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William A. S. Paddock III
Department of Plant Biology, Michigan State University, East Lansing

Stephen D. Davis
Division of Natural Science, Pepperdine University, Malibu, California

R. Brandon Pratt
Department of Biology, California State University, Bakersfield

Anna L. Jacobsen
Department of Biology, California State University, Bakersfield

Michael F. Tobin
Department of Biology, California State University, Bakersfield

See next page for additional authors

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FACTORS DETERMINING MORTALITY OF ADULT CHAPARRAL SHRUBS IN AN EXTREME DROUGHT YEAR IN CALIFORNIA

William A. S. Paddock, III,[1] Stephen D. Davis,[2] R. Brandon Pratt,[3] Anna L. Jacobsen,[3] Michael F. Tobin,[3] Jorge López-Portillo,[4] and Frank W. Ewers[5,6]

[1]*Michigan State University, Department of Plant Biology, East Lansing, Michigan 48824;*
[2]*Pepperdine University, Division of Natural Science, Malibu, California 90263;*
[3]*California State University Bakersfield, Department of Biology, Bakersfield, California 93311;*
[4]*Instituto de Ecología, A. C., Red de Ecología Funcional, Xalapa 91070, Veracruz, Mexico;*
[5]*California State Polytechnic University Pomona, Biological Sciences, Pomona, California 91768*
[6]*Corresponding author (fwewers@csupomona.edu)*

ABSTRACT

We measured dieback and mortality in a chaparral shrub community at a chaparral/desert ecotone following four years of below-average rainfall. Ecotones are important systems in which to examine plant and community responses to extreme and prolonged drought conditions and the potential impact of global change on plant distributions and community composition. Following a particularly severe drought year, dieback and mortality were documented for seven co-dominant shrub species. We examined whether mortality was related to species ecology, leaf traits, or water relations. Dieback and mortality were greatest in two non-sprouting species. These species also had high xylem cavitation resistance and low specific leaf area compared to several sprouting species. Among two sprouting congeners, mortality was greater in the more shallowly rooted species, even though this species was more cavitation resistant. Across all species, those that were more resistant to cavitation had greater mortality. Evidently, high resistance to xylem cavitation does not prevent adult plant mortality at chaparral/desert ecotones. A series of extreme drought years could preferentially reduce or eliminate non-sprouting species from mixed chaparral populations, causing a shift in community structure and contributing to desertification.

Key words: cavitation resistance, chaparral, climate change, desert, ecotone, life history type, non-sprouter, sprouter, water potential, water relations.

INTRODUCTON

Ecotones are regions where species and communities are often at the limits of their environmental tolerances making them particularly susceptible to even minor changes in climate. For this reason, it is important to study ecotones in the context of climate change as these regions may serve as early indicators of changes in species or community distributions.

In Southern California the ecotone between desert and chaparral communities is of particular interest. Changes in rainfall and temperature are predicted to impact the chaparral species at this ecotone, perhaps leading to local dieback and extinction of some species. Chaparral refers to the evergreen sclerophyllous shrub vegetation found in southwestern North America and is the most extensive vegetation type in California (Wieslander and Gleason 1954; Hanes 1995). Chaparral is a vegetation type found in one of five Mediterranean-type ecosystems of the world, each of which is characterized by winter rains and rain-free summers, high biodiversity, and risk of desertification.

Chaparral species are often categorized by life history type according to their post-fire regeneration method. After fire, some species sprout from a basal root crown or lignotuber (i.e., ''sprouters''). Other species never sprout after fire but recruit exclusively from seed (i.e., ''non-sprouters''; Keeley and Keeley 1981; Keeley 2000). These species are dependent on fire disturbance to establish seedlings, and recruitment rarely occurs in the absence of fire. Such species persist because of refractory seeds (seeds whose dormancy is hard to break) and

the accumulation of a long-lived seed bank (Keeley 1977; Parker and Kelly 1989). Sprouters and non-sprouters tend to have different seasonal water relations. For example, sprouting chaparral species *Malosma laurina* (Nutt.) Nutt. ex Abrams, *Quercus durata* Jeps., *Rhamnus californica* Eschsch., *Rhus integrifolia* (Nutt.) Benth. & Hook. f. ex W.H.Brewer & S.Watson, and *R. ovata* generally maintain water potentials above −3.0 MPa even when exposed to seasonal drought conditions (Poole and Miller 1975; Davis and Mooney 1986). In contrast, the non-sprouting chaparral species *Arctostaphylos viscida* Parry, *A. glauca*, *Ceanothus crassifolius* Torr., *C. cuneatus* (Hook.) Nutt., *C. greggii*, and *C. megacarpus* Nutt. exhibit much more negative seasonal low water potentials ranging from −6 to −11 MPa depending on the year (Poole and Miller 1975; Parsons et al. 1981; Davis et al. 1999, 2002; Pratt et al. 2007*b*).

