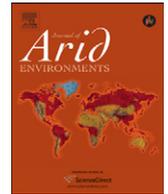




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Soil-dependent canopy die-back and plant mortality in two Mojave Desert shrubs

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ABSTRACT

Recent drought has led to unprecedented levels of plant mortality across the Southwestern US. An unaddressed feature of this drought's impact is how soil characteristics and soil hydrological behavior affect desert plant canopy die-back and mortality. Here, we present a multi-year study in the Mojave Desert assessing canopy die-back and whole-plant mortality of white bursage (*Ambrosia dumosa*) and creosotebush (*Larrea tridentata*) in soils varying in surface and sub-surface horizon development, and topographic (hillslope vs. channel) positions. Canopy die-back and mortality was more widespread *A. dumosa* than in *L. tridentata*, and dead plants tended to be smaller than surviving plants, especially in channel and hillslope locations. This suggests that juveniles were particularly vulnerable where plants depended heavily on augmentation of incident precipitation by runoff. Canopy die-back was greater in young, weakly developed soils that fostered extensive plant growth, while plants growing in older, well-developed soils showed markedly lower branch and plant mortality, especially in *A. dumosa*. We attributed these differences in plant response in part to variation in distributions of large rocks within soil profiles, which might affect soil hydrological heterogeneity and intensity of plant competition for water.

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1. Introduction

Recent severe drought conditions across the arid Southwest have resulted in annual precipitation totals 50–70% below long-term averages (Breshears et al., 2005; Hereford et al., 2006), and have been credited in inducing widespread plant mortality in higher-elevation forest (Breshears et al., 2005) and lower-elevation desert scrub communities (Bowers, 2005; Hereford et al., 2006; Miriti et al., 2007). Such widespread mortality indicates this drought is far more severe than the predictable seasonal dry periods characteristic of North American deserts (Miriti et al., 2007; Smith et al., 1997), and may represent the start of a protracted and prolonged climatic drought across the arid Southwest, which have occurred over the last few millennia on an inter-decadal and inter-centennial basis (Swetnam and Betancourt, 1998). Protracted drought may produce significant ecological disturbance across this region, since such conditions can kill adult plants, the loss of which strongly affects plant demography, resulting in a persistent effect in the recovering plant community (Bowers and Turner, 2001; Miriti et al., 2001, 2007; Swetnam and Betancourt, 1998). In addition, loss of established plants has a lasting effect on desert ecosystem processes by altering the spatial distribution and availability of soil nutrients that accumulated under long-lived plants prior to their deaths (Schlesinger and Pilmanis, 1998).

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Plant mortality in response to this widespread regional drought may be influenced by soil characteristics. Soil water availability is the primary driver of ecological processes in deserts (Noy-Meir, 1973). Temporal persistence of soil moisture is largely a function of the depth of soil moisture storage, as influenced by precipitation amount, the amount infiltrating into the soil surface, and the depth of percolation. The strength of horizon development in desert soils affects both surface infiltration and subsurface percolation (McAuliffe, 2003). Fine-textured vesicular A horizons that frequently underlie stone pavements in deserts greatly limit infiltration, while deeper horizons enriched by clay or calcium carbonate greatly influence percolation depth and water availability (Alizai and Hulbert, 1970; Hamerlynck et al., 2002; McAuliffe, 1994, 2003).

Another critical feature of desert soil hydrology is the contribution of landform features to the production and/or receipt of overland flow, which can greatly augment the amount of incident precipitation (Abrahams and Parsons, 1991; Schlesinger et al., 1989). In general, overland flow generated on shallow slopes is transmitted into channels where it can accumulate and generate channel flow, the degree of which depends on transmission losses that are determined by the channel's soil characteristics and overall morphology (Abrahams and Parsons, 1991; Atchley et al., 1999). Taken together, these soil hydrological features strongly affect individual plant performance (Hamerlynck et al., 2000, 2002; Huxman et al., 2004; Schlesinger and Jones, 1984; Schlesinger et al., 1989; Smith et al., 1995), plant density and biomass (McAuliffe, 1994; Shreve and Mallery, 1933), rooting patterns (Gile et al., 1998) plant–plant interactions (Briones et al., 1996, 1998; Schenk et al., 2003), community structure (McAuliffe, 1994), and nutrient cycling (Lathja and Schlesinger, 1986, 1988).

