

DESERT WILDFIRE AND SEVERE DROUGHT DIMINISH SURVIVORSHIP OF THE LONG-LIVED JOSHUA TREE (*YUCCA BREVIFOLIA*; AGAVACEAE)¹

LESLEY A. DEFALCO^{2,4}, TODD C. ESQUE², SARA J. SCOLES-SCIULLA², AND JANE RODGERS³

²U.S. Geological Survey, Western Ecological Research Center, 160 N. Stephanie Street, Henderson, Nevada 89074 USA; and

³U.S. National Park Service, Grand Canyon National Park, 823 San Francisco Street, Suite F, Flagstaff, Arizona 86001 USA

Extreme climate events are transforming plant communities in the desert Southwest of the United States. Abundant precipitation in 1998 associated with El Niño Southern Oscillation (ENSO) stimulated exceptional alien annual plant production in the Mojave Desert that fueled wildfires in 1999. Exacerbated by protracted drought, 80% of the burned *Yucca brevifolia*, a long-lived arborescent monocot, and 26% of unburned plants died at Joshua Tree National Park by 2004. Many burned plants <1 m tall died immediately, and survival of all but the tallest, oldest plants declined to the same low level by 2004. Postfire sprouting prolonged survival, but only at the wetter, high-elevation sites. During succeeding dry years, herbaceous plants were scarce, and individuals of *Thomomys bottae* (pocket gopher) gnawed the periderm and hollowed stems of *Y. brevifolia* causing many of them to topple. *Thomomys bottae* damage reduced plant survivorship at low-elevation, unburned sites and diminished survival of burned plants in all but the driest site, which already had low survival. Accentuated ENSO episodes and more frequent wildfires are expected for the desert Southwest and will likely shift *Y. brevifolia* population structure toward tall, old adults with fewer opportunities for plant recruitment, thus imperiling the persistence of this unique plant community.

Key words: Agavaceae; climate change; El Niño Southern Oscillation; herbivory; invasive alien annuals; Mojave Desert; pocket gophers; *Thomomys bottae*; *Yucca brevifolia*.

Pronounced El Niño Southern Oscillation (ENSO) episodes in western North America have drawn recent attention to the role of extreme climate events in shaping arid plant communities. Rapid growth and abundant biomass of Eurasian annual grasses including *Bromus tectorum*, *B. madritensis* subsp. *rubens*, and *Schismus* spp. are associated with heavy winter and spring precipitation that typically falls during El Niño phases in North American warm deserts (Hunter, 1991; Esque and Schwalbe, 2002; Salo, 2002; Brooks and Matchett, 2006). Shoots of these alien annual grasses senesce and persist during the succeeding dry La Niña phases and provide the continuity between sparsely distributed shrubs for sustaining wildfire. Few native perennials in Mojave Desert shrublands resprout in response to scorching or burning of aboveground tissues, and

survival is typically low (O'Leary and Minnich, 1981; Brown and Minnich, 1986; Loik et al., 2000a). The accentuated amplitude of ENSO events in recent decades (Allan and Soden, 2008) and the rapid transition from wet to dry years during El Niño and La Niña phases has enhanced the frequency and size of wildfires in the American Southwest (Swetnam and Betancourt, 1990, 1998; Littell et al., 2009). Despite the prominent impacts to desert shrublands, the long-term consequences of wildfire on stand-level structure of desert plants in combination with greater prevalence of predicted climate extremes are unknown for the North American desert region.

The ENSO cycle not only predisposes the Southwest desert region to wildfires, but also to extreme drought events that may have a profound impact on population structure and community dynamics of long-lived desert plant species. Droughts lasting several years can selectively remove the most common perennial species from desert plant communities (Webb et al., 2003; Hereford et al., 2006; Miriti et al., 2007). Many of these perennial plants influence the availability of food, cover, and structure for a variety of small desert animals; therefore, attrition of selective sizes of these perennial plants may have cascading effects on desert plant stand structure and their associated animal communities (Brown et al., 1997). As food resources decline, shifts in diet, and intensified use of limited available resources may result in further declines of adult perennial plants and hinder seedling establishment, but this dynamic has not been well documented for desert regions.

Yucca brevifolia Engelm. (Joshua tree) is a slow-growing, long-lived endemic of the Mojave Desert (Comanor and Clark, 2000; Gilliland et al., 2006) and can vigorously resprout after disturbances such as wildfire (Webber, 1953; Vogl, 1968; Conrad, 1987; Loik et al., 2000a; USDA, 2002). Although the long-term effects of wildfire on population structure of *Y. brevifolia* are unknown, recent studies indicate that a large proportion of *Y. brevifolia* populations die after fire, yet resprouting may be a

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⁴ Author for correspondence (e-mail: Lesley_DeFalco@usgs.gov)

more rapid means of establishing reproductive adults than postfire recruitment (Minnich, 1995; Loik et al., 2000a). Fueled by a continuous stand of annual plants resulting from above-average rainfall in 1998, the Juniper Fire Complex spread across nearly 5700 ha in Joshua Tree National Park in May 1999. This wildfire provided an opportunity to examine the long-term effects of alien-grass-fueled fires on *Y. brevifolia* ecology and population dynamics. In this study, we monitored attrition of *Y. brevifolia* during the 5 yr following this moderate-intensity fire and examined how climate variability interacts with sprouting and herbivory to impact short-term survival of this desert icon.

MATERIALS AND METHODS

Site selection—Ten months after the fire, study sites were randomly selected within burned and adjacent unburned areas in Joshua Tree National Park using a Geographic Information System (Fig. 1). We selected burned and unburned areas at five sites with similar slopes, exposures, and soils, but they differed in elevation. Adjacent burned and unburned areas were typically separated by a road such that the fire was stopped arbitrarily and not by biological or edaphic factors. We characterized the temporal and spatial patterns in precipitation for each site using the PRISM Climate Mapping Program (PRISM Group, Oregon State University, <http://www.prismclimate.org>, created 24 September 2008).

