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ADULT MORTALITY OF CHAPARRAL SHRUBS
FOLLOWING SEVERE DROUGHT

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WILLIAM ALBERTSON STEBBINS PADDOCK III

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ADULT MORTALITY OF CHAPARRAL SHRUBS FOLLOWING SEVERE DROUGHT

By

William Albertson Stebbins Paddock III

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ABSTRACT

ADULT MORTALITY OF CHAPARRAL SHRUBS FOLLOWING SEVERE DROUGHT

By

William Albertson Stebbins Paddock III

While drought is an annual event in chaparral systems, adult mortality of the woody shrubs is extremely rare. We examined a chaparral shrub community that was at an ecotone with a desert system and that had experienced widespread dieback following a severe 5-year drought. The initial aim of the study was to quantify patterns of dieback, detect whole plant mortality, and make comparisons of dieback among seven co-dominant evergreen sclerophyllous species. Since mortality did occur, and varied dramatically among species, we attempted to relate the mortality to post fire regeneration strategy and to various physiological parameters such as xylem resistance to cavitation, specific leaf area, predawn and midday xylem pressure potential and leaf stomatal conductance, and transpiration rate. As expected, no general relationship between water stress and mortality was observed. Contrary to predictions, mortality was significantly higher in the two nonsprouting species, which had the most cavitation-resistant xylem and lowest specific leaf area. An explanation for the surprising relationship between mortality and water stress resistance is offered, based on rooting depth. Deep rooted species appear to avoid water stress, possibly by accessing deep water resources available even during the prolonged drought. Shallow rooted species (with roots < 1 m deep) are denied this resource so they must tolerate water stress during annual summer droughts. They were apparently unable to do so during the severe 4-year drought from 1998 to 2002.

DEDICATION

This work is dedicated to everyone that made it possible, from friends and family to colleagues and mentors. I am fortunate to have been surrounded by so many great people. Most of all I dedicate this to my wife, Carrie Tansy, who makes so much possible for me.

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INTRODUCTION

The observation of widespread adult mortality in a community of chaparral shrubs is a rare event. A recent observation of such an event by Stephen D. Davis (Pepperdine University, pers. comm., 2003), following a prolonged severe drought, provided a special opportunity to observe and measure plant responses to water limitation. Most chaparral communities experience annual summer drought punctuated by winter rain; however, the particular community we studied was at an ecotone with desert communities and thus appears to have been particularly responsive to regional decreases in precipitation. In this study, we looked for physiological characteristics that may relate to patterns in the mortality of the woody shrubs in the community.

The Chaparral

"Chaparral" refers to the evergreen sclerophyllous shrub vegetation found in southwestern North America. The chaparral is the most extensive vegetation type in California, dominating the foothills from the Sierra Nevada to the Pacific Ocean (Wieslander and Gleason, 1954). These shrublands form a nearly continuous cover of shrubs, often of similar height (i.e., 1.5-2.0 m) and with intertwining branches (Hanes, 1995).

While physiognomy is relatively consistent throughout the region, there is a great amount of species diversity. More than 100 evergreen shrub species are found in the chaparral, only some of which are widespread in distribution (Keeley and Keeley, 1988; Keeley, 2000). Local communities typically have multiple co-occurring species. There are several factors that are known to affect local species composition, including moisture, elevation, latitude, slope, aspect, fire history, and substrate (Hanes, 1995; Keeley, 2000).

The climate in this region is a key factor in the ecology of the chaparral. The chaparral occurs in a region of Mediterranean-type climate with cool, moist winters and hot, dry summers. In the winter (November to April) the chaparral receives limited rainfall (i.e., 200-1000 mm), which often falls in a few intense storms (Miller and Hajek 1981). Because winter rainfall typically occurs irregularly, there may be prolonged dry periods even in the wet season (Keeley, 2000). There is usually no rain in the summers, creating extremely dry conditions and resulting in annual drought. Hot, dry winds in the late summer and early autumn add to the severity of the drought stress of the shrubs (Hanes, 1995). The dry conditions of the vegetation in the summer, and the density of shrubs which create large areas of contiguous fuel, provide ideal conditions for propagation of wild fire.