To date, no study has taken a soils- and landform approach to determine the effects that recent, intense drought conditions have had on plant mortality in the arid Southwest. Here, we present results on the effects of the drought on two important Mojave Desert shrubs, the evergreen creosotebush (*Larrea tridentata*) and the drought deciduous white bursage (*Ambrosia dumosa*); together, these two species are biomass co-dominants across much of the Mojave Desert, frequently to the near exclusion of other species (Hamerlynck et al., 2002; Smith et al., 1997). We selected five sites differing in either soil development, or the degree to which they either acted as source for runoff or a place augmented by run-on. We developed four hypotheses to test:

- (1) The drought-deciduous *A. dumosa* would show greater evidence of canopy die-back and whole-plant mortality compared with the evergreen *L. tridentata*. Drought-deciduous shrubs like *Ambrosia dumosa* avoid seasonal drought by going dormant. However, protracted multi-year drought may be a particular problem because these plants may not receive enough rain to break dormancy and establish sufficient leaf area to fix enough carbon in order to survive the duration of the drought (Comstock and Ehleringer, 1986; Smith et al., 1997). In contrast, *L. tridentata* is highly drought-tolerant, capable of positive net photosynthetic rates at water potentials as low as -8 MPa (Hamerlynck et al., 2000; Odening et al., 1974), has xylem architecture that is more resistant to cavitation than *A. dumosa* at similar low water potentials (Jacobsen et al., 2007), and, depending on soil characteristics, can utilize even modest seasonal rains (Hamerlynck et al., 2000). Thus, *L. tridentata* might be expected to be better able to endure prolonged drought conditions.
- (2) Canopy die-back and plant mortality would be more evident in smaller plants, since seedling and juvenile desert plants are particularly susceptible to drought-induced mortality (Casper, 1996; Miriti et al., 2001, 2007).
- (3) Canopy die-back and mortality would be more extensive in soils with stronger soil horizon development and potentially less favorable soil hydrologies, as we hypothesized in previous work examining plant water relations (Hamerlynck et al., 2002). Fine-textured soil horizons can strongly limit surface infiltration and sub-surface percolation and plant water availability (Alizai and Hulbert, 1970; McAuliffe, 2003), and could potentially magnify the effects of drought.
- (4) Canopy die-back and mortality would be less pronounced in channel areas that could accumulate overland flow than in areas having more limited potential for augmentation of incident precipitation. Channel locations usually have more persistent soil moisture, greater growth and better nutrient status (Atchley et al., 1999), and thus we expected less extreme effects of climatic drought in these locations.

2. Materials and methods

2.1. Study sites

Fieldwork was conducted on the west-facing alluvial piedmont of the Providence Mountains in the Mojave National Preserve, CA ($34^{\circ}54'–58'N$, $115^{\circ}36'–39'W$). Five sites were selected from those previously studied in this area (Hamerlynck et al., 2000, 2002; McDonald et al., 2003). Three sites were located along a chronosequence of soils derived from the same mixed plutonic (PM) alluvial parent material (McDonald et al., 1996). The first of these was located on a ~ 6000 -year-old Holocene fan deposit of coarse gravelly alluvium, hereafter referred to as the *Young Alluvial* site. Soil at this site is weakly developed, with minimal horizon development. The second and third sites were located on older, late Pleistocene deposits, one on a $\sim 12,000$ -year-old deposit (hereafter referred to as the *Intermediate Alluvial* site), the other on a $\sim 50,000$ -year-old deposit (hereafter referred to as the *Old Alluvial* site), both consisting of cobbly to bouldery alluvium. Soil at the Intermediate Alluvial site has a fairly well-developed, fine-textured vesicular (A_v) horizon directly beneath the surface of

moderately developed stone pavement, and a moderately developed, clay-enriched argillic (B_t) horizon about 20–35 cm below the surface. Soil at the Old Alluvial site has a very strongly developed A_v horizon underlying a well-developed stone pavement, and a strongly developed argillic B_t horizon at 20–60 cm. Calcium carbonate is found throughout Young, Intermediate, and Old Alluvial soil profiles, but there are no cemented calcic horizons (“caliche”) in any of these soils. *Slope* and *Channel* plots were established on side slopes and channels receiving overland flow run-off from the soil surface of a late Pleistocene (12,000 YBP) mixed volcanic (VX) alluvial fan deposit (McDonald et al., 1996). This location was selected because the strong A_v and stone pavement limit infiltration of all but the strongest rains into this soil (Hamerlynck et al., 2000), and enhance chances that run-off will be generated from the surface and be delivered onto the lateral slopes and into the channels incising the surface. Slope sites therefore characterize locations of production and transfer of overland flow, while Channel sites represent areas of overland flow accumulation.

2.2. Canopy die-back and mortality surveys

Canopy die-back and plant mortality data were gathered from May 3–10, 2003 and 2004 at both sites. At each of the three PM Alluvial soil sites, a 100 m transect was established, and two 100 m² plots were created by sampling all plants in 1 m swaths along the left and right sides of the transect. Transects were oriented along similar compass bearings, and the co-ordinates of each end recorded using a hand-held GPS unit. At the Slope sites, six 100 m² circular plots were established, three on north-facing and three on south-facing exposures, while six 100 m² Channel plots were established by spreading 50 m transects along the main channel beds, and sampling along a 2 m swath centered on the transect. Canopy mortality was determined visually, using the following categorical scale: 0 = all branches dead; and scores of 1 = less than 1/8 branches alive; 2 = $\frac{1}{8}$ – $\frac{1}{4}$; 3 = $\frac{1}{4}$ – $\frac{1}{2}$; 4 = $\frac{1}{2}$ – $\frac{3}{4}$; 5 = $>\frac{3}{4}$ branches live. Only plants that had died within the previous 12 months were counted as class 0 plants based on the retention of dehydrated, dead leaves and shoots produced in the previous growing year; plants that had apparently died in previous years were not included. Visual estimates such as these allow rapid and repeatable estimates of canopy die-back (Bowers and Turner, 2001). Following classification, individual plant canopy diameters (major and minor axes) were measured, then aerial coverage of individual canopies was computed as ellipses and summed for all plants to estimate total canopy cover for the plot. For *L. tridentata*, position along each transect and perpendicular distance from transect were recorded in order to re-visit these plants and ascertain if mortality classification had changed between years.