Sampling design—We randomly selected four to five 300–600-m point-centered quarter line transects within paired burned and unburned areas at the five sites for a total of 46 transects (Brower et al., 1998). Each transect had sampling points at 100 m intervals so that *Y. brevifolia* plants selected for the study did not overlap between adjacent points. At each sampling point, the closest *Y. brevifolia* within each of four quadrants (NE, SE, SW, and NW) was marked with a numbered aluminum tag attached to the trunk at a height of 1 m. For plants <1 m tall, we attached tags with wire wrapped loosely around the stem. When the closest plant in a quadrant was dead, it was tagged and measured, but the next-closest live plant in that quadrant was also marked so we would have a robust sample size to monitor the effects of fire after the initial loss of plants. In addition, if the plant selected in a burned quadrant was <1 m tall, the second-closest live plant in that quadrant was also marked in anticipation of greater attrition in this smaller size class. These additional tagged plants were important for long-term monitoring of the population because nearly 40% of burned plants <1 m tall appeared dead at the initial sampling date. We assumed all scorched plants selected and tagged on burned plots were alive at the time of the fire; plants presumed to be dead before the fire burned completely so that only their ash silhouettes remained on the ground surface.

Assessment of survival for *Y. brevifolia* that sprouted or sustained herbivore damage—For each tagged *Y. brevifolia*, we first determined whether the plant was alive or dead. A plant was considered dead when no green leaf blades were found on any leaf axil and green sprouts were absent from the stem and the root crown. Two to three observers visually estimated and averaged among them the scorch damage for *Y. brevifolia* plants in burned areas as a percentage of total aboveground plant surface area blackened by the fire. For burned and unburned plants, height was measured from ground level using a telescoping fiberglass rod graduated in cm. Live and dead root and stem sprouts were counted separately, and damage by herbivores was noted. Tissue damage by *Thomomys bottae* (pocket gopher) predominated, although damage by other herbivores (e.g., lagomorphidae or sciuridae) was also noted. *Thomomys bottae* damage was easily identified when subterranean burrows extended into the inner portions of *Y. brevifolia* stems and soil was backfilled into scarred parts of the plant. This tissue damage often weakened the *Y. brevifolia* stem resulting in the plant toppling to the ground.

Data analysis—We used the LIFEREG procedure in SAS (SAS Institute, SAS version 9.1.3. Cary, North Carolina, USA) to compare the declining survivor functions (Allison, 1995), which characterized the probability of survival during the 5 yr following the fire. Before we conducted each survival analysis, we used LIFEREG to select the appropriate model fit among the exponential, Weibull, gamma, log-normal, and log-logistic distributions based on log-likelihood. Then we tested the differences in survivor functions using Wald's χ^2 . We

first compared survivor functions between burned and unburned plants (Burn), among sites (Site), and among the different sizes of *Y. brevifolia* (Height) as well as the two-way interactions. Survivor functions for plants with different degrees of scorching (Scorch) were also compared for burned plants only. We then compared survivor functions between *Y. brevifolia* with and without sprouts (Sprout), among sites, and the two-way interaction in separate burned and unburned analyses. Finally, we compared survivor functions between *Y. brevifolia* with and without *T. bottae* damage (Damage), among sites, and the interaction to examine the influence of herbivory on survival in the separate burned and unburned areas.

RESULTS

Study sites—The Mile Marker 21, Cap Rock, and Lost Horse sites occur at lower elevation and generally received less precipitation than the Upper and Lower Covington Flats sites during the study (Fig. 2). Above-average precipitation occurred at all sites in September 1997 and the following February and May 1998. The subsequent dry period that lasted from September 1998 through March 1999 produced conditions that led to the Juniper Fire Complex in May 1999. Below-average rainfall generally prevailed the succeeding 19 mo except for heavy summer monsoon activity in July 1999 and August 2000 and average precipitation that fell in February 2000 at high-elevation sites. Average precipitation returned to high-elevation sites and partially to low-elevation sites in January and February 2001 but was immediately followed by a protracted drought period that lasted through January 2003. Precipitation during the remainder of the study period generally rebounded to average levels with pulses and deficits occurring during summer monsoonal periods and winter months, respectively.

Survival of burned *Y. brevifolia*—Survival of burned *Y. brevifolia* at the lowest elevation site, Mile Marker 21, declined at a greater rate relative to unburned controls than burned plants at high-elevation sites (Burn \times Site, $\chi^2 = 20.1$, $p < 0.01$). By the spring 2004 census, the average survival for burned plants was 20% compared with 74% for unburned plants (Burn, $\chi^2 = 349.7$, $p < 0.01$). Plants that sustained more than 30% scorch damage had lower than 30% survival by 2004 (Scorch, $\chi^2 = 77.1$, $p < 0.01$; Fig. 3). Survivor functions for the different scorch damage classes did not differ among sites (Scorch \times Site, $\chi^2 = 37.0$, $p = 0.56$).

Survival of the larger unburned plants declined more slowly than smaller plants during the 5-yr study, but immediate declines in survival were striking for all sizes of burned *Y. brevifolia* (Burn \times Height, $\chi^2 = 8.7$, $p = 0.07$; Fig. 4). In unburned areas, slow declines in the smallest *Y. brevifolia* were detected by the 2001 census following two consecutive dry years. Declining survival of the intermediate (1 m to <3 m) and tallest (3 m and greater) unburned plants was detected at 4 and 5 years, respectively. In contrast, survival of small burned *Y. brevifolia* dropped the first year after the fire and steadily declined during each census. Survival for all sizes of burned *Y. brevifolia* declined uniformly to the lowest survival probability of approximately 20% after 5 yr except for the tallest plants that declined to 30%.

Survival of sprouting *Y. brevifolia*—Most *Y. brevifolia* did not produce sprouts (Table 1), but of those that did, more were burned (33%) than unburned (15%). Unburned plants at the high-elevation Upper Covington Flat site maintained high survival regardless of whether they sprouted; at the lower elevation Lost Horse and Cap Rock sites, unburned plants with