In the present study we explored factors responsible for differential dieback and mortality of chaparral shrubs (Table 1) at a desert/chaparral ecotone. This dieback coincided with several years of below-average rainfall between 1998 and 2002, culminating in an extreme drought year in the winter of 2002–2003. We hypothesized that there would be species-specific differences in drought-induced mortality, with non-sprouting species exhibiting greater adult dieback and mortality because (1) non-sprouting species tend to be relatively shallow rooted (Hellmers et al. 1955; Kummerow et al. 1977; Thomas and Davis 1989) and (2) non-sprouting species normally exhibit lower water potentials than sprouting species, a discrepancy

Table 1. Seven chaparral shrubs sampled in this study, with abbreviations used in tables and figures. Ability to sprout following a fire event is based on Hanes (1965), Stone and Juhren (1951), Nixon (2002), Keeley and Zedler (1978), and Keeley (1977).

Species	Species abbreviation	Sprouter
Adenostoma fasciculatum Hook. & Arn.	Af	Yes
Adenostoma sparsifolium Torr.	As	Yes
Arctostaphylos glauca Lindl.	Ag	No
Bernardia myricifolia (Scheele) Benth. & Hook. f.	Bm	?
Ceanothus greggii A.Gray	Cg	No
Quercus cornelius-mulleri Nixon & K.P.Steele	Qc	Yes
Rhus ovata S.Watson	Ro	Yes

that is magnified during extreme drought years (Jacobsen et al. 2007).

Applying the same reasoning to the two sprouting congeners *Adenostoma fasciculatum* and *A. sparsifolium* growing at the same location, we predicted that the more shallowly rooted *A. fasciculatum* would show greater mortality than *A. sparsifolium* which is deeper rooted (Redtfeldt and Davis 1996). Lastly, we hypothesized that for species with high mortality, smaller adults with smaller canopies would be more likely to show mortality than larger adults, since, in even-aged stands, smaller individuals may be more shallowly rooted (Schlesinger et al. 1982).

To take account of the apparently contradictory findings that non-sprouters tend to be more cavitation resistant than sprouters (Jacobsen et al. 2007; Pratt et al. 2008) and that cavitation resistance is often associated with drought tolerance, at least in seedlings, we also examined cavitation resistance and other parameters of water relations in the chaparral species at the ecotone.

MATERIALS AND METHODS

Study Area

The shrub community we examined was located in Riverside County, California, at the dry edge of the local chaparral range, in the rain-shadow of the Santa Rosa Mountains, bordering a Sonoran Desert ecosystem (Table 2). All data were collected from an area of about 4000 ha located in the San Bernardino National Forest in Riverside County, north of Santa Rosa Mountain along State Route 74 (33°35′N 116°27′W), near Pinyon Pines. The community is bounded by desert to the north and east and by forest to the south and west. Further details on the community are given in Paddock (2006).

Characterization of the Drought Period

Climatic data were collected from the National Climatic Data Center's (NCDC) on-line database (NOAA 2005). The data files we obtained from the NCDC contained monthly precipitation from the Anza and Deep Canyon sites (NOAA 2001). The two data collection stations were located about 20 km to the east (Anza 33°33′N, 116°40′W) and about 20 km to the west (Deep Canyon 33°39′N, 116°23′W) of the study area. Precipitation at the study area was estimated as the arithmetic mean of data from the two stations.

Annual precipitation was calculated by summing monthly precipitation from July of one year to June of the next. This is most biologically relevant because this includes all of the rain from one wet season within a data point.

Quantifying Dieback

We defined dieback as the death of leaves and branches without necessarily the loss of whole individuals. Mortality involved death of all the leaves and branches of an individual, as described below. Dieback was quantified among all woody species present at eight sites between April 2003 and September 2004 (Table 2). Sites were chosen to represent the diversity in both community composition and environmental factors such as slope and aspect. Sixty plants were selected within each of seven sites (Sites A–F and H) using a modified wandering quarter method (Catana 1963). At each site, a 30 m base transect was set out perpendicular to the slope of the site. A 90° angle was described using compass bearings so that the apex of the angle fell on the 0 m point of the base transect and the bisector of the angle was pointing up the slope, perpendicular to the base. The closest plant within this 90° angle was selected for data collection; this plant was then used as the apex of the next 90° angle within which the next closest plant would be selected. This process was used to select 15 plants. A total of four such wandering transects were used at each site beginning at 0 m, 10 m, 20 m, and 30 m along the base transect. To allow for intensive sampling of the two co-occurring congeners, *Adenostoma fasciculatum* and *A. sparsifolium*, we used the point quarter sampling method (Cox 1985)

Table 2. Location, elevation, slope, and aspect of eight sampling sites in the chaparral-desert ecotone. Sites are listed in order of increasing distance from the desert side. Species abbreviations are as in Table 1. Species numbers indicate the amount of individuals captured in the dieback survey within a given site.