2.3. Statistical analyses

A χ^2 analysis (Statistix v8.0, Analytical Software, Tallahassee, FL) was made to test for differences in the proportions of mortality scores across the five sites. One-way analysis of variance (ANOVA, Statistix v8.0) was used to test for size-specific differences between canopy die-back classifications within each of the five sites, and for differences in total cover, density, percent mortality, and canopy diameters of *A. dumosa* and *L. tridentata* between the sites. All percentage-based data were arcsine transformed to meet ANOVA data distribution assumptions; *post hoc* means tests using LSD were made at an associated adjusted α of 0.05. Linear and non-linear regression (SYSTAT v8.0, SPSS Chicago, IL) was used to find which type of relationship best described the co-variation of plant mortality with plant density and mean individual plant size.

3. Results

Total canopy cover was similar across the five sites (Table 1), averaging 20.40% (± 2.14 SE) across the sites, mainly due to changes in the relative contributions of *A. dumosa* or *L. tridentata* to total cover (Fig. 1). Total plant densities differed significantly between the five study sites (Table 1), and were significantly higher at Old Alluvial (84.0 ± 13 SE per 100 m² plot) and Intermediate Alluvial (84.5 ± 7.50 SE) sites compared with Young Alluvial (40.0 ± 2.0 SE) and Channel sites (44.2 ± 9.45 SE), which in turn had higher densities than Slope locations (20.5 ± 2.63 SE; Fig. 1). Differences in total plant density were driven by changes in *A. dumosa* density, which had the highest densities of all species across the five sites

Table 1

One-way analysis of variance (ANOVA) results comparing percent total plant cover, plant density, plant size (m² canopy area) and percent mortality of white bursage (*Ambrosia dumosa*) and creosotebush (*Larrea tridentata*) in five soil/landscape positions following severe drought conditions

Attribute	Location MS	Error MS	$F_{(4,13)}$ (df)	<i>p</i>
% Cover	0.0130	0.0141	0.92	0.4836
Total density	2454.19	257.29	9.54	0.0008
<i>A. dumosa</i> individual canopy area	0.0126	0.0016	7.88	0.0019
<i>L. tridentata</i> individual canopy area	1.530	0.102	15.1	0.0001
<i>A. dumosa</i> % mortality	0.4582	0.0664	6.90	0.0033
<i>L. tridentata</i> % mortality	0.0067	0.0063	1.06	0.4137

Analyses for percentage-based data are after arcsine transformation to meet ANOVA data distribution assumptions. Significant results ($p \leq 0.05$) are in bold.