Fire frequency in the chaparral averages about once every 20 to 30 years, although historically fire may have occurred less frequently (Keeley, 2000). Human activity is the primary cause of present-day wildfires (Keeley, 2000); historically, lightning strikes were the natural sources of fire ignition in the region. Chaparral fires typically kill all aboveground biomass. The rate of shrub recovery varies with patterns of precipitation, elevation, slope, aspect, and degree of coastal influence (Keeley and Keeley, 1981; Hanes, 1995). Communities tend to return rapidly to their pre-fire composition, illustrating the resilience of chaparral to fire disturbance (Keeley, 1986; Keeley, 2000).

Chaparral species are often categorized by life history strategy according to their post fire regeneration method. After fire, some species resprout from a basal root burl (i.e., "sprouters"). The seeds of these species are typically short-lived and germinate readily with adequate moisture, but are killed in the intense heat of a fire. Thus, these species fail to establish seedlings after a fire but persist at a site because individuals survive fire events (Keeley, 1997; Keeley, 2000). Other species recruit from seed following fire (i.e., "non-sprouters") (Keeley and Keeley, 1988; Keeley, 2000). These species are dependent on the fire disturbance to establish seedlings; recruitment is almost non-existent in the absence of fire. Individuals do not survive fire events but species persist at a site because of the existence of a long-lived seed bank (Keeley, 1977; Parker and Kelly, 1989). Germination of these species is triggered by intense heat or by chemical stimulus from charred wood or smoke (Keeley, 2000). A third, intermediate, life history type has been termed "facultative sprouter" (Keeley and Keeley, 1988; Keeley, 2000). These species use a combination of both sprouting and seed germination. These species produce fire-resistant seeds but also have the capacity to resprout from a basal burl (Keeley, 1986).

These patterns of post-fire regeneration result in what Hanes (1971) termed "autosuccession" because with time a post-fire chaparral stand essentially regenerates itself with much the same composition that was present pre-fire. The succession pattern in the chaparral after fire is unusual compared to most plant communities; following fire disturbance, the chaparral community does not return entirely to earlier seral stages (Hanes, 1971). Although some of the same individual plants are present following fire, other species may be present only temporarily following fire in the chaparral. In the first year after fire, there is an abundant growth of herbaceous and suffrutescent vegetation, often comprised of annuals. Many of these species are short lived, and by the third or fourth year woody shrubs commonly dominate the site (Keeley, 2000). Further, many shrub species are present on recently burned sites but are not found in mature chaparral stands. These pioneer species may dominate burned sites several years after a fire, but will die out gradually as the stand ages (Hanes, 1995). Hanes refers to the great bulk of California chaparral as being in some stage of secondary succession; an apparently mature, stable community is actually part of a cycle between stand regeneration from seed and resprouts punctuated by destruction due to episodic fire.

From a biogeographical perspective, it is interesting to note that the dominant woody genera of the California chaparral (i.e., *Adenostoma, Arctostaphylos, Ceanothus, Heteromeles,* and *Rhus*) are absent from other regions having a similar Mediterranean-type climate (Hanes, 1995). Axelrod (1958) concluded that the entire California chaparral evolved in place. Keeley (2000) and Axelrod (1989) reviewed the evolutionary history of the chaparral shrub community and described several key environmental factors driving the evolution of the system including topography, drought, edaphic factors, and fire. While both sprouting and non-sprouting species are successful in chaparral in the present day, according to Wells (1969) the sprouting strategy is ancestral while the nonsprouting strategy is the derived trait. Axelrod (1989) proposed that fire was important in driving speciation in the nonsprouting species, which are common in the genera *Arctostaphylos* and *Ceanothus.*

In addition to evolutionary implications, post fire regeneration strategy appears to have associations with certain morphological characteristics. Sprouters (i.e., those that regenerate from a root burl) tend to be more deeply rooted, whereas the non-sprouting species tend to have more shallow root systems (Hellmers et al., 1955). Conversely, the leaves of all chaparral shrubs are generally sclerophyllous, meaning "hard-leaved" (Schimper, 1903), and having low specific leaf area (Fahn and Cutler, 1992). Furthermore, many additional xeromorphic traits are seen in various chaparral species, including sunken stomata, waxy cuticle, resistance to xylem cavitation, and dense xylem (Krause and Kummerow, 1977; Blake-Jacobson, 1985; Langan et al., 1997; Ackerly et al., 2002).