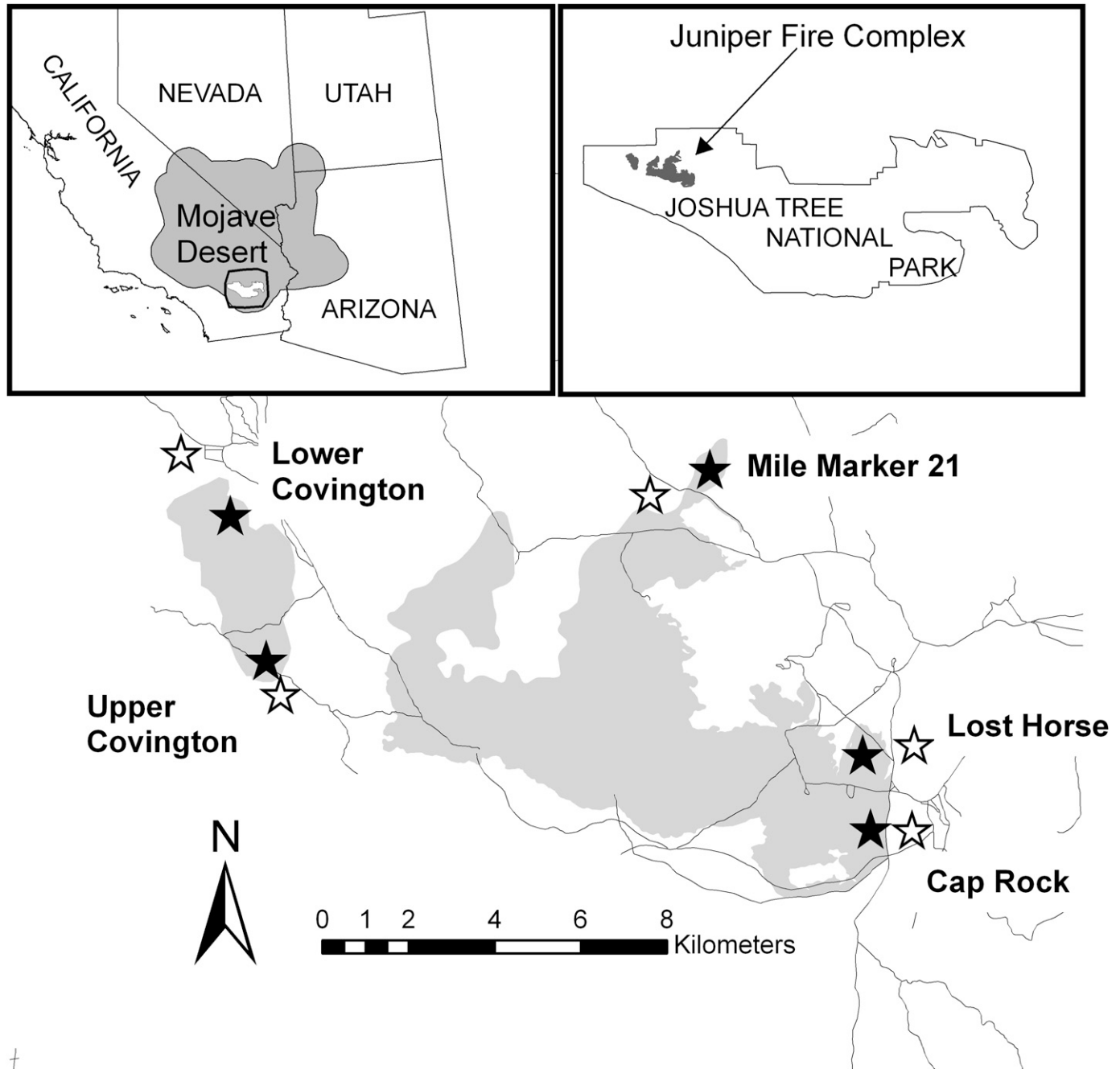


Fig. 1. Five study areas within the Juniper Fire Complex at Joshua Tree National Park, California. Each site contains replicated transects within adjacent burned (black stars) and unburned areas (clear stars).

sprouts had higher survival after 5 yr than those without sprouts (Sprout \times Site, $\chi^2 = 16.4$, $p < 0.01$, Fig. 5A). Surprisingly, survival of unburned *Y. brevifolia* that sprouted at the Lower Covington Flat and Mile Marker 21 sites declined more dramatically than plants without sprouts (Fig. 5A). Alternatively, sprouting generally prolonged survival for burned *Y. brevifolia* (Sprout, $\chi^2 = 2265.1$, $p < 0.01$, Fig. 5B). While the survival of *Y. brevifolia* that sprouted in burned areas of the Upper and Lower Covington Flats sites declined much more slowly than those without sprouts, *Y. brevifolia* survival at the lower elevation sites converged at the same low level by year 5 (Sprout \times Site, $\chi^2 = 107.6$, $p < 0.01$).

Survival of *Y. brevifolia* damaged by *T. bottae*—Damage to the stems of *Y. brevifolia* was the most dramatic form of herbivory observed, although damage to periderm on the lower stems of *Y. brevifolia* by *Lepus californicus* (jackrabbit) and *Neotoma* spp. (woodrat) was also confirmed from tooth patterns. The majority of *Y. brevifolia* did not have *T. bottae* damage in unburned (86%) and burned areas (72%). In addition, damage to *Y. brevifolia* occurred predominantly at the low-elevation sites and was virtually absent from Lower and Upper Covington Flats (Table 1). Damaged *Y. brevifolia* plants in these unburned, low-elevation sites had slightly lower survival