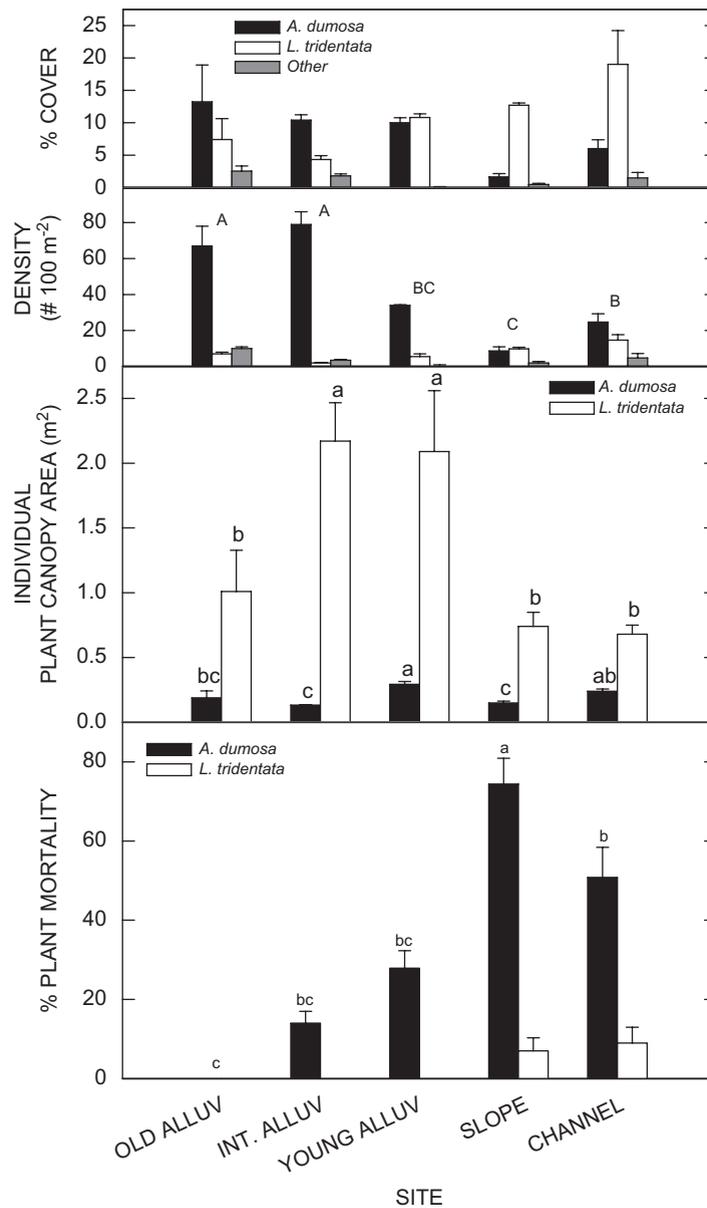


Fig. 1. Percent cover and plant density of all species, and individual plant canopy areas and % mortality of *Ambrosia dumosa* and *Larrea tridentata* growing in five different soil locations. Bars are mean and SE of 2 (Alluvial soils) or 6 (Channel and Slope) plots, letters differ at $p < 0.05$ (LSD of ANOVA results); lower case letters are within-species comparisons, capital letters compare pooled results.

(Fig. 1). Individual plant canopy areas changed in a soil-specific manner (Table 1). Canopy areas of individual *A. dumosa* were greatest at the Young Alluvial and Channel sites compared with smaller, yet similar, plant sizes at the Old Alluvial, Intermediate Alluvial, and Slope sites (Fig. 1). Individual *L. tridentata* had largest canopies at Young and Intermediate Alluvial sites and smaller canopies at the remaining sites (Fig. 1). Plant mortality levels were significantly different between the sites only for *A. dumosa* (Table 1), with the highest mortality at the Slope site, followed by significantly lower mortality levels at the Channel, Young Alluvial, and Intermediate Alluvial sites, with no *A. dumosa* mortality evident at the Old Alluvial site (Fig. 1). Though *L. tridentata* mortality was noted at Slope and Channel locations, these levels did not vary significantly from zero (Fig. 1).

There was a significant quadratic relationship between *A. dumosa* density and mean individual canopy area (Table 2) that was driven by site-specific variation in size and density (Fig. 2). The Young Alluvial site and some Channel site plots provided the peak size/density combination, and similar small canopy areas at the Slope and Intermediate Alluvial PM sites anchored the two ends of the density spectrum (Fig. 2); linear regression failed to explain this relationship (Table 2).

Table 2

Comparison of different regression relationships individual plant canopy area (A in m^2) and densities of *Ambrosia dumosa* and *Larrea tridentata* (D ; plants/ m^2 for *A. dumosa* and plants per $100 m^{-2}$ for *L. tridentata*) across five contrasting soil sites

Species	Type	Regression	R^2	$F_{(df)}$
<i>A. dumosa</i>	Quadratic	$A = 0.162 + 0.256D - 0.103D^2$	0.33	83.33 _(3,15)
<i>A. dumosa</i>	Linear	$A = 0.202 - 3.31 \times 10^{-5}D$	0.0002	0.00 _(1,16)
<i>L. tridentata</i>	Inv. Quad.	$A = -0.025 + (9.6/D) - (10.18/D^2)$	0.66	49.38 _(3,15)
<i>L. tridentata</i>	Linear	$A = 1.64 - 0.0596D$	0.30	6.82 _(1,16)

Significant ($p \leq 0.05$) coefficients of variation (R^2) and associated F -tests are in bold.