One final feature of chaparral vegetation is that, outside of fire events, adult mortality is uncommon. In an extensive study of chaparral succession Hanes (1971) sampled chaparral sites with costal and desert exposure in the San Gabriel and San Bernardino mountains. Hanes reported the percentage of individuals that were dead, in coastal stands of 4 age classes. Stands growing for 2-8, 9-21, 22-40, and over 40 years since fire contained dead individuals representing 14%, 8%, 15%, and over 25% of the communities, respectively. Hanes reported that while the desert communities were less dense than the costal chaparral, desert stands contained smaller proportions of dead individuals than similarly aged coastal chaparral. Compared to the rate of mortality in adults, the regular summer drought in chaparral causes widespread mortality in seedlings. Frazer and Davis (1988) reported mortality rates of 99.9% and 46% in *Malosma laurina* and *Ceanothus megacarpus*, respectively, during the first summer drought after germination. However, while there is evidence of drought-induced branch dieback in adults (Davis et al., 2002); we are unaware of documentation of widespread whole-plant mortality in adult chaparral shrubs following drought.

The Study Site

This study involved a community of chaparral shrubs located in Riverside County, CA, near Pinyon Pines (Figure 1). The soils throughout the site are of the Trigo family with rock outcrops common. The Trigo family soils are "loamy, mixed, nonacid, thermic, shallow Typic Xerothents" (USDA, 2006). The site is particularly useful for the study of water stress because it is located at the dry edge of the local chaparral range. The area has been described by Hanes (1995) as desert chaparral. This indicates that the plants are at the edge of their physiological tolerance for water stress. For chaparral communities throughout California, the majority of rainfall occurs in the winter and is limited, averaging from 200 to 1000 mm annually (Miller and Hajek, 1981). From 1963 to 2003, the average annual rainfall at our study site was 236mm, which is near the lowest known for chaparral systems (NOAA, 2005).

Severe Drought

Based upon data collected at two weather stations in close proximity to the study site, the area experienced a severe multiyear drought beginning in 1998. During this time, drought was occurring throughout the southwestern United States. From 1998 to 2002 the average annual rainfall at the study site was only 103mm (NOAA, 2005). The drought culminated during the 2001-2002 rainy season when only 73mm of rain fell (NOAA, 2005). No drought of this duration and magnitude had occurred in the previous 30 years (NOAA, 2005). This drought was followed by the rare observation of widespread dieback in the adult shrubs around the study site, providing a special opportunity to observe species differences in adult mortality.

Research Objectives

Our first objective was to quantify dieback and determine if adults were experiencing whole plant mortality. We wanted to determine: 1) if plants were only experiencing partial dieback of branches or if whole individuals were being killed following the drought event, 2) if the frequency of dieback was different among the co-dominant shrub species of the area, and 3) if certain physiological parameters associated with water stress resistance, namely xylem vulnerability to cavitation and specific leaf area, were associated with the patterns of mortality among species.

Our second objective was to determine if the life history strategy of these species was related to the extent of drought-induced dieback experienced. Since differences in water stress resistance have been associated with post fire regeneration strategy, we were interested in determining if there was an association between life history strategy and the dieback observed.

Our third objective was to determine if particular measures of water stress were associated with the patterns of mortality among species. We used xylem pressure potential, stomatal conductance, and transpiration rates to characterize the water stress that species were experiencing.

Hypotheses

Based on the widespread occurrence and severe nature of the dieback we initially observed, we hypothesized that we would find whole plant death for some individuals in the community. We predicted that there would be species differences in this drought induced mortality based on water stress resistance. We reasoned that species with low xylem vulnerability (i.e., high resistance) to cavitation and low specific leaf area (i.e., thick leathery leaves) should be more resistant to water stress and should thus exhibit low mortality.

Furthermore, we predicted that there would be differences in species' mortality based on life history type; nonsprouting chaparral species tend to be more resistant to water stress (Davis, 1989) and thus should experience less dieback and mortality following drought.

Finally, we predicted that the water stress that species experienced might be a poor predictor of mortality following extreme drought since some species are known to be more resistant to water stress (e.g., can tolerate more negative xylem pressure potentials) than others (Blake-Jacobson, 1985).

MATERIALS AND METHODS

The Study Site

The widespread shrub mortality in this community was first recognized by Stephen D. Davis (Pepperdine University, pers. comm., 2003). Seven sites were selected within the community to capture the variation in slope, aspect, and altitude of the area. All data were collected from a community of chaparral shrubs of about 4000 ha located in the San Bernardino National Forest in Riverside County, CA, USA, located north of Santa Rosa Mountain along State Route 74 (N33°35' W116°27'), near Pinyon Pines (Figure 1). The community is bounded by desert to the north and east, by forest to the south and west, and is interspersed with Pinyon-Juniper woodland. Elevations of the study sites ranged from 1100 m in the northeast to 1600 m in the southwest.