Site	Latitude (deg N)	Longitude (deg W)	Elevation (m)	Slope (deg)	Aspect (deg)	Species						
						Ag	Cg	Af	As	Bm	Qc	Ro
A	33.604	116.422	1103	12	108	22	-	-	-	28	6	4
B	33.587	116.437	1339	30	250	48	-	-	4	-	7	2
C	33.592	116.444	1265	07	168	5	-	-	-	22	21	4
D	33.568	116.444	1453	26	020	2	41	-	10	-	5	2
E	33.577	116.460	1259	06	035	-	46	1	-	-	7	2
F	33.565	116.477	1502	30	008	-	53	-	1	-	4	2
G	33.574	116.495	1310	03	305	-	13	112	34	-	-	-
H	33.549	116.508	1591	11	225	-	13	29	18	-	-	-

at one of the transects (site G, Table 2), instead of the wandering quarter sampling method described above. Each of 40 random points along a 500 m transect was divided into four quadrats (N, S, E, W) and the closest plant within each quadrat was sampled.

Each plant was identified to species, and measured for height and two perpendicular crown diameters. Plant volume was then calculated as the product of canopy area and height. Each plant was given a dieback score. Recently dead foliage could be distinguished from long-dead plants because, like most chaparral shrubs, these species have tough, sclerophyllous foliage that remains on the stems for a prolonged period after death (Davis et al. 2002). In the present study we found that chaparral plants retained their dead foliage for more than a year. Dieback was visually assessed on a scale from one to five. A value of 1 indicated that the plant had essentially no dead foliage on the branches whereas a score of 5 indicated that the plant had no live foliage.

After the rainy season of 2003–2004, during which the 5-year drought eased, we returned to the area in June 2004 to determine if the plants that had previously scored 5 (i.e., no living foliage) were indeed dead. A sub-sample of 90 individuals that had been scored 5 in 2003 were located and scored for dieback again in 2004.

We used Kruskal-Wallis analysis of variance on ranks (KW) to compare the median dieback score among species, followed by Dunn's multiple comparisons. Only the species with more than seven individuals were included in the analysis. For the three most common species Mann-Whitney U-tests were carried out to compare between the median dimensions of dead (dieback score = 5) vs. alive (dieback scores 1–4) individuals. Before the comparisons, normality and equal variance tests were done for each species.

Xylem Vulnerability to Cavitation

To assess the vulnerability of the xylem to cavitation, stem segments were collected from healthy individuals in August 2003. "Survivor bias" could not be avoided since we could make the physiological measurements only on the surviving plants.

A single stem was taken from each individual sampled. Stems were collected from *Arctostaphylos glauca, Bernardia myricifolia, Quercus cornelius-mulleri,* and *Rhus ovata* at site C, and from *Adenostoma fasciculatum, Adenostoma sparsifolium,* and *Ceanothus greggii* at site H (Table 2). We were unable to sample *B. myricifolia* at the same time as the other species, and this species was sampled later (January 2010) from site C. Six stem samples of each species were collected and analyzed. Each sample came from a stem that had living foliage to ensure that the xylem was conductive.

To avoid the introduction of air embolisms upon harvest, shoots approximately 2 m in length were cut from each plant and double-bagged in heavy plastic bags with moist paper towels to prevent desiccation during transport. For *B. myricifolia,* shorter stems were harvested, but they were cut from plants in the field underwater to prevent the introduction of air into the xylem, and the cut end was kept submerged in water during transport to a laboratory. Plant material was usually processed in the laboratory within 12 hours of collection. In the laboratory the branches were cut to the desired length underwater in preparation for vulnerability analysis by the centrifuge method (Alder et al. 1997). For most species 140-mm segments were used. In the case of *C. greggii,* it was necessary to use 271-mm segments and a larger custom rotor to spin stems. The larger rotor is capable of subjecting longer stems to greater tensions. In all cases the stem segments used were 5–8 mm in diameter. After cutting the samples to the desired length, the ends of each segment were shaved smooth with a razor blade to remove any obstruction to the flow of water.

Cochard et al. (2010) suggested that artifacts were likely when measuring vulnerability to cavitation in species with long vessels using centrifuge techniques. The species we used were all shrubs with relatively short vessels (Hacke et al. 2009). More importantly, we have not found vessel length artifacts with the centrifuge technique used in the present study (Sperry et al. 2012; Jacobsen and Pratt 2012; Tobin et al. in press).

Samples were installed in a tubing manifold, and the xylem was flushed with a 0.01 M pH 2 solution of HCl (or 20 mM KCl for *Bernardia*), which had been degassed and filtered to 0.1 μm, at a pressure of 100 kPa for at least 1 h to remove native embolisms. Following flushing, each stem was placed in another tubing manifold to measure hydraulic conductivity with corrections made for background flow (Stiller and Sperry 1999). Next, the stems were subjected to a tension of −0.5 MPa. Any xylem vessels that cavitate at this very low tension have likely experienced "cavitation fatigue" and thus would not be likely to be conductive in vivo (Hacke and Sperry 2001). Therefore, the hydraulic conductivity measured after the stem had experienced −0.5 MPa was used as the maximum hydraulic conductivity, and any loss in conductivity was divided by that maximum to determine fatigue-corrected percent loss in conductivity (PLC).