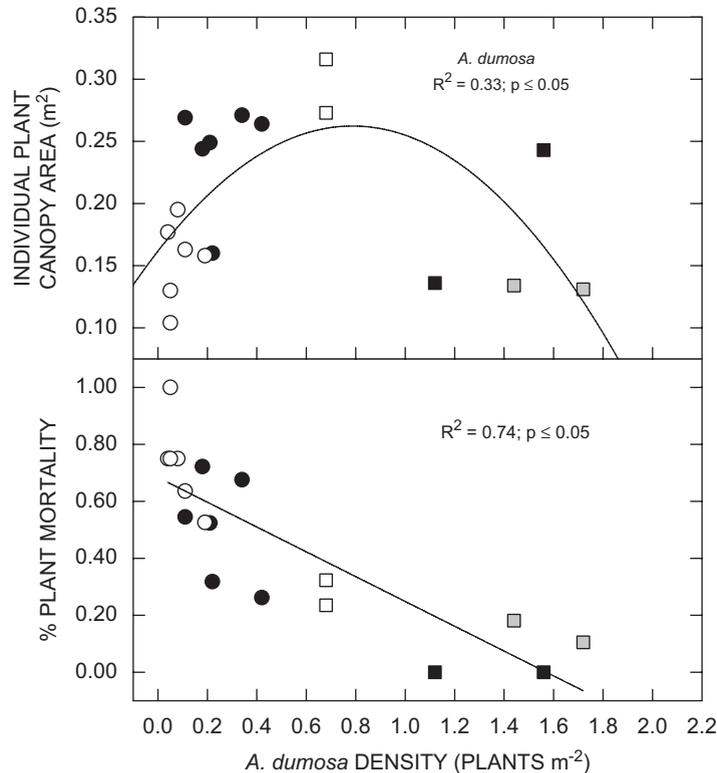


Fig. 2. Relationships of plant size and plant mortality with density of *Ambrosia dumosa*. Symbols indicate ● = Channel, ○ = Slope, ■ = Old Alluvial, ■ = Intermediate Alluvial and □ = Young Alluvial sites.

The strong contrast in mortality between similar sized plants from Slope, Intermediate and Old Alluvial sites resulted in a strongly significant inverse relationship between *A. dumosa* mortality and density (Table 3), with Channel and Young Alluvial sites providing intermediate values (Fig. 2). *A. dumosa* was the most common species in all plots (Fig. 1), and its density accounted for nearly 90% of the variation in total plant density (total density = $13.36 + 1.008 * A. dumosa$ density ± 0.86 SE; $R^2 = 0.895$; $p \leq 0.001$). *A. dumosa* density better explained *A. dumosa* mortality than did summed densities of *A. dumosa* and *L. tridentata*, or total density of all plant species (Table 2). Means of individual *L. tridentata* plant sizes showed a significant inverse quadratic relationship with *L. tridentata* density, which explained markedly more variation in plant size than did a linear model (Table 2). There was no significant relationship of any sort between *L. tridentata* mortality and density (Fig. 3).

χ^2 analysis showed the proportion remaining living plant canopy varied significantly between the five sites for both *A. dumosa* ($\chi^2 = 310.98$; $p \leq 0.001$) and *L. tridentata* ($\chi^2 = 45.13$; $p = 0.029$). Branch mortality was most severe in *A. dumosa* at Young Alluvial site, where the most frequent classification was $< \frac{1}{8}$ live canopy, and no plants with $> \frac{3}{4}$ live canopy were found (Fig. 4). *A. dumosa* canopy die-back at the Intermediate and Old Alluvial sites shifted sharply to the right, centering on $\frac{1}{4}$ – $\frac{1}{2}$ and $\frac{1}{2}$ – $\frac{3}{4}$ live canopy classes, respectively (Fig. 4). While whole *A. dumosa* plant mortality was markedly higher at the Slope and Channel sites (Figs. 1 and 4), canopy die-back distributions in living *A. dumosa* at these two sites were similar to Old Alluvial site plants (Fig. 4). Canopy die-back in *L. tridentata* was more severe at the Slope and Channel sites compared

Table 3

Linear regression results of *Ambrosia dumosa* percent mortality as a function of *A. dumosa* density, *A. dumosa* and *Larrea tridentata* densities, and total plant densities

Density basis (<i>D</i>)	Regression	R^2
<i>A. dumosa</i> only	Mortality = $0.767 - 9.74 \times 10^{-3}D$	0.74
<i>A. dumosa</i> + <i>L. tridentata</i>	Mortality = $0.869 - 9.90 \times 10^{-3}D$	0.70
All species	Mortality = $0.854 - 8.71 \times 10^{-3}D$	0.67

All regressions are significant at $p \leq 0.001$.

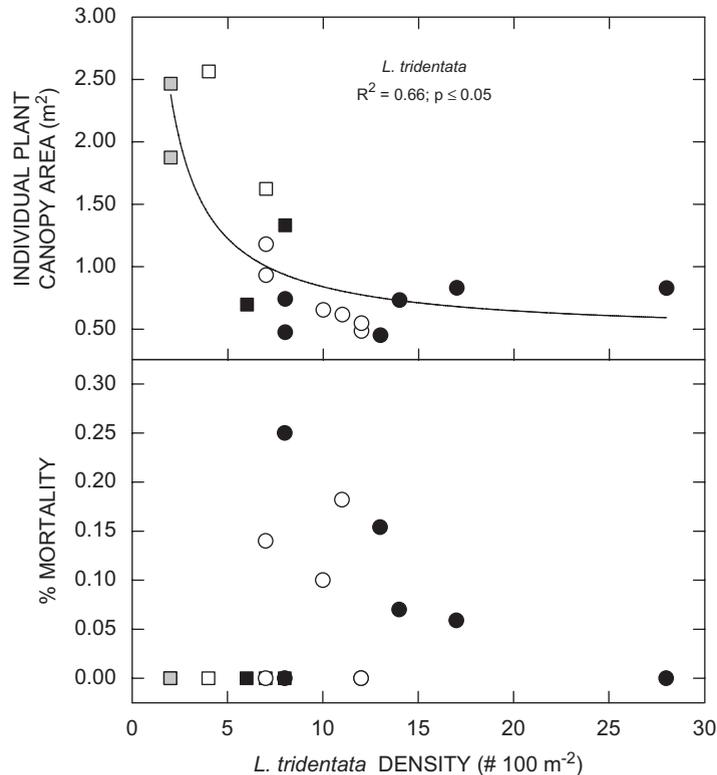


Fig. 3. Relationships of plant size and plant mortality with density of *Larrea tridentata*. Symbols indicate ● = Channel, ○ = Slope, ■ = Old Alluvial, ■ = Intermediate Alluvial and □ = Young Alluvial sites.