Quantifying Dieback

The community was sampled between April of 2003 and September of 2004. To quantify differences in dieback among all woody species present, seven sites (Table 1) were chosen to represent the diversity in both community composition and environmental factors such as slope and aspect (Figure 1). Sixty plants were selected within each site using a modified wandering quarter method (Catana, Jr., 1963). This method provides an objective way to select plants and allows estimation of population density. 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 was used at each site beginning at 0 m, 10 m, 20 m, and 30 m along the base transect. This sampling identified seven co-dominant shrub species, which are listed in Table 2.

Each plant was identified to species; height and two perpendicular crown diameters were measured. The two crown diameters were used to calculate the crown area by estimating it as an ellipse. The distance between the center of each plant and the previous one was recorded and used to estimate density. Finally, 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 which remains on the stems for a prolonged period after death. Dieback was assessed visually on a scale from one to five. A value of one indicated that the plant had essentially no dead foliage on the branches whereas a five indicated that the plant had essentially no live foliage (and typically much dead foliage).

Differences in dieback among species were determined with pairwise comparisons using Cochran-Mantel-Haenszel Statistics, controlling for differences among sites. Within each species logistic regression was used to determine if plant height, crown size, or distance from adjacent plants were correlated with mortality (i.e., a score of 5). Forward selection was used to determine which parameters contributed significantly to the logistic regression.

After the rainy season of 2003-2004, during which the 5-year drought eased somewhat, we returned to the site in June 2004 to determine if the plants that had previously scored 5 (i.e., no living foliage) were able to recover and produce any functional photosynthetic tissue. A sub-sample of individuals that had been scored 5 was located using GPS and markers left at the site in 2003. Once located, each plant was scored for dieback again and a photograph was taken.

Xylem Vulnerability to Cavitation

To assess the vulnerability of the xylem to cavitation for each species, stem segments were collected from healthy individuals at the site in August of 2003. A single stem was taken from each individual sampled. Because it was not possible to locate all seven species in one location, stems were collected from sites 4 and 7 (Figure 1). At site 4, samples of *Bernardia incana*, *Quercus cornelius-mulleri*, *Rhus ovata*, and *Arctostaphylos glauca* were collected. At site 7, samples of *Adenostoma fasciculatum*, *Adenostoma sparsifolium*, and *Ceanothus greggii* were collected. Six stem samples of each species were collected and analyzed. Samples were free of side branches and foliage and were selected to be as straight as possible. Each sample came from a stem that supplied living foliage to indicate that the xylem was conductive. The presence of conductive xylem was later verified by a lack of discolored xylem tissue in the samples.

To avoid the introduction of air embolisms into the xylem of the desired segment, shoots approximately 2 m in length were cut from each plant and double-bagged in heavy plastic bags with moist paper towel to prevent desiccation during transport. 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. The xylem of this species is very resistant to cavitation and the centrifuge 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.

Rubber gaskets were placed on the ends of each stem sample and the samples were then installed in a tubing manifold. The xylem was flushed with a 0.01 M solution of HCl, which had been degassed and filtered to 0.1 μm, at a pressure of 100 kPa for at least 1 h to remove any native embolisms. Following flushing, each stem was placed in another tubing manifold to measure hydraulic conductivity (k_h=mass flow rate per pressure gradient, in $m^4mPa^{-1}s^{-1}$) (Pockman and Sperry, 2000). Gravity was used to create a pressure of approximately 2 kPa (4 kPa for *A. glauca* and *A. sparsifolium*) on one side of the stem sample, which was sufficiently small to avoid displacing embolisms during conductivity measurement. The mass of water leaving the other side of the sample was measured on an electronic balance for a period of 60 s and an average flow rate was calculated. In addition, flow rates were measured with the stem in the apparatus, but before and after pressure was applied, so any background flow could be eliminated from the measure of flow through the sample (Stiller and Sperry, 1999).