Each stem was subjected to alternating cycles of conductivity measurement and centrifuge treatment through a series of increasing tensions (Alder et al. 1997). The tension which caused 50% loss in conductivity (P_{50}) was determined for each sample by fitting the data with a second-order polynomial model and then solving the model for the pressure at 50% loss in conductivity. Comparison of fatigue-corrected P_{50} was performed with ANOVA using log-transformed data and Tukey's test for means separations to control for Type-1 experimental error rate. We used a linear regression model to relate percent mortality with P_{50}. We used an arcsine transformation for normalization of the mortality data.

Specific Leaf Area

In June of 2004, leaves were collected from 12 individuals of each species from sites C and H (Table 2) including the same individuals used for vulnerability analysis and additional plants. All individuals used had mortality scores between 1 and 3. For the broad-leaved species three leaves were collected from each plant. For *Adenostoma fasciculatum* and *A. sparsifolium* 15 leaves were collected due to their small size. All leaves collected had expanded in the previous year, were from sunlit branches, and exhibited no senescence, physical damage, or apparent disease.

The leaves were bagged, immediately placed in a cooler, and stored for less than 48 hours before being processed. In the lab,

the petioles were removed, fresh mass was recorded, and projected area was measured (LI-3100 Leaf Area Meter Li-Cor, Inc., Lincoln, Nebraska). The leaves were dried at 80°C for several 24-hour periods until a repeatable mass was obtained for each sample.

As an estimate of sclerophylly, specific leaf area (SLA) was calculated according to the following equation:

$$SLA = \frac{fresh\ projected\ leaf\ area}{dry\ mass}$$

ANOVA was performed on log_{10}-transformed data.

Stomatal Conductance and Field Water Potential

In August 2004 an LI-1600 Steady State Porometer (Li-Cor, Inc.) was used to measure transpiration rates and stomatal conductance in the same 12 individuals per species for which the SLA was measured. Both in June and August 2004, leaves from the same 12 individuals per species were also used to measure predawn and midday water potential with a pressure chamber (Scholander et al. 1965). Repeated measures ANOVA was performed, and Tukey's test was used to control experimental error ($P < 0.0001$) for means separations.

<div align="center">RESULTS</div>

Precipitation Data

The drought period preceding the observation of dieback was particularly severe. For chaparral communities throughout California, the majority of rainfall occurs in the winter, averaging from 200 to 1000 mm annually (Miller and Hajek 1981). From 1963 to 2003, the average annual rainfall at the study area was calculated (mean of two closest stations) to be 236 mm, which is near the lowest known for chaparral systems (Franklin 1998). The average annual rainfall for the 5-year period from 1998 to 2003 was only 103 mm, less than 44% of the area's 40-year average. The drought was the most severe in the year leading to the dieback. From July 2002 to June 2003 only 73 mm of rain fell (31% of the average), though easing to 143 mm of rain (61% of the average) during the following year from July 2003 to June 2004.

Dieback

Mortality was highest in the three most abundant species, *Adenostoma fasciculatum*, *Arctostaphylos glauca,* and *Ceanothus greggii*. Seven species were observed in sufficient quantities ($N > 7$) to allow analysis of the dieback scores (Fig. 1). There were significant differences among species in this parameter ($H = 224$, $P < 0.001$, 6 d.f.). The two species with the highest median dieback score of 5 were *Arctostaphylos glauca* and *C. greggii*, with a value significantly greater than the rest. The median dieback score of *Adenostoma fasciculatum* was intermediate at 3, and significantly different from the other species. The median dieback score for the other four species was 2 (Fig. 1).