with any of the Alluvial soil sites, with frequency distributions fairly evenly distributed across all classes; these were the only locations where whole-plant *L. tridentata* mortality was noted (Fig. 4). Along the mixed plutonic soil chronosequence, *L. tridentata* did best at the Old and Intermediate Alluvial sites, with little evidence of extensive canopy mortality, while there was evidence of fairly severe canopy die-back ($\frac{1}{4}$ – $\frac{1}{2}$ and $\frac{1}{2}$ – $\frac{3}{4}$ classifications) at the Young Alluvial site (Fig. 4).

Plant sizes sometimes varied significantly between canopy die-back classifications (Table 4). At Old Alluvial and Young Alluvial sites, *A. dumosa* sizes were the same across all classifications, while at the Intermediate Alluvial, Slope and Channel sites, dead *A. dumosa* were significantly smaller than living plants, and surviving individuals had similar mean plant sizes (Fig. 5). For the evergreen *L. tridentata* at the Slope and Channel sites, the mean size of dead plants were significantly smaller than surviving plants (Fig. 5).

4. Discussion

As expected, canopy die-back and whole-plant mortality were more extensive in the drought-deciduous *A. dumosa* compared with the evergreen *L. tridentata* (Fig. 1). Physiological activity and canopy development of drought deciduous shrubs are coordinated with heaviest seasonal rains (Comstock and Ehleringer, 1986; Smith et al., 1997). Compared with desert evergreen shrubs, drought-deciduous species frequently have larger leaves, greater stomatal conductance and

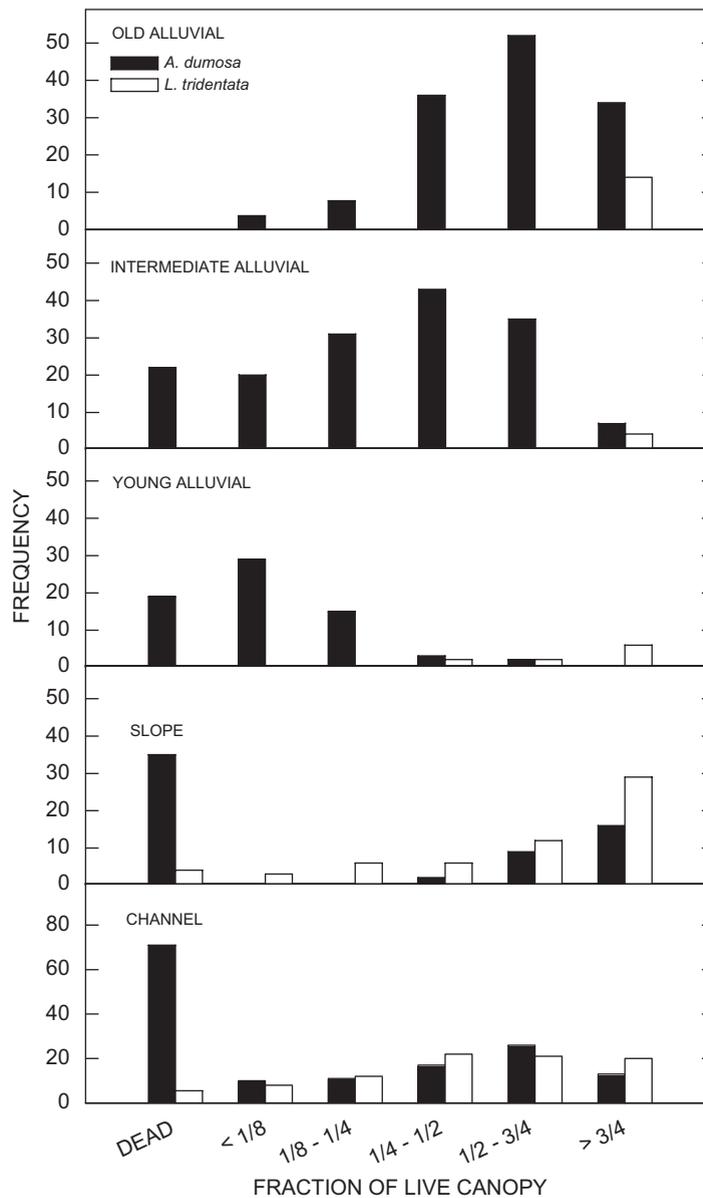


Fig. 4. Frequency distributions of canopy die-back classes of *Ambrosia dumosa* and *Larrea tridentata* growing in five different soil locations.