After the initial measurement of hydraulic conductivity the stems were spun in a centrifuge to exert tension on the water column in the xylem. The stems were placed in a specialized rotor that allowed the cut ends of the stems to be submerged in water as the tension was applied (Figure 2). By controlling the speed of rotation the tension on the xylem water can be carefully controlled (Alder et al., 1997). Initially 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 never be conductive *in vivo* (Hacke et al., 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 percent loss in conductivity (PLC).

Each stem was subjected to alternating cycles of conductivity measurement and centrifuge treatment through a series of increasing tensions. A vulnerability curve was constructed for each stem by curvilinear regression of PLC as a function of tension exerted by the centrifuge. These curves illustrate the cavitation vulnerability of the xylem over a wide range of xylem tensions. A curve representing the means of each species is shown in Figure 3.

The tension which caused 50% loss in conductivity (Ψ_{50}) was determined for each sample by interpolating the regression curve. Comparison of Ψ_{50} was performed with ANOVA using log transformed data and Tukey's test for means separations to control experimentwise error.

Specific Leaf Area

In June of 2004, leaves were collected from 12 individuals of each species. As discussed above, it was not possible to locate all seven species in one location; therefore, stems were collected from sites 4 and 7 (Figure 1). At site 4, samples of *B. incana*, *Q. cornelius-mulleri*, *R. ovata*, and *A. glauca* were collected. *Adenostoma fasciculatum, A.*

sparsifolium, and *C. greggii* were collected from site 7. Leaves were collected from the same individuals used for vulnerability analysis and from additional plants to achieve a total of 12 plants per species. All individuals used had mortality scores between 1 and 3. For the broad leaved species 3 leaves were collected. However, due to the small leaf size of *A. fasciculatum* and *A. sparsifolium*, 15 leaves were collected from each plant. All leaves collected met the following conditions: had expanded in the previous year, from sunlit branches, with no senescence, no physical damage, and no apparent disease.

The leaves were cut from the plants, placed in zip closure bags, and immediately placed in a cooler. The leaves were stored for less than 48 hours before being processed. In the lab, the petioles were removed and fresh mass was recorded. Then a LI-3100 Leaf Area Meter (Li-Cor, Inc.) was used to determine the projected area of the leaves. 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

$$\mathrm{SLA} = \frac{\text{fresh projected leaf area}}{\text{dry mass}} \qquad (1)$$

ANOVA was performed on $\log_{10}$ transformed data and Tukey's test was used to control experimentwise error ($p < 0.050$) for means separations.

Xylem Pressure Potential

In June of 2004, and again in August of the same year, leaves were collected for measurement of xylem pressure potential from the same individuals used to measure SLA. Again, 12 individuals from each species were measured each sampling period.

One sample from each plant was collected predawn (before 6am). A second was collected midday (typically 1pm-3pm). The samples were cut, placed in a small zip closure bag, and placed in a cooler for 1-2 h at which time water potential was measured with a pressure chamber (Scholander et al., 1965).

The samples collected at midday in August were used to characterize minimum seasonal pressure potential. Repeated Measures ANOVA was performed and Tukey's test was used to control experimentwise error ($p < 0.0001$) for means separations.

Repeated Measures ANOVA showed no significant difference between predawn water potentials from June to August ($p > 0.05$); therefore, the predawn data were aggregated for analysis. The predawn data are used as an estimation of soil water potential in the soil surrounding the plant's roots (Slatyer, 1967). Repeated Measures ANOVA was performed and Tukey's test was used to control experimentwise error ($p < 0.0001$) for means separations.

Transpiration Rates and Stomatal Conductance

In August of 2004 an LI-1600 Steady State Porometer (Li-Cor, Inc., Lincoln, Nebraska) was used to measure transpiration rates and stomatal conductance. The measurements were made at the end of the dry season because this is the time when the greatest variance among species occurs. Measurements were made according to the Li-Cor instruction manual (Li-Cor, 1989); however, the leaf temperature was also measured, with an infrared thermometer, so that measurements of transpiration rate could be corrected for true leaf temperature (Pearcy et al., 1991). Two different aperture caps were needed because of the different leaf morphologies among the seven species. For *Q.*

cornelius-mulleri, R. ovata, and *A. glauca* the 1600-06 Small Aperture (0.66 cm^2, Li-Cor, Inc.) was used. For *B. incana, A. fasciculatum, A. sparsifolium*, and *C. greggii* the 1600-07 Cylindrical Chamber (Li-Cor, Inc.) was used.