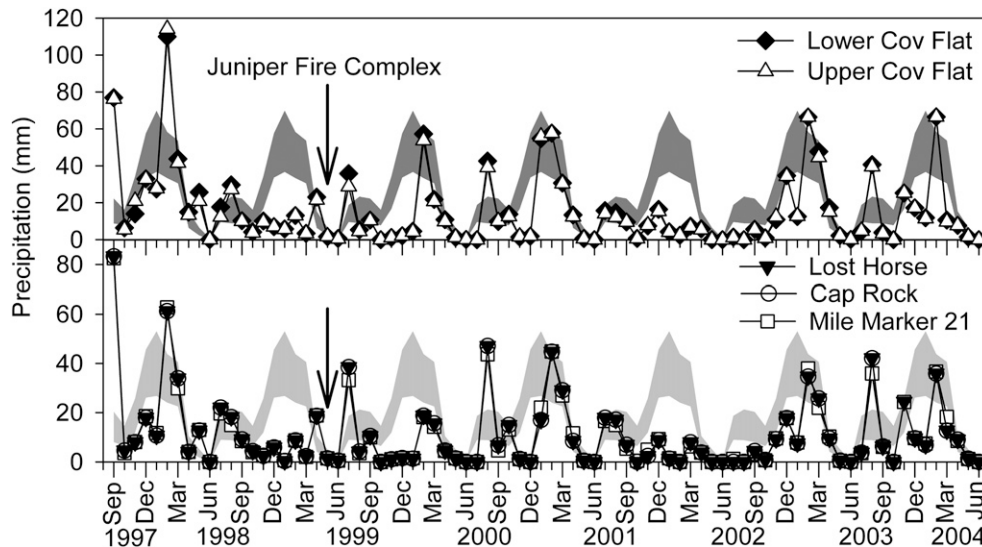


Fig. 2. Monthly precipitation for higher-elevation Lower Covington (1502 m a.s.l.) and Upper Covington (1307 m) sites (upper panel), and lower-elevation Lost Horse (1286 m), Cap Rock (1286 m), and Mile Marker 21 (1232 m) study sites (lower panel) at Joshua Tree National Park. The 95% confidence interval around the 1935–1995 seasonal averages for upper elevation (dark gray shading) and lower elevation (light gray shading) were derived from the Lower Covington Flat and Mile Marker 21 sites, respectively. Arrow denotes occurrence of May 1999 Juniper Fire Complex. Elevation and monthly precipitation were derived from the PRISM Climate Mapping Program, Oregon State University (<http://www.prismclimate.org>).

than undamaged plants (Damage, $\chi^2 = 3.1$, $p = 0.07$, Fig. 6A). In the burned areas, survival declined rapidly for animal-damaged *Y. brevifolia* at low-elevation Cap Rock and Lost Horse sites but was similar between damaged and undamaged plants at Mile Marker 21 where survival for these plants declined early to the same low level (Damage \times Site, $\chi^2 = 11.3$, $p = 0.01$, Fig. 6B).

DISCUSSION

Low survival of burned *Y. brevifolia*—Five years after the Juniper Fire Complex of May 1999, approximately 80% of burned *Y. brevifolia* died compared with 26% in adjacent unburned sites. This high postfire mortality of *Y. brevifolia* is consistent with other studies including 90% mortality six years after a 1978 fire in Lower Covington Flat at Joshua Tree National Park (Allison, 1984) and 64–95% mortality at sites censused 1 to 47 yr after fires in Mojave and Sonoran deserts of California (Minnich, 1995). Declining survival during the first year is attributed to immediate losses of small *Y. brevifolia* (<1 m tall) whose active meristems close to the ground are vulnerable to extreme fire temperatures and flames that consume whole plants (Brooks, 2002; Esque, 2004). As they age and grow taller, *Y. brevifolia* shed leaves from the trunk and are less likely to burn, unlike younger plants whose aging leaves are still attached and provide ladder fuel (T. C. Esque, personal observation). Thus, taller plants likely sustained less proportional burn injury to the outer periderm tissue during the fire, and steep declines in this size class occurred only after the consecutive dry periods that began in the autumn months during 1999 and 2000. Furthermore, the slower decline in survival for burned *Y. brevifolia* at the more mesic, high-elevation sites underscores the importance of post-fire climate conditions on defining the demographic structure of recovering *Y. brevifolia* populations.

Low survival of *Y. brevifolia* exacerbated by drought—Mortality of more than one-quarter of the unburned *Y. brevifolia*

during the 5-yr duration of this study demonstrates how even in the absence of wildfire, drought is changing the demography of long-lived species within the desert Southwest. Survival of unburned *Y. brevifolia* <1 m tall diverged from other size classes in 2001 after 2 yr of low autumn through spring precipitation. Deficits of precipitation that continued into 2003 reduced survival of plants in the middle size classes (1 m to <3 m tall) as well as the largest plants by 2004; thus, even the oldest adult *Y. brevifolia* were susceptible to prolonged drought.

The recent drought that persisted for several years throughout western North America (Cook et al., 2004) caused widespread mortality of other desert species including *Ambrosia dumosa*, *Sphaeralcea ambigua*, and *Eriogonum fasciculatum* in the Colorado Desert (Miriti et al., 2007); *A. dumosa* and *Larrea tridentata* in the eastern Mojave Desert (Hamerlynck and McAuliffe,

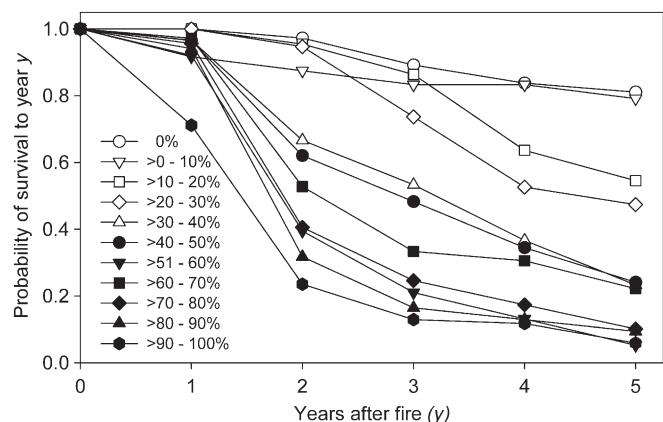


Fig. 3. Estimated survivorship functions for burned *Yucca brevifolia* that sustained different percentages of scorching of aboveground tissue at Joshua Tree National Park 5 yr after the Juniper Fire (year 0 = May 1999). Analysis included 559 *Y. brevifolia*.

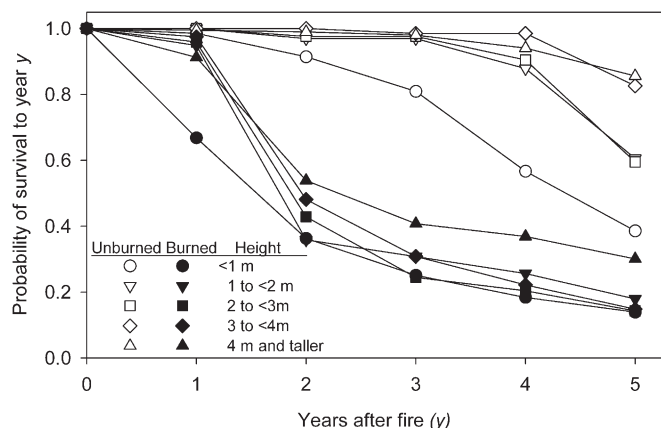


Fig. 4. Estimated survivorship functions for unburned (open symbols) and burned (black symbols) *Yucca brevifolia* at Joshua Tree National Park 5 yr following the Juniper Fire (year 0 = May 1999). Analysis included 1154 *Y. brevifolia*.