Table 4

One-way analysis of variance (ANOVA) *F*-test results testing differences in individual plant canopy area between canopy die-back classifications of the drought-deciduous white bursage (*A. dumosa*) and evergreen creosotebush (*L. tridentata*)

Site/species	<i>F</i>	df	<i>p</i>
Old Alluvial/ <i>A. dumosa</i>	0.46	4, 129	0.7662
Int. Alluvial/<i>A. dumosa</i>	2.31	5, 152	0.0468
Young Alluvial/ <i>A. dumosa</i>	0.71	4, 63	0.5881
Slope/<i>A. dumosa</i>	5.21	3, 58	0.0030
Channel/<i>A. dumosa</i>	5.06	5, 142	0.0003
Young Alluvial/ <i>L. tridentata</i>	3.84	2, 8	0.0678
Slope/<i>L. tridentata</i>	4.07	5, 54	0.0033
Channel/<i>L. tridentata</i>	3.26	5, 85	0.0097

F-test results significant at $p \leq 0.05$ are in bold, at $p \leq 0.1$ in italics.

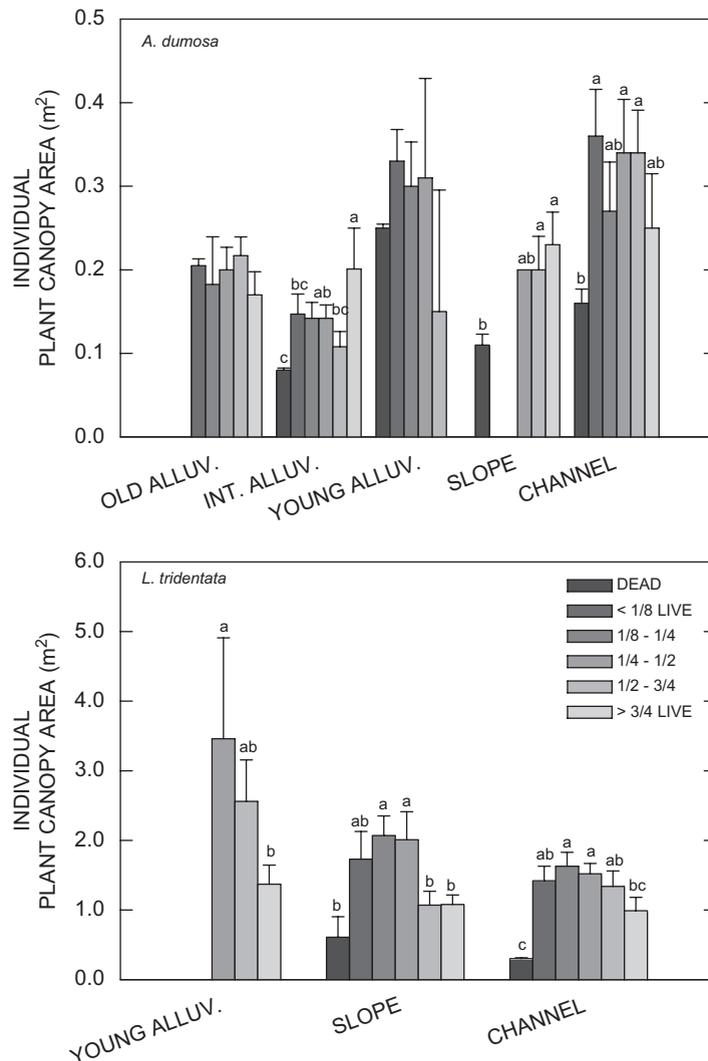


Fig. 5. Size distributions of canopy die-back classes of *Ambrosia dumosa* and *Larrea tridentata* growing in five different soil locations. Letters differ within a site at $p \leq 0.05$ (LSD of ANOVA results).

higher transpiration rates (Smith et al., 1997). These leaf-level characteristics likely require xylem with larger vessel elements, capable of readily delivering soil water (Maherali et al., 2004). However, under water-limited conditions, such xylem structure such is more prone to cavitation (Jacobsen et al., 2007; Pockman and Sperry, 2000), likely leading to higher levels of branch death in *A. dumosa* observed in this study (Fig. 4).