Verification of mortality in 2004 showed that 99% of plants scored as having 100% death of foliage in 2003 (with a dieback score of 5) still had scores of 5 in June of 2004. Ninety individuals that had been given a dieback score of 5 in 2003 were verified; only one (an *Arctostaphylos glauca* individual)
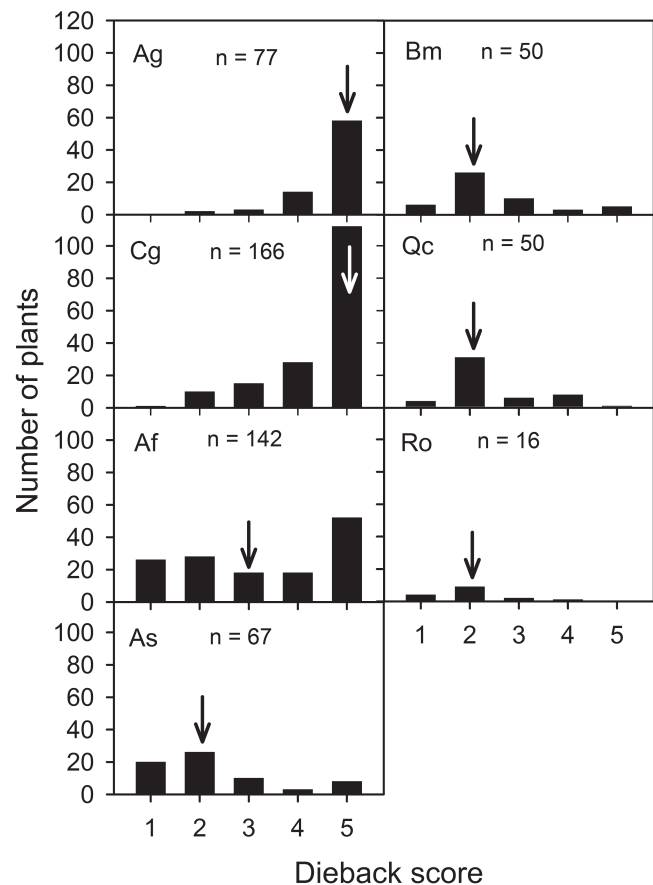

Fig. 1. Dieback score frequency distribution for the seven most abundant species in 2003. Dieback scores ranged from 1 (no dead foliage) to 5 (all foliage dead). Arrows indicated the median dieback score. Species abbreviations as in Table 1.

was observed to have any living foliage in 2004. Thus we considered a score of 5 to represent mortality.

The living plants tended to be larger than the dead ones within a species. Within the three species with moderate or high mortality, there were significant differences when comparing the median dimensions of dead (dieback score of 5) versus living plants (dieback score = 1–4) using Mann-Whitney Rank Sum tests ($P < 0.001$; Table 3). With the exception of the median height in *Arctostaphylos glauca* and *C. greggii*, which was statistically similar between dead and live plants ($P > 0.3$), all other comparisons indicated a significantly lower median height, canopy mean diameter and canopy volume of the dead individuals when compared to living individuals ($P < 0.001$, Table 3).

Xylem Vulnerability

Species that exhibited high mortality had xylem that was extremely cavitation resistant. Based upon the mean ($\pm$SE) pressure potentials resulting in 50% loss of conductivity (P_{50}), *Arctostaphylos glauca* ($P_{50} = -9.22 \pm 0.76$ MPa) and *C. greggii* (-7.01 ± 0.60 MPa) had more negative P_{50} values than species that exhibited lower levels of mortality. Of the congeners *Adenostoma sparsifolium* and *A. fasciculatum*, the former had significantly lower dieback and mortality though slightly more vulnerable xylem than the latter (Fig. 2, Table 4).

Table 3. The dimensions of living and dead plants for the three most abundant species in the survey, including median height, median canopy diameter, and median canopy volume. Numbers within parentheses are 25% and 75% quartiles. * = significant difference between living and dead plants ($P < 0.001$).

Species	Condition	n	Height (m)	Diameter (m)	Volume (m^3)
Adenostoma fasciculatum	living	90	1.4 (1.1–1.6)*	0.8 (0.5–1.3)*	0.73 (0.27–1.9)*
	dead	52	1.0 (0.8–1.2)	0.5 (0.3–0.8)	0.18 (0.01–0.5)
Arctostaphylos glauca	living	19	1.4 (1.1–1.5)	3.2 (1.5–3.5)*	10.7 (5.5–14.8)*
	dead	58	1.2 (1.0–1.6)	2.0 (1.3–2.5)	3.9 (1.8–6.2)
Ceanothus greggii	living	54	1.5 (1.2–1.6)	1.0 (0.8–1.3)*	1.1 (0.5–2.2)*
	dead	112	1.4 (1.1–1.6)	0.8 (0.6–1.1)	0.6 (0.3–1.2)

The two species with the most vulnerable xylem were *Q. cornelius-mulleri* ($P_{50} = -3.17 \pm 0.28$ MPa) and *R. ovata* (-2.36 ± 0.32 MPa), both of which had very low mortality (Fig. 2, Table 4). There was a significant inverse linear regression between species mortality and P_{50} values, that is, species with more negative P_{50} values tended to have greater mortality (Fig. 3).

Bernardia myricifolia was an outlier (open symbols, Fig. 3), since it showed low mortality combined with xylem that was relatively resistant to cavitation. We could not find reports of whether this species is a sprouter or a non-sprouter (Table 1), perhaps because this is mostly a desert plant where fires are not as common as in chaparral. This species also differed from the others in this study by being facultatively deciduous in extreme drought years.