2008); and *Cercidium microphyllum*, *A. dumosa*, *L. tridentata*, *Encelia farinosa*, and *Krameria grayi* in the northern Sonoran Desert (Bowers and Turner, 2001; Bowers, 2005). Indeed, episodic mortality during past decades and centuries indicates that extremes in precipitation have altered plant composition and stand age structure in North American warm deserts (Turner, 1990; Pierson and Turner, 1998; Hereford et al., 2006). However, predicted changes in the regional climate present novel threats to these desert plant communities. We expect that the greater frequency and amplitude of the rapid switches between El Niño wet phases that promote alien annual plant production followed by dry La Niña phases (McCabe et al., 2004; IPCC, 2007; Seager et al., 2007; Allan and Soden, 2008) will continue to promote desert wildfires that injure and kill all size classes of *Y. brevifolia*. Future ENSO periods will likely favor a demographic shift toward taller, older *Y. brevifolia* populations. These shifts in stand structure due to drought- and fire-induced losses of smaller *Y. brevifolia* may prevail over plant responses that enhance survival such as freezing tolerance that facilitates plant migration as atmospheric CO₂ concentrations increase (Huxman et al., 1998; Loik et al., 2000b; Dole et al., 2003). Furthermore, given that the recruitment of *Y. brevifolia* seedlings is phenomenologically linked to the canopies of perennial shrubs and grasses during high precipitation years (Brittingham and Walker, 2000), greater frequency of recruitment failure on postfire landscapes will be detrimental to aging *Y. brevifolia* populations in the future.

Herbivore-induced losses of *Y. brevifolia*—The loss of *Y. brevifolia* was not only amplified by the lack of precipitation following the wildfire but also by herbivores that damaged burned plants. Herbaceous annual plants were scarce during the growing season following the 1999 fire, and many perennials were dormant due to low autumn through spring precipitation that triggers germination and breaks leaf dormancy (Went, 1948; Beatley, 1974). Widespread incidence of tissue damage by *T. bottae* in burned areas implies that the roots and periderm of *Y. brevifolia* that did not die immediately in the fire offered an alternative succulent food source in denuded areas where shrubs and grasses were incinerated. We did not monitor densities of *T. bottae* among the sites during this study, so we cannot eliminate the possibility that higher densities of *T. bottae* that may have occurred at low-elevation, burned sites were responsible for greater *Y. brevifolia* mortality. Similar to our results, the shift from wet to dry ENSO periods has caused herbivore-mediated plant mortality in other systems: bromeliads were eaten by frugivorous collared peccaries during fruit shortages on Barro Colorado Island, Panama (Ticktin, 2003), bush lupines in coastal California were eaten by herbivorous moths after nematode predation on moths declined (Preisser and Strong, 2004), and mesquite tree establishment in north central Chile was hindered by prevalence of exotic herbivores (Holmgren et al., 2006). Thus, *Y. brevifolia* mortality as a consequence of a switch in *T. bottae* diet driven by a shortage of herbaceous plants in 2000 is a compelling hypothesis that requires further investigation.

Sprouting in *Y. brevifolia* does not always ensure survival—In our study, 33% of *Y. brevifolia* that were censused in burned areas sprouted from the root crown or stem after the fire compared with 15% in unburned areas. One year after a 1978 fire in Covington Flats, Allison (1984) found 25% of the *Y. brevifolia* sprouting from the root crown, and Loik et al. (2000a) observed 30% of plants sprouting from the root crown or the stem one year after a 1995 fire in Lower Covington Flats. In unburned areas, survival of *Y. brevifolia* was enhanced by sprouting at the low-elevation sites, Cap Rock and Lost Horse, while survival of the higher-elevation Upper Covington Flat site remained high regardless of sprouting. Sprouting, in response to the combination of shallow soils or substrate instability and low-level disturbances such as high winds, has been demonstrated to extend the life span of individuals of other species (Del Tredici, 2001). Accordingly, we considered that *Y. brevifolia* that sprout after burn injury are able to quickly re-establish as reproductive adults and thereby circumvent the challenges of plant establishment during seed dispersal, seed

TABLE 1. Number of *Yucca brevifolia* with and without new leaf sprouts and with and without *Thomomys bottae* damage during the study. Percentage of population by site and burn area are shown in parentheses. Some *Y. brevifolia* could not be found for assessment of sprouts in some years; thus, table values reflect only the *Y. brevifolia* that could be definitely assessed out of the total number of plants in the study (i.e., 14% of unburned and 2% burned *Y. brevifolia* could not be found in all years for assessment of sprouts and were omitted for the sprout analysis).

Site	Unburned		Burn		Unburned		Burn	
	No sprouts	Sprouts	No sprouts	Sprouts	No damage	Damage	No damage	Damage
Mile Marker 21	64 (51)	13 (10)	106 (81)	19 (15)	90 (72)	35 (28)	75 (57)	56 (43)
Cap Rock	99 (80)	19 (15)	90 (67)	43 (32)	107 (86)	17 (14)	91 (67)	44 (33)
Lost Horse	105 (88)	12 (10)	79 (58)	55 (40)	96 (80)	24 (20)	80 (58)	57 (42)
Upper Cov Flat	65 (67)	25 (26)	55 (64)	28 (33)	97 (100)	0 (0)	86 (100)	0 (0)
Lower Cov Flat	59 (66)	16 (18)	59 (54)	50 (46)	90 (100)	0 (0)	96 (88)	13 (12)
Total	392 (71)	85 (15)	389 (65)	195 (33)	480 (86)	76 (14)	428 (72)	170 (28)