While using the small aperture, readings were taken from the top and bottom of each leaf sampled because the aperture only measures transpiration on one side of a leaf; these two sub samples were combined for analysis as one sample to make them comparable to measurements taken with the cylindrical chamber. Two leaves per individual were sampled. The porometer was set to 0.65 cm^2 and the readings were later corrected for the true aperture of 0.66 cm^2 with the following calculation

$$g_{\text{corrected}} = g_{\text{measured}} \times \frac{0.65\,\text{cm}^2}{0.66\,\text{cm}^2} \qquad (2)$$

with $g_{\text{corrected}}$ equal to corrected stomatal conductance, and g_{measured} equal to measured stomatal conductance.

While using the cylindrical chamber, all surfaces of the several leaves on a single branchlet contributed to the transpiration measured for each sample. Two samples were measured for each individual. After measurement with the porometer the branchlet was collected and stored in a zip-closure bag and immediately placed in a cooler. Back in the lab the leaves were cut from their petioles and projected area for all leaves of each sample was measured with a Li-3100 leaf area meter (Li-Cor, Inc.). This projected area was doubled since the cylindrical chamber measures transpiration from both the top and bottom surfaces of leaves. During measurement the porometer was set to use a leaf area of 1 cm^2 so the actual leaf area (i.e., 2 x projected area) was used to correct measurements using the following equation

$$g_{\text{corrected}} = g_{\text{measured}} \times \frac{1\,\text{cm}^2}{2 \times A_l\,\text{cm}^2} \qquad (3)$$

with $g_{\text{corrected}}$ equal to corrected stomatal conductance, g_{measured} equal to measured stomatal conductance, and A_l equal to projected leaf area.

For measurements made both with the small aperture and the cylindrical chamber transpiration rate was further adjusted for temperature. Any differences in temperature inside and outside the cuvette make the measured transpiration (inside the cuvette) different from the native transpiration rate (outside the cuvette); Pearcy et al. (1991) described the calculations which can correct for this source of error.

For both stomatal conductance and transpiration rates ANOVA was performed on $\log_{10}$ transformed data and Tukey's test was used to control experimentwise error ($p < 0.050$) for means separations.

Characterization of the Drought Period

Climatic Data were collected from the National Climatic Data Center's (NCDC) on-line database located at http://www.ncdc.noaa.gov/oa/ncdc.html (NOAA, 2005). The primary data used were from two data collection stations: Anza and Deep Canyon. These stations are located to the east (Anza 33°33'N / 116°40'W) and west (Deep Canyon 33°39'N / 116°23'W) of the study site.

RESULTS

Dieback

Seven species were observed in sufficient quantities to allow analysis of the dieback scores: *A. fasciculatum*, *A. glauca*, *A. sparsifolium*, *B. incana*, *C. greggii*, *Q. cornelius-mulleri*, and *R. ovata* (Table 2). Two species, *C. greggii* and *A. glauca*, had significantly higher dieback than all other species, but did not differ from each other ($p=0.5296$). The five remaining species also did not differ from each other ($p=0.3208$); thus the seven species could be divided into low- and high-dieback groups, which differed at $p<0.0001$ (Figure 4a).

Logistic regression of the mortality of *A. glauca* showed a small but significant negative correlation ($p=0.0150$) with crown area: as crown area increased, dieback tended to decrease. A similar relationship was observed for *C. greggii* ($p=0.0277$). This relationship was only significant in the two species with high mortality; neither height nor distance to adjacent plants were significantly correlated with mortality for any species ($p>0.05$ for all comparisons).

Verification of mortality in 2004 showed that the vast majority of plants with 100% death of foliage in 2003 (score of 5) were completely dead. Ninety individuals that were given a dieback score of 5 in 2003 were verified; only one was observed to have any living foliage in 2004. This was an *A. glauca* individual. Since it is clear that a score of 5 represented mortality, the two groups of species described above will hereafter be referred to as the "low-mortality" and "high-mortality" groups. Percentages of mortality observed in 2003 were 66% and 75% for *C. greggii* and *A. glauca*, respectively. In the low mortality group percentages ranged from 0% to 15% (Figure 4b).