Specific Leaf Area

Specific leaf area (SLA) was low in the high-mortality species but no significant difference in SLA ($P = 1.0$) was detected between *R. ovata* (low mortality) and *Arctostaphylos glauca* (high mortality). When comparing the two congeners, SLA was significantly lower in the moderate-dieback *Adenostoma fasciculatum* than the low-dieback *A. sparsifolium* (Table 4).

Fig. 2. Vulnerability curves for seven species showing mean ±SE percent loss of conductivity (PLC) as a function of xylem pressure potential. Species abbreviations as in Table 1.

Field Water Potentials and Stomatal Conductance

Dry-season water potentials were significantly more negative in *Adenostoma fasciculatum*, *B. myricifolia* and *C. greggii* than in the other sampled species (Table 4). Similarly, these three species also had the largest seasonal drop in water potential when comparing June and August 2004 predawn values. The dry season $\Delta\Psi$ for those three species were 3.5, 2.1, and 2.7 MPa, respectively (data not shown). In August 2004 the levels of stomatal conductance were fairly low for all seven species and were not related to the P_{50} or to water potentials across species (Table 4).

DISCUSSION

The weather data from sites adjacent to the study area indicated that a particularly severe drought period preceded the dieback and mortality of plants at the chaparral-desert ecotone. We believe that adult dieback and mortality observed in some of the species in 2003 and 2004 was due either to the particularly intense drought of 2002, or to the longer-term drought of about five years.

The results supported our hypothesis that non-sprouting species are more vulnerable to severe drought than sprouting species, despite the fact that their xylem is very resistant to cavitation. Measurements of ground water depth from wells less than 5 km from the study site show that ground water fluctuates between 6 m and 15 m below the surface (California Department of Water Resources 2006). Considering differential rooting depths observed in sprouting and non-sprouting chaparral species by Hellmers et al. (1955) and Thomas and Davis (1989), and given the higher field water potentials we found for sprouters, it is reasonable to hypothesize that deep-rooted sprouting species were accessing ground water, while the shallow-rooted non-sprouters were not, leading to dieback and mortality of non-sprouters. *Arctostaphylos glauca* is a very shallow rooted species, with roots occurring predominantly at 0.3 m depth (Miller and Ng 1977) and always less than 1 m deep (Hellmers et al. 1955). Like *Arctostaphylos glauca*, *C. greggii* is a shallow-rooted species with roots growing less than 1 m deep (Hellmers et al. 1955; Miller and Ng 1977). The latter species experienced the lowest pressure potentials of all species in August 2004.

The sprouting species in the present study tended to have higher SLA values and lower resistance to xylem cavitation, yet they had very low dieback and low mortality. Sprouting species have an older root system than non-sprouters that must establish an entire new root system following a wildfire event.
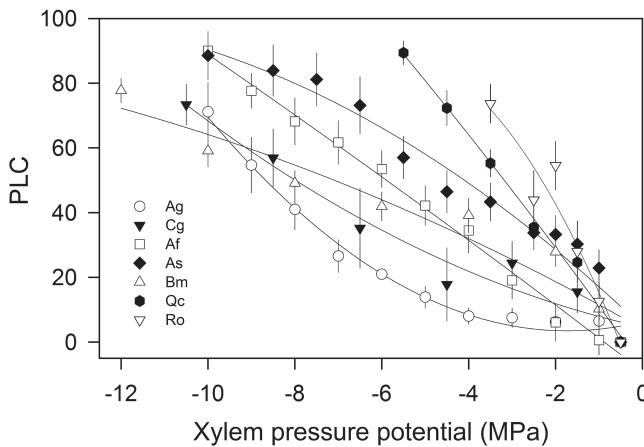
Table 4. Species results for mortality, plant height, canopy diameter, specific leaf area, August 2004 measurements of stomatal conductance, predawn and midday water potential (ψ), and the fatigue-corrected P_{50} (xylem tension at 50% loss conductivity). Letters (a, b, c, d) indicate significant differences within a column. Species are listed in order from highest to lowest mortality. Species abbreviations are as in Table 1.