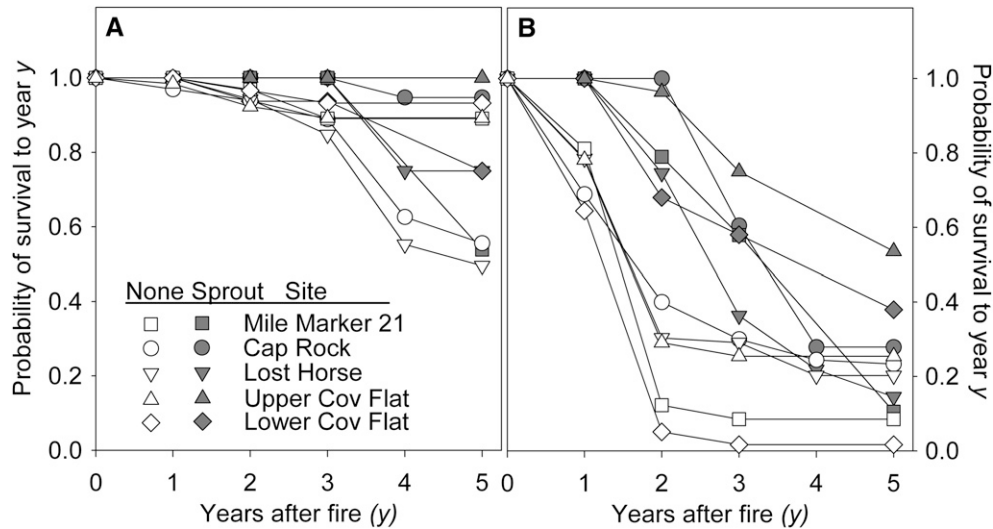


Fig. 5. Estimated survivorship functions for (A) unburned and (B) burned *Yucca brevifolia* without sprouts (open symbols) and with sprouts (gray symbols) among five sites at Joshua Tree National Park 5 yr after the Juniper Fire (year 0 = May 1999). Analysis included 584 burned and 477 unburned *Y. brevifolia*.

germination, and development toward reproductive size in a variable environment.

Fire-adapted plants in systems where high intensity fires are frequent can remobilize carbohydrates stored in belowground structures so that plants can sprout from the root crown (Bond and Midgley, 2001). *Yucca brevifolia* is shallow-rooted with little or no developed taproot system (Rundel and Gibson, 1996) so after burn injury, the belowground resources of *Y. brevifolia* may be insufficient or energetically too costly to mobilize for new sprouts. Alternatively, stem sprouting after injury can occur by remobilizing carbohydrates stored in the aboveground tissues as observed in subtropical coastal sand dune trees (Nzunda et al., 2008). Results from a study in Lost Horse Valley at Joshua Tree National Park (Smith et al., 1983) imply

that carbon gain during January through May can provide a surplus of resources after the annual cost of leaf production, root and shoot growth, and maintenance respiration is considered, potentially leaving any surplus storage that could be used for sprouting. In our study, larger plants generally sustained less proportional surface burning than smaller plants; therefore, we speculate that the larger plants in general had greater reserves available for sprouting, which prolonged survival. Webber (1953) suggested that *Y. brevifolia* is highly adapted to fire, and in addition with others (Loik et al., 2000a), speculated that *Y. brevifolia* sprouting is a successful means of repopulating disturbed sites. Our data indicate that *Y. brevifolia* sprouting can provide some advantage to survival only when precipitation is sufficient (e.g., at higher-elevation sites or during wet

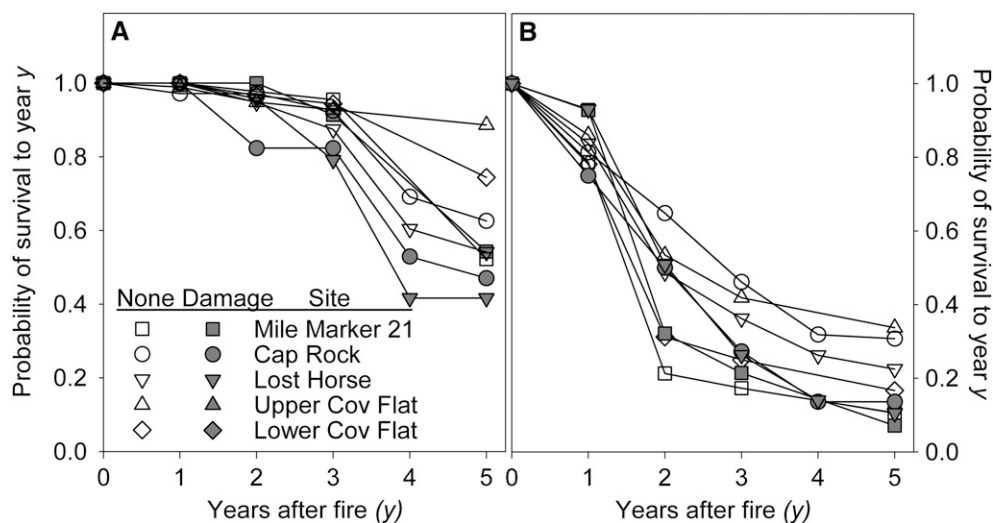


Fig. 6. Estimated survivorship functions for (A) unburned and (B) burned *Yucca brevifolia* without damage (open symbols) and with damage (gray symbols) by *Thomomys bottae* among five sites within Joshua Tree National Park 5 yr after the Juniper Fire (year 0 = May 1999). Functions for damaged *Y. brevifolia* were not analyzed for Upper and Lower Covington Flat sites due to lack of or too few plants that were damaged by *T. bottae*. Analysis included 512 burned (excludes Upper Covington) and 369 unburned *Y. brevifolia* (excludes Upper and Lower Covington Flats).

years). Thus, sprouting of *Y. brevifolia* in the Mojave Desert presents an uncertain recovery strategy in postfire landscapes, especially in the face of herbivory and recurring low-precipitation years, and merits further long-term research attention.

The recruitment of *Y. brevifolia* is a slow process even without the impediments introduced by accelerated fire-return intervals. At 13 burned sites in Joshua Tree National Park, few arboreal species recolonized even 47 yr after a single fire (Minnich, 1995). *Yucca brevifolia* re-established so slowly in comparison to other perennial species on plowed fields that after 70 yr there were virtually no arboreal species on disturbed sites (Carpenter et al., 1986). A 20-yr study of *Y. brevifolia* on three 0.1-ha plots in southern California found only two seedlings, both of which died within a year (Comanor and Clark, 2000), though sample sizes were small for drawing demographic conclusions. After the 1999 fire in Joshua Tree National Park, burned sites were nearly denuded of shrub and perennial grass cover, and this postfire landscape lacked the safe sites beneath nurse plants necessary for *Y. brevifolia* seedlings to establish (Brittingham and Walker, 2000; Loik et al., 2000a). Mortality of seed-producing adults over expansive areas and loss of suitable establishment sites are important limitations to *Y. brevifolia*'s recolonization after fires.