Xylem vulnerability

In general, the high-mortality species tended to have xylem that is relatively cavitation resistant. *Arctostaphylos glauca* and *C. greggii* had more negative mean pressure potentials resulting in 50% loss of conductivity (Ψ_{50}) than the low-mortality species (Figure 5a). However, not all of the differences were statistically significant. *Arctostaphylos glauca* did have xylem that was significantly more cavitation-resistant than that of all low-mortality species ($p=0.003$) with the exception of *A. fasciculatum* ($p=0.138$). The two species with the most vulnerable xylem were *Q. cornelius-mulleri* and *R. ovata*; both were in the low-mortality group. The remaining species had xylem of intermediate vulnerability (Figure 5a).

Specific Leaf Area

Specific leaf area (SLA) was generally higher in the low-mortality group. The SLA was significantly higher for all low-mortality species than high-mortality species ($p<0.005$) with one exception: *R. ovata* (low mortality) had a SLA not different ($p=1.00$) from *A. glauca* (high mortality) (Figure 5b).

Xylem pressure potential

Predawn xylem pressure potential was used to characterize functional rooting depth based on the assumption that the soil-plant continuum approaches water potential equilibrium during nighttime stomatal closure (Slatyer, 1967). Predawn pressure potential divided the seven species into three significantly different groups. The group with the least negative predawn pressure potentials included *R. ovata*, *A. sparsifolium*, *Q. cornelius-mulleri*, and *A. glauca*. All these species experienced low-mortality except *A. glauca*. The intermediate group consisted of two low-mortality species, *A. fasciculatum* and *B. incana*. *Ceanothus greggii* had significantly more negative predawn pressure potential than all other species. Pairwise comparisons within all groups resulted in $p>0.36$, but between all groups $p<0.001$. The two high-mortality species were at opposite ends of the range of predawn pressure potentials observed, thus there was no apparent relationship between predawn water potential and mortality (Figure 5c).

Minimum seasonal pressure potential, measured in 2004 at the end of the dry season at midday, was used to estimate the maximum water stress experienced by each species. *Rhus ovata* had a mean minimum seasonal pressure potential of -2.30 MPa which was significantly less negative than all other species ($p<0.0001$). The remaining six species fell into two significantly different groups. Those with intermediate minimum seasonal pressure potentials included one high-mortality species, *A. glauca*, and two low-mortality species, *A. sparsifolium* and *Q. cornelius-mulleri* which were not significantly different from each other ($p=1$). Another group of three species formed a group that had the most negative minimum seasonal pressure potentials but were not significantly different from each other ($p>0.76$); this group included two low-mortality species, *A. fasciculatum* and *B. incana*, and one high-mortality species, *C. greggii*. There was no overall relationship observed between minimum seasonal pressure potential and mortality (Figure 5d).

Stomatal Conductance

One species, *C. greggii,* had a lower mean stomatal conductance than all other species ($p<0.001$) based upon measurements made in August of 2004. *Ceanothus greggii* is in the high-mortality group. The other high-mortality species, *A. glauca*, was not significantly different from the three low-mortality species with the highest stomatal conductances, *R. ovata*, *Q. cornelius-mulleri*, and *B. incana* ($p>0.051$). The two remaining species (both having low mortality) had intermediate stomatal conductance and were significantly different than either high-mortality species ($p<0.001$). Thus, no relationship between mortality and stomatal conductance was observed (Figure 5e).

Transpiration Rates

The pattern of transpiration rates among species was similar to the pattern in stomatal conductance. *Ceanothus greggii*, a high-mortality species, had a lower mean transpiration rate than all other species ($p<0.001$) with the exception of one low-mortality species, *A. sparsifolium* ($p= 0.089$). The other high-mortality species, *A. glauca*, was not significantly different from the three low-mortality species with the highest transpiration rates, *R. ovata*, *Q. cornelius-mulleri*, and *B. incana* ($p>0.114$). The remaining species, *A. fasciculatum* (low mortality), had an intermediate mean transpiration rate significantly different than either high-mortality species ($p<0.001$). Thus, no relationship between mortality and transpiration rate was observed (Figure 5f).

Precipitation Data

The data files we obtained from the NCDC contained monthly precipitation for

Anza, Deep Canyon, and for each climatic division in which the stations are located. Anza is located in the South Coast Drainage Climate Division while Deep Canyon is in the Southeast Basin Climate Division (NOAA, 2001). The study site is located on the border of two of these areas.

Due to the westerly movement of weather systems in the region and the decrease in elevation from west to east, the Anza station generally receives more precipitation than the study site while Deep Canyon generally receives less. Therefore, the precipitation at the study site was estimated as the arithmetic mean