Species	Mortality (%)	Height (m)	Canopy diameter (m)	Specific leaf area ($cm^2\,g^{-1}$)	Stomatal conductance ($mmol\,m^{-2}\,s^{-1}$)	Predawn ψ (MPa)	Midday ψ (MPa)	P_{50} (MPa)
Ag	75	1.29 ± 0.03 c	2.3 ± 0.13 c	31.2 ± 1.4 b	17.48 ± 1.74 cd	-3.15 ± 0.23 a	-5.03 ± 0.22 b	-9.22 ± 0.76 a
Cg	67	1.40 ± 0.03 bc	0.9 ± 0.03 a	21 ± 0.6 a	2.73 ± 0.31 a	-6.12 ± 0.23 c	-8.21 ± 0.22 c	-7.01 ± 0.6 ab
Af	37	1.75 ± 0.07 cd	0.8 ± 0.04 a	40.9 ± 1.4 c	7.36 ± 1.11 b	-4.76 ± 0.23 b	-7.52 ± 0.22 c	-5.85 ± 0.58 ab
As	12	2.21 ± 0.12 a	1.8 ± 0.11 b	62.6 ± 3.2 d	7.33 ± 1.56 b	-3.02 ± 0.23 a	-4.78 ± 0.22 b	-4.68 ± 0.99 bc
Bm	10	1.03 ± 0.09 d	1.0 ± 0.09 a	61.2 ± 2.5 d	17.59 ± 2.77 cd	-4.91 ± 0.22 b	-7.50 ± 0.21 c	-6.13 ± 0.95 ab
Qc	2	2.17 ± 0.09 ab	2.7 ± 0.19 d	43.9 ± 1.3 c	32.19 ± 2.20 d	-2.79 ± 0.23 a	-4.90 ± 0.22 b	-3.17 ± 0.28 cd
Ro	0	1.94 ± 0.21 ab	3.0 ± 0.43 d	31 ± 1.0 b	13.64 ± 3.20 bc	-2.3 ± 0.23 a	-3.00 ± 0.22 a	-2.36 ± 0.32 d

Thus, well established adult sprouters may have an advantage during extreme drought events (Hellmers et al. 1955; Krause and Kummerow 1977; Davis 1989). In contrast, high resistance to cavitation and low SLA of non-sprouters could have an advantage at the seedling establishment stage, when rooting depths and access to soil moisture are limited and similar across life history types (Pratt et al. 2008, 2010).

The present study is consistent with results of Horton and Kraebel (1955) and Parsons et al. (1981) with regard to higher mortality of non-sprouting species than sprouting species in Southern California following severe drought periods. Horton and Kraebel (1955) tracked vegetation for a 25-year period. For sprouting species, there was zero mortality for the duration of the study. In contrast, the non-sprouting species showed significant mortality of adult plants corresponding to a severe drought in 1947–1950. Similarly, Parsons et al. (1981) found high dieback and some mortality for non-sprouting *Arctostaphylos viscida* in California following the severe drought of 1975–1977, while the surrounding sprouting chaparral species showed no dieback.

In the present study the mortality in *Adenostoma fasciculatum* and *C. greggii* may have been due to catastrophic dysfunction of the xylem (Tyree and Sperry 1989; Tyree and Ewers 1991; Rood et al. 2000; Davis et al. 2002), given that

Fig. 3. Species mortality as a function of the pressure potential at 50% loss of xylem conductivity (P_{50}). Solid symbols are for evergreen species, the open symbol is for the drought-deciduous species *Bernardia myricifolia*.

their seasonal low water potentials in 2004 were considerably lower than the P_{50} values. The hydraulic safety margin (difference between dry season predawn water potential and the P_{50}), which was only 0.89 and 1.09 MPa in these two species in 2004, may have been eroded in 2003, which was an even more severe drought year.

In contrast to the other high-dieback species, the mortality in *Arctostaphylos glauca* may not have been due to xylem dysfunction, given the large safety margin in that species in 2004 (6.07 MPa), along with the modest dry-season decline in water potential (0.77 MPa). McDowell et al. (2008) predicted that during severe drought "isohydric" species (species maintaining a constant water potential) would show mortality first due to carbon starvation (lack of stored carbohydrate) and associated insect and pathogen attacks, as observed in piñon-juniper woodland (West et al. 2008). Isohydric species maintain higher water potentials through stomatal control (Tardieu and Simonneau 1998). However, carbon starvation seems an unlikely cause of mortality in *Arctostaphylos glauca* because it is not isohydric by most standards. Our results are consistent with those of Poole and Miller (1975) who observed that *Arctostaphylos glauca* can maintain fairly high stomatal conductance even while xylem pressure potentials get quite low (i.e., to -5.5 MPa). Perhaps the only survivors of this species were on relatively favorable microsites in the 2004 data; our results may show a "survivor bias" in this case. Since then, for this species at other sites, we have found lower minimum field water potentials (-6.7 MPa in 2010) than in 2004.

Results from the co-occurring congeners *Adenostoma fasciculatum* and *A. sparsifolium* are a particularly informative contrast. Consistent with previous reports, *A. fasciculatum* was more resistant to xylem cavitation and had lower SLA than *A. sparsifolium*. Despite those apparent advantages, *A. fasciculatum* showed more dieback and greater mortality than its congener. This high mortality was likely due to the more highly negative field water potentials associated with the shallower root system in *A. fasciculatum* (Redtfeldt and Davis 1996).