Alien annual grasses introduce a complication in the slowly recovering landscape of the Mojave Desert because in addition to causing fires, they compete with native species for water and nutrients (Brooks, 2000; DeFalco et al., 2003, 2007). These annual grasses are ubiquitous in the Mojave Desert, and production is intimately tied to above-average autumn and winter precipitation during wet El Niño phases. The success of alien annual grasses in postfire habitats prolongs the period during which recolonizing *Y. brevifolia* are susceptible to fire (D'Antonio and Vitousek, 1992). The larger the burned area, the more difficult it will be for native plants to recolonize their original range (Carpenter et al., 1986; Vitousek et al., 1997), especially for species such as *Y. brevifolia* that require animal dispersal (Vander Wall et al., 2006; Waitman, 2009). Continued monitoring of long-lived plant species such as the iconic *Y. brevifolia* will provide insights into how population- and community-level dynamics will respond to a future changing climate and determine how scientists and managers can plan for and possibly mitigate such changes.

LITERATURE CITED

- ALLAN, R. P., AND B. J. SODEN. 2008. Atmospheric warming and the amplification of precipitation extremes. *Science* 321: 1481–1484.
- ALLISON, A. E. 1984. Post-fire regeneration: Mohave Desert, pinyon-juniper belt. Research report, Joshua Tree National Park, Twentynine Palms, California, USA.
- ALLISON, P. D. 1995. Survival analysis using the SAS system: A practical guide, SAS Institute, Cary, North Carolina, USA.
- BEATLEY, J. C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology* 55: 856–863.
- BOND, W. J., AND J. J. MIDGLEY. 2001. Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology & Evolution* 16: 45–51.
- BOWERS, J. E. 2005. Effects of drought on shrub survival and longevity in the northern Sonoran Desert. *Journal of the Torrey Botanical Society* 132: 421–431.
- BOWERS, J. E., AND R. M. TURNER. 2001. Dieback and episodic mortality of *Cercidium microphyllum* (foothill paloverde), a dominant Sonoran Desert tree. *Journal of the Torrey Botanical Society* 128: 128–140.
- BRITTINGHAM, S., AND L. R. WALKER. 2000. Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. *Western North American Naturalist* 60: 374–383.
- BROOKS, M. L. 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. *American Midland Naturalist* 144: 92–108.
- BROOKS, M. L. 2002. Peak fire temperatures and effects on annual plants in the Mojave Desert. *Ecological Applications* 12: 1088–1102.
- BROOKS, M. L., AND J. R. MATCHETT. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *Journal of Arid Environments* 67: 148–164.
- BROWER, J. E., J. H. ZAR, AND C. N. VON ENDE. 1998. Field and laboratory methods for general ecology. Wm. C. Brown, Dubuque, Iowa, USA.
- BROWN, D. E., AND R. A. MINNICH. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. *American Midland Naturalist* 116: 411–422.
- BROWN, J. H., T. J. VALONE, AND C. G. CURTAIN. 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences, USA* 94: 9729–9733.
- CARPENTER, D. E., M. G. BARBOUR, AND C. J. BAHRE. 1986. Old field succession in Mojave Desert scrub. *Madroño* 33: 111–122.
- COMANOR, P. L., AND W. H. CLARK. 2000. Preliminary growth rates and a proposed age-form classification for the Joshua Tree, *Yucca brevifolia* (Agavaceae). *Haseltonia* 7: 37–46.
- CONRAD, C. E. 1987. Common shrubs of chaparral and associated ecosystems of southern California. General Technical Report PSW-99, U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.
- COOK, E. R., C. A. WOODHOUSE, C. M. EAKIN, D. M. MEKO, AND D. W. STAHL. 2004. Long-term aridity changes in the western United States. *Science* 306: 1015–1018.
- D'ANTONIO, C. M., AND P. M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics* 23: 63–87.
- DeFALCO, L. A., D. R. BRYLA, V. SMITH-LONGOZO, AND R. S. NOWAK. 2003. Are Mojave Desert annual species equal? Resource acquisition and allocation for the invasive grass *Bromus madritensis* ssp. *rubens* (Poaceae) and two native species. *American Journal of Botany* 90: 1045–1053.
- DeFALCO, L. A., G. C. J. FERNANDEZ, AND R. S. NOWAK. 2007. Variation in the establishment of a non-native annual grass influences competitive interactions with Mojave Desert perennials. *Biological Invasions* 9: 293–307.
- DEL TREDICI, P. 2001. Sprouting in temperate trees: A morphological and ecological review. *Botanical Review* 67: 121–140.
- DOLE, K. P., M. E. LOIK, AND L. C. SLOAN. 2003. The relative importance of climate change and the physiological effects of CO₂ on freezing tolerance for the future distribution of *Yucca brevifolia*. *Global and Planetary Change* 36: 137–146.
- ESQUE, T. C. 2004. The role of fire, rodents and ants in changing plant communities in the Mojave Desert. Ph.D. dissertation, University of Nevada, Reno, Nevada, USA.
- ESQUE, T. C., AND C. R. SCHWALBE. 2002. Alien annual plants and their relationships to fire and biotic change in Sonoran Desert scrub. In B. Tellman [ed.], *Invasive exotic species in the Sonoran region*, 165–194. Arizona-Sonora Desert Museum and University of Arizona Press, Tucson, Arizona, USA.
- GILLILAND, K. D., N. J. HUNTLY, AND J. E. ANDERSON. 2006. Age and population structure of Joshua trees (*Yucca brevifolia*) in the northwestern Mojave Desert. *Western North American Naturalist* 66: 202–208.
- HAMERLYNCK, E. P., AND J. R. McAULIFFE. 2008. Soil-dependent canopy die-back and plant mortality in two Mojave Desert shrubs. *Journal of Arid Environments* 72: 1793–1802.
- HEREFORD, R., R. H. WEBB, AND C. J. LONGPRE. 2006. Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave Desert regions, 1893–2001. *Journal of Arid Environments* 67: 13–34.