As expected, dead *A. dumosa* and *L. tridentata* tended to be smaller plants (Table 4, Fig. 5). This was particularly evident at Slope and Channel sites, where plant mortality levels were higher (Figs. 1 and 2). These results corroborate long-term studies showing juvenile desert plants are particularly susceptible to drought-induced mortality (Casper, 1996; Miriti, 2006; Miriti et al., 2001, 2007; Toft, 1995). The higher overall mortality at these two sites also suggests that landscape positions that can accumulate run-on may be especially prone to booms and busts in plant establishment and growth. In locations such as the Channel sites, overland flow may dramatically augment incident precipitation in normal to above normal precipitation years (Atchley et al., 1999; Schlesinger and Jones, 1984; Schlesinger et al., 1989). This augmentation could extend seasonal moisture availability, and facilitate plant establishment and extensive canopy development. However, under severe drought conditions, rainfall may not be of sufficient duration or intensity to generate run-off, and incident precipitation would be insufficient to support the plants that had been dependent on runoff. The balance between active absorbing root area and transpiring leaf area developed by these plants under wetter, augmented conditions may make them more susceptible to drought-induced loss of xylem function (Pockman and Sperry, 1997, 2000; Sperry et al., 1998, 2002). Also, most desert shrubs, especially juvenile individuals, have limited carbon reserves, and rely on current carbon-fixation to drive seasonal canopy growth (Smith et al., 1997). Thus, sustained drought could curtail canopy

development to the point that insufficient carbon could be fixed to offset losses stemming from protracted dormancy (Comstock and Ehleringer, 1986; Smith et al., 1997), driving widespread juvenile plant mortality observed at these locations.

Along the PM soil chronosequence, partial canopy die-back and whole-plant mortality was most pronounced at the Young Alluvial site; contrary to our hypothesis that drought effects would be more severe in more well-developed soils at the Intermediate and Old Alluvial site (Figs. 1 and 2). Strong drought effects at the Young Alluvial site may be similar to those postulated above for the run-on accumulating Channel sites. The highly permeable soil may foster extensive plant growth during years of normal or above normal precipitation as indicated by the large size of plants of both species at this site (Fig. 1). However, under strong drought, large plants with extensive root systems and canopies could rapidly exhaust limited soil water reserves, thereby causing considerable branch mortality. This supports findings showing that strong inter- and intra-species competition for water prevails in soils that favor plant growth (Schenk et al., 2003), and support our previous conclusion that plant–plant interactions may influence seasonal ecophysiological performance in weakly developed, sandy-gravelly desert soils (Hamerlynck et al., 2002).

The large *L. tridentata* plants at Young Alluvial site often exhibited ring-like clonal growth forms (McAuliffe et al., 2007; Vasek, 1980), and based on past growth rate estimates, plants at this site may be centuries to possibly millennia old (Hamerlynck et al., 2002), and the large size of *A. dumosa* at this site suggest it may be many decades old (Miriti et al., 2001). A frequent feature of extensive growth and clonal development in desert plants is axis splitting of the root-stock, which maintains favorable root-shoot ratios, water relations and survival of genetic individuals (Jones, 1984; Schenk, 1999). However, axis splitting is a basal process that results in discreet sections of the canopy completely dying, while the surviving portion remains largely unaffected (Jones, 1984). The pattern of branch mortality we observed was distributed distally throughout the plant, and thus does not likely reflect increased levels of active axis splitting.

The strong drought effects in Young Alluvial soils may also reflect the hydrological importance of the occurrence of large stones within the soil. Considerably less mortality (entire or partial) for both species at Intermediate and Old Alluvial sites is in agreement with the unexpectedly high plant water relations and gas exchange rates observed previously at these sites (Hamerlynck et al., 2002). We attributed this strong plant performance to the presence of large stones and cobbles that occur frequently through soil profiles at the Intermediate and Old Alluvial sites (McAuliffe, personal obs.; Hamerlynck et al., 2002). Such stones may act as evaporative barriers and also serve as accumulation points for infiltrating and downward percolating water (Nobel et al., 1992), and soil water modeling suggests they facilitate long-term persistence of moisture at plant rooting depths (Hamerlynck et al., 2002). Heterogeneous distribution of large stones could result in many favorable hydrological micro-sites, thereby buffering drought effects at this site (Figs. 2 and 3). Additionally, the presence of large rocks concentrates soil moisture in the remaining fine soil fraction. Large soil rocks could therefore facilitate wide-spread plant establishment, yet limit rooting volumes and plant growth, leading to the high densities of small plants observed at the Intermediate and Old Alluvial sites (Fig. 3). The lack of such soil heterogeneity in Young Alluvial site soils may therefore have fostered greater plant growth and development of strong root-mediated competitive regimes, leading to lower densities of large plants (Brisson and Reynolds, 1994; Mahall and Callaway, 1992), which may have negatively influenced seasonal plant performance at this site (Hamerlynck et al., 2002), as well as contributing directly to higher levels of canopy die-back observed during extended drought (Figs. 2 and 3).

In summary, we found that canopy die-back and plant mortality in these two Mojave Desert dominants to be soil-specific, and unexpectedly greater in soils that favored extensive plant growth during moist climatic intervals. The changes in leaf area display are likely to be sufficient enough to change site-water balance (Smith et al., 1995), and more likely in a way that favors more extensive water use by the evergreen shrub, *L. tridentata*, which had much lower proportional die-back and mortality responses to the current drought, as has been found at other locations in the Southwest (Miriti et al., 2007). Moreover, this study highlights the importance in soils and topographic position in influencing the ways in which severe drought affects basic desert ecological processes.

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