In the present study, species with lower field water potentials, greater resistance to cavitation, and lower SLA were more vulnerable to drought. The exception was *B. myricifolia*, but we discovered that in very dry years this desert species is drought deciduous, giving it another means to cope with low soil water potentials. This species more commonly inhabits desert communities than chaparral ones (Hickman 1993), and in our study it occurred only at the low elevation
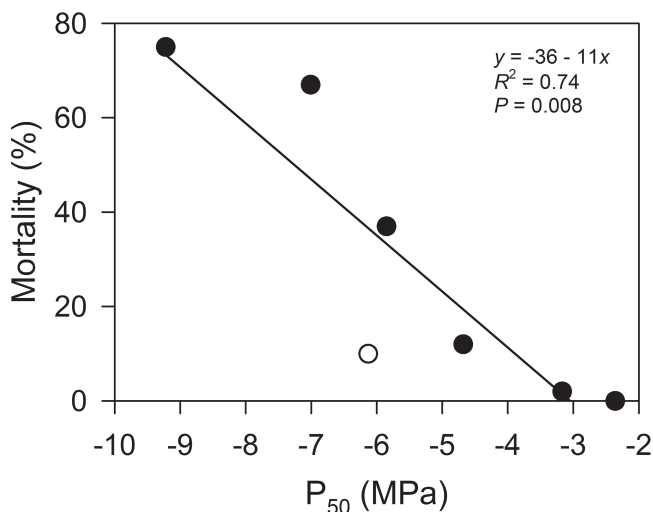
sites close to the desert side of the ecotone. In contrast, the shrubs that commonly occur in chaparral communities are strictly evergreen.

The inverse relation between mortality and plant size in the three most abundant species may be due to differences in rooting depth and/or differences in water storage capacity. Larger plants may have better-established root systems. Schlesinger et al. (1982) found for the non-sprouter *Ceanothus megacarpus* that in even-aged stands the smaller individuals showed lower water potentials and suffered greater mortality. They attributed this to a shallower rooting depth. Further, in species with low seasonal water potential, there seems to be little xylem capacitance (water storage) to buffer drops in water potential under extreme conditions (Pratt et al. 2007*a*; Meinzer et al. 2009). Perhaps greater plant size can ameliorate limited shoot capacitance.

Rhus ovata and *Q. cornelius-mulleri* were the most isohydric species at our study area and exhibited a fairly tight correlation between leaf stomatal behavior and stem xylem resistance to cavitation. *Rhus* and *Quercus* harbor some of the deepest-rooted species ever excavated in chaparral (Hellmers et al. 1955; Thomas and Davis 1989). Poole and Miller (1975) showed that stomatal closure occurred quickly in *R. ovata,* before xylem pressure potentials reach low values (i.e., -3 MPa), further suggesting it is rather isohydric for a chaparral plant. *Rhus ovata* and *Q. cornelius-mulleri* did not experience great stress in terms of lower water potentials at the end of the summer drought in 2004, suggesting that they would not need highly resistant xylem in order to survive drought. This contrasts with proposed carbon-starvation models of plant mortality (McDowell et al. 2008) and suggests that, even following long periods of drought, carbon starvation may be unlikely for some species.

The rather counter-intuitive correlation between resistance to xylem cavitation and adult dieback and mortality during extreme droughts periods is not unique to the present study. Rice et al. (2004) reported that during the extreme 1992–1997 El Niño drought period in Queensland, Australia, tree species with greater resistance to xylem cavitation showed the most dieback, which they attributed to shallower root systems. In response to a record drought in 2007 in central North Carolina, USA, tree species with the greatest resistance to cavitation showed the greatest canopy dieback (Hoffmann et al. 2011), which the authors attributed both to greater leaf retention and shallower root systems in the cavitation-resistant species. Similarly, Maseda and Fernández (2006) and Miranda et al. (2010) reported that in addition to resistance to xylem cavitation and stomatal conductance, other factors such as root-to-shoot ratio and leaf abscission patterns may be critical to survival of the hydraulic system.

Climate change effects may be particularly acute in southern California and other Mediterranean-type ecosystems, which have been identified as worldwide global change "hot spots" (Kelly and Goulden 2008; Kerr 2008). Desert and dry shrublands are projected to have among the most rapid increases in mean temperature (Loarie et al. 2009). Based on recent climate models, it is possible that the climate in the California chaparral will become drier, and it is especially likely that rainfall will become less consistent from year to year (Smith et al. 2001). The predictability of rainfall may be of particular importance to chaparral species since, unlike many coastal sage and desert plants, chaparral shrubs generally do not have the ability to shed leaves in response to drought, nor the ability to store large amounts of water in stems or leaves. As a result, some species may shift their average elevational range upward, a trend reported for many plants in the Santa Rosa Mountains (Kelly and Goulden 2008) and in west Europe (Lenoir et al. 2008). Non-sprouting chaparral species might experience widespread mortality and potentially be locally extirpated at the desert ecotones.

CONCLUSIONS

High resistance to xylem cavitation did not prevent adult plant mortality at a chaparral/desert ecotone. Plants with more extensive rooting systems, such as resprouting chaparral shrubs, appear to be best equipped to tolerate successive severe drought years. In contrast, a series of extreme drought years could reduce or eliminate populations of shallow rooted, non-sprouting chaparral species, contributing to shifts in plant community structure and desertification.

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