (1) do these species behave in concert as a community, experiencing similar mortality from extreme drought, or (2) do species respond individualistically, with mortality differing dramatically among species that dominate the landscape. If the first alternative is true, recovery might or might not repopulate the community with roughly the same proportions of species as existed before the die-off.

If the second alternative is true, reflecting quite different demographic rhythms among species, different species are likely to replace dead adults, leading to changes in relative proportions of species that successfully recruit adults. In the latter case, the imprint of each episode of death and recovery may persist for at least decades.

A demographic study of marked individuals has limitations. This is not a physiological study, nor is it a regional analysis of broad patterns of plant community change. Our unique contribution is a window into the process of persistence, mortality, recovery, and eventually recruitment of thousands of tagged individual plants across all common species over more than 20 years.

## METHODS

Numerical data for >8000 individuals of six common species of shrubs and cacti are from five censuses taken at five-year intervals from 1984 to 2004 in a permanent study hectare in Joshua Tree National Park, California (Miriti et al. 2001). The site is on a bajada that gently slopes ($\leq$4%) to the northwest of the Eagle Mountains, in the transition between the Colorado Desert and the Mojave Desert (115°47′ W; 33°46′ N; elevation, 1006 m). Rainfall typically occurs during the winter months, and averages 11.1 cm/yr, determined from records at neighboring stations from 1980 to 2004. Plant censuses were in March or April as shrubs leafed and flowered.

From 1984 to 2004, woody perennial shrubs and cacti of 23–26 species were tagged, measured, and mapped to 0.1 m on a fixed grid. Reproductive status was determined by evidence of flowers or fruit (Wright and Howe 1987, Miriti et al. 1998). Plant height, length, and width were used to determine plant volume, calculated treating shrubs as oblate spheroids (Wright and Howe 1987, Miriti et al. 2001). We tested for differences in the growth of plants that remained alive from 1989 to 2004 compared to those that were alive from 1989 to 1999 but were recorded as dead in 2004. Because growth is strongly influenced by plant size, we divided plants into size classes that were determined using demographic criteria (see Miriti et al. 2001) to account for differences

TABLE 1. Location of stations in southeastern California, USA, within 81 km of the study site that were used to collect precipitation data from 1980 to 2004.

| Station name | County | Latitude, longitude | Distance to Eagle Mountain (km) |
|---|---|---|---|
| Blythe | Riverside | 33°37′ N, 114°36′ W | 71.38 |
| Blythe Airport | Riverside | 33°37′ N, 114°43′ W | 71.38 |
| Eagle Mountain | Riverside | 33°49′ N, 115°27′ W | 0 |
| Habitat | Imperial | 33°21′ N, 116°01′ W | 73.81 |
| Hayfield Pumping Plant | Riverside | 33°42′ N, 115°38′ W | 21.34 |
| Indio Fire Station | Riverside | 33°43′ N, 116°13′ W | 71.74 |
| Iron Mountain | San Bernardino | 34°09′ N, 115°07′ W | 21.34 |
| Mecca Fire Station | Riverside | 33°34′ N, 116°05′ W | 64.85 |
| Niland | Imperial | 33°17′ N, 115°31′ W | 59.62 |
| Palm Desert | Riverside | 33°44′ N, 116°23′ W | 69.34 |
| Palm Springs | Riverside | 33°50′ N, 116°31′ W | 77.6 |
| Palm Springs Thermal Ap | Riverside | 33°38′ N, 116°10′ W | 69.34 |
| Twentynine Palms | San Bernardino | 34°08′ N, 116°02′ W | 64.29 |

TABLE 2. Six common shrubs and one cactus in Joshua Tree National Park, California.

| Age and species | 1984 | 1989 | 1994 | 1999 | 2004 |
|---|---|---|---|---|---|
| Juveniles | | | | | |
| *Ambrosia dumosa* | 1459 | 3361 | 1561 | 1878 | 350 |
| *Eriogonum fasciculatum* | 134 | 263 | 113 | 74 | 0 |
| *Larrea tridentata* | 2 | 15 | 7 | 7 | 19 |
| *Opuntia ramossisima* | 34 | 139 | 111 | 105 | 19 |
| *Simmondsia chinensis* | 65 | 88 | 64 | 63 | 17 |
| *Sphaeralcea ambigua* | 67 | 209 | 12 | 39 | 0 |
| *Tetracoccus hallii* | 82 | 109 | 80 | 81 | 16 |
| Adults | | | | | |
| *Ambrosia dumosa* | 1555 | 1564 | 1714 | 1600 | 523 |
| *Eriogonum fasciculatum* | 148 | 166 | 250 | 256 | 11 |
| *Larrea tridentata* | 162 | 166 | 162 | 162 | 158 |
| *Opuntia ramossisima* | 82 | 82 | 81 | 82 | 37 |
| *Simmondsia chinensis* | 156 | 156 | 161 | 164 | 69 |
| *Sphaeralcea ambigua* | 59 | 81 | 50 | 59 | 0 |
| *Tetracoccus hallii* | 648 | 651 | 632 | 651 | 274 |

in growth attributable to size. Growth was recorded as the percentage change in plant volume ($\log_2$[cubic centimeters]) that occurred during each census interval. Differences in growth of plants that survived or died in 2004 were determined by bootstrap analysis of all plants within each of the six size classes. Significance was determined at the 95% confidence interval by 10 000 iterations of the bootstrap.

Dormant shrubs sometimes resemble dead ones. In May 2005, after a wet winter and spring, we checked a random sample of 100 *Ambrosia dumosa* and 95 *Tetracoccus hallii*, and conducted a comprehensive check for *Eriogonum fasciculatum* and *Sphaeralcea ambigua* for living foliage or other signs of recovery. One year after the 2004 census, no *A. dumosa* reported dead in 2004 had recovered; of 29 of 95 *T. hallii* recorded as dead in 2004, 11 (38%) partly revived in 2005, and may or may not fully recover. After a 95% mortality of adults, eight *E. fasciculatum* alive in 2004 died by 2005, and only three showed one or two branches with foliage. All *S. ambigua* were dead.

RESULTS

Demographic data collected from a perennial community in Joshua Tree National Park from 1984 to 2004

showed starkly different patterns of juvenile and adult mortality over 20 years (Table 2). Using the Friedman nonparametric analysis of variance as an analog for a repeated-measures ANOVA (Zar 1999), juvenile rankings across species varied dramatically over the first 15 years of this study (Friedman statistic = 12.7, Kendall coefficient = 0.606, df = 3, $P = 0.005$), but adult rankings did not (Friedman statistic = 4.5, Kendall coefficient = 0.216, df = 3, $P = 0.23$). In five censuses at five-year intervals over 20 years, juvenile rankings continued to vary widely (Friedman statistic = 15.6, Kendall coefficient = 0.558, df = 4, $P = 0.005$), while a catastrophic die-off of adults of common species between 1999 and 2004 also altered numbers and rankings of well-established adults (Friedman statistic = 17.0, Kendall coefficient = 0.608, df = 4, $P = 0.005$). The site has undergone sudden adult attrition of 55–100% (72% ± 8%, mean ± SE) for six of the seven most common desert perennials.

Statistical analyses of growth of *A. dumosa* and *T. hallii* adults and juveniles indicated that evidence of stress foretold mortality for the codominant, *A. dumosa*, but not *T. hallii*. The study site experienced two major drought episodes, the first occurring during the 1989–1994 interval and the second during the 1999–2004 interval (Fig. 1). The first drought was marked by a 54% reduction in the number of juveniles of *A. dumosa* (Table 2), but adult numbers were not strongly affected. Adult responses to the first drought were subtle. Comparisons of growth, measured as the change in plant volume during a census interval, revealed that adult plants that survived the first drought but died by 2004 experienced greater reduction in volume and wider fluctuations in volume than those that survived (Table 3); adult plants that were most adversely affected by the first drought did not survive the more recent drought. No significant relationship between growth and mortality was found for similar samples of *T. hallii*.

The most far-reaching potential effects on desert community structure follow from mortality of 55–68% of the adult individuals of four robust shrub species, including the two codominants *Ambrosia dumosa* (68% mortality between 2000 and 2004) and *Tetracoccus hallii* (58% mortality; Table 2). One hundred percent mortal-

TABLE 3. The data presented below distinguish the relative growth of *Ambrosia dumosa* that survived within each of six size classes (volume cut-offs presented in parentheses) from 1989 to 2004, and those that survived from 1989 to 1999 but died in 2004.

| Size class ($\log_2$cm$^3$) | 1989–1994 | | 1994–1999 | | 1999–2004 | |
|---|---|---|---|---|---|---|
| | Dead, 2004 | Alive, 2004 | Dead, 2004 | Alive, 2004 | Dead, 2004 | Alive, 2004 |
| J1 (<9.5) | 89.75 | 76.21 | 4.76 | 1.05 | −1.47* | 5.21* |
| J2 (9.5–10.6) | 32.43 | 29.20 | −0.12 | 3.21 | −2.67 | 1.92 |
| J3 (10.6–15) | 10.97 | 12.78 | −1.97 | −0.59 | 1.82* | 5.82* |
| A1 (15–16.7) | 1.65* | 3.08* | −1.98 | −1.34 | 0.16 | 0.71 |
| A2 (16.7–17.5) | −0.91* | 0.11* | −3.03 | −2.46 | 0.329 | 1.14 |
| A3 (>17.5) | −2.79* | −1.56* | −3.42* | −2.03* | 1.309 | 0.27 |

*Notes:* The bootstrap sampling mean for the relative growth of plants is presented as the percentage change in plant volume that occurred over the census interval. Asterisks indicate growth differences that are significant at $P < 0.05$. Juveniles are J1–J3; adults, A1–A3.

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ity of one short-lived perennial (*Sphaeralcea ambigua*), and virtual elimination (99% mortality by 2005) of a common and often large long-lived perennial (*Eriogonum fasciculatum*), may have long-term consequences for this site if they fail to reestablish from dispersed or dormant seed. Both species still grow in more mesic washes 200–500 m away. Remarkably, no significant mortality was documented for juveniles or adults of *Larrea tridentata* over these 20 years. Overall, 81% of subadults and 64% of reproductive-age perennials died during the 2000–2004 interval. The sheer number of spaces opened by death or canopy die-back of adult plants of most common species will likely have profound consequences for community diversity and structure.

## DISCUSSION

Our results highlight the disproportionate effects of rare extreme events (Gutschick and BassiriRad 2003) in both changes in species richness of a long-standing desert community and potential succession to a different state. Two points follow.

First, a report of a mortality event of this magnitude that includes most common species, with death not caused by grazing, invasive species, or fire, is unprecedented in a desert perennial community. Mortality of up to 25% has been reported for one desert shrub (*Chrysothamnus nauseosus*) in northern California in the 1988–1990 drought (Toft 1995), but the community-wide die-off we recorded appears unique. Pulsed events such as this unique mortality event are thought to drive species interactions and community dynamics in arid and semiarid plant communities (Tausch et al. 1993, Schwinning et al. 2004, but see Watson et al. 1997). Death across several species of different demographic characteristics, ranging from short-lived perennial mallow *Sphaeralcea ambigua* that rarely survives three five-year censuses to the persistent spurge *Tetracoccus halli* that rarely dies, implies that synchronous mortality of an aging recruitment cohort including several species (Wiegand et al. 1995) is unlikely. A recruitment pulse of several species is anticipated, but surveys of the site in springs of 2004, 2005, and 2006 show no evidence of it yet.

Second, mortality and persistence were not random across species, suggesting that the community trajectory may shift substantially after a die-off. An extreme example of such a shift occurred after major drought in 1250–1288 in northeastern Utah, when packrat middens and fossils indicate that a catastrophic die-off of *Juniperus osteosperma*, which had been dominant for ~8700 years, was replaced by *Pinus edulis* (Gray et al. 2006). This degree of radical change is not indicated in our system; it is clear at Joshua Tree that some species held space far better than others. Creosote bush (*Larrea tridentata*) had negligible recruitment or mortality during 20 years of observation, while large perennial buckwheat (*Eriogonum fasciculatum*) virtually disappeared in the early millennium drought. A codominant,

*A. dumosa* established seedlings in open spaces and nursed perennial seedlings over 15 years, suggesting a dynamic contribution to desert dominance and recruitment (McAuliffe 1988, Miriti et al. 1998), but lost most adult individuals between 2000 and 2004. This contrasted with grudging persistence of the *Tetracoccus hallii*, which did not require a nurse and did not nurse other species. Individual *T. hallii* and *L. tridentata* alive today may not be thousands of years old, but they yield space in the face of severe drought far less readily than other common shrubs. A question is whether dynamics set in motion by severe drought represent early stages of community change involving increased dominance over *A. dumosa* by its regional endemic.

Our observations also indicate that the roles of facilitation and competition change with extreme drought. Desert plant communities reflect a dynamic balance of facilitation and competition (Callaway and Walker 1997, Tielbörger and Kadmon 2000). Facilitation is expected to increase and competition decrease with decreasing habitat quality (Callaway et al. 1996, Goldberg and Novoplansky 1997), but extreme stress may compromise this trade-off (Tielbörger and Kadmon 2000, Maestre et al. 2005). Crown shrinkage that preceded death in *A. dumosa*, total mortality of seedlings, and exceedingly high mortality of older juveniles in response to drought show that facilitation decreased in importance as abiotic conditions worsened. Such shifts in the importance of facilitation and habitat conditions have previously been considered along resource gradients (Michalet et al. 2003), but not through time. Facilitative or competitive ability depends on both species identity and habitat conditions (McAuliffe 1988, Callaway et al. 1996, Tewksbury and Lloyd 2001, Toft and Fraizer 2003). Because some species provide better spaces for regenerating seedlings than others (e.g., Nunez et al. 1999; M. N. Miriti, *unpublished manuscript*), differences in numbers, proportions, and spatial patterns of episodic die-offs may echo for decades to centuries.

The mortality event reported here punctuated a period of apparent stasis, and likely represents the beginning of a process of recovery that will play out over years. Climatic histories show periods of severe drought, as well as periods of several years of unusually high precipitation, or "pluvials," in deserts of western North America (Cook et al. 2004, Jackson et al. 2005). The pluvial of the early 20th century in western North America (Cook et al. 2004) was strongly represented in data from southern California (S. T. Gray, *personal communication*). It is possible that species established early in the last century simply do not persist in drier times. Time, and continued monitoring of processes of birth, death, and persistence, will tell.

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