- HOLMGREN, M., B. C. LÓPEZ, J. R. GUTIÉRREZ, AND F. A. SQUEO. 2006. Herbivory and plant growth rate determine the success of El Niño Southern Oscillation-driven tree establishment in semiarid South America. *Global Change Biology* 12: 2263–2271.
- HUNTER, R. B. 1991. *Bromus* invasions on the Nevada Test Site: Present status of *B. rubens* and *B. tectorum* with notes in their relationship to disturbance and altitude. *Great Basin Naturalist* 51: 176–182.
- HUXMAN, T. E., E. P. HAMERLYNCK, M. E. LOIK, AND S. D. SMITH. 1998. Gas exchange and chlorophyll fluorescence responses of three southwestern *Yucca* species to elevated CO₂ and high temperature. *Plant, Cell & Environment* 21: 1275–1283.
- INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE. 2007. Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- LITTELL, J. S., D. MCKENZIE, D. L. PETERSON, AND A. L. WESTERLING. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. *Ecological Applications* 19: 1003–1021.
- LOIK, M. E., T. E. HUXMAN, E. P. HAMERLYNCK, AND S. D. SMITH. 2000b. Low temperature tolerance and cold acclimation for seedlings of three Mojave Desert *Yucca* species exposed to elevated CO₂. *Journal of Arid Environments* 46: 43–56.
- LOIK, M. E., C. D. ST. ONGE, AND J. ROGERS. 2000a. Post-fire recruitment of *Yucca brevifolia* and *Yucca schidigera* in Joshua Tree National Park, California. In J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham [eds.], Second interface between ecology and land development in California, 79–85. Open-File Report 00-62, U.S. Geological Survey, Sacramento, California, USA.
- MCCABE, G. J., M. A. PALECKI, AND J. L. BETANCOURT. 2004. Pacific and Atlantic Ocean influences on multi-decadal drought frequency in the United States. *Proceedings of the National Academy of Sciences, USA* 101: 4136–4141.
- MINNICH, R. A. 1995. Wildland fire and early postfire succession in Joshua tree woodland and blackbrush scrub of the Mojave Desert of California. In R. E. Reynolds and J. Reynolds [eds.], Ancient surfaces of the east Mojave Desert, 99–106. San Bernardino County Museum Association Quarterly, vol. 42, San Bernardino, California, USA.
- MIRITI, M. N., S. RODRÍGUEZ-BURITITICÁ, S. J. WRIGHT, AND H. F. HOWE. 2007. Episodic death across species of desert shrubs. *Ecology* 88: 32–36.
- NZUNDA, E. F., M. E. GRIFFITHS, AND M. J. LAWES. 2008. Sprouting by remobilization of above-ground resources ensures persistence after disturbance of coastal dune forest trees. *Functional Ecology* 22: 577–582.
- O'LEARY, J. F., AND R. A. MINNICH. 1981. Postfire recovery of creosotebush scrub vegetation in the western Colorado Desert. *Madroño* 28: 61–66.
- PIERSON, E. A., AND R. M. TURNER. 1998. An 85-year study of saguaro (*Carnegiea gigantea*) demography. *Ecology* 79: 2676–2693.
- PREISSER, E. L., AND D. R. STRONG. 2004. Climate affects predator control of an herbivore outbreak. *American Naturalist* 163: 754–762.
- RUNDEL, P. W., AND A. C. GIBSON. 1996. Ecological communities and processes in a Mojave Desert ecosystem: Rock Valley, Nevada. Cambridge University Press, New York, New York, USA.
- SALO, L. F. 2002. Ecology and biogeography of red brome (*Bromus madriensis* subspecies *rubens*) in western North America. Ph.D. dissertation, University of Arizona, Tucson, Arizona, USA.
- SEAGER, R., M. TIND, I. HELD, Y. KUSHNIR, J. LU, G. VECCHI, H. P. HUANG, ET AL. 2007. Model projections on an imminent transition to a more arid climate in southwestern North America. *Science* 316: 1181–1184.
- SMITH, S. D., T. L. HARTSOCK, AND P. S. NOBEL. 1983. Ecophysiology of *Yucca brevifolia*, an arborescent monocot of the Mojave Desert. *Oecologia* 60: 10–17.
- SWETNAM, T. W., AND J. L. BETANCOURT. 1990. Fire–Southern Oscillation relations in the southwestern United States. *Science* 249: 1017–1020.
- SWETNAM, T. W., AND J. L. BETANCOURT. 1998. Mesoscale disturbance and ecological response to decadal climate variability in the American Southwest. *Journal of Climate* 11: 3128–3147.
- TICKTIN, T. 2003. Relationships between El Niño Southern Oscillation and demographic patterns in a substitute food for collared peccaries in Panama. *Biotropica* 35: 189–197.
- TURNER, R. M. 1990. Long-term vegetation change at a fully protected Sonoran Desert site. *Ecology* 71: 464–477.
- USDA [U.S. DEPARTMENT OF AGRICULTURE]. 2002. Fire Effects Information System [online]. Website <http://www.fs.fed.us/database/feis> [accessed 29 October 2008].
- VANDER WALL, S. B., T. C. ESQUE, B. A. WAITMAN, D. F. HAINES, AND M. G. GARNETT. 2006. Joshua tree (*Yucca brevifolia*) seeds are dispersed by seed-caching rodents. *Ecoscience* 13: 539–543.
- VITOUSEK, P. M., C. M. D'ANTONIO, L. L. LOOPE, M. REJMÁNEK, AND R. WESTBROOKS. 1997. Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* 21: 1–16.
- VOGL, R. J. 1968. Fire adaptations of some southern California plants. In Proceedings of the California Tall Timbers Fire Ecology Conference, Lake County, California, 78–107. Tall Timbers Research Station, Tallahassee, Florida, USA.
- WAITMAN, B. 2009. Rodent mediated seed dispersal of Joshua tree (*Yucca brevifolia*). M.S. thesis, University of Nevada, Reno, Nevada, USA.
- WEBB, R. H., M. B. MUROV, T. C. ESQUE, D. E. BOYER, L. A. DEFALCO, D. F. HAINES, D. OLDERSHAW, ET AL. 2003. Perennial vegetation data from permanent plots on the Nevada Test Site, Nye County, Nevada. Open-File Report 03-336, U.S. Geological Survey, Tucson, Arizona, USA.
- WEBBER, J. M. 1953. Yuccas of the southwest. Agricultural Monograph No. 17. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- WENT, F. W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. *Ecology* 29: 242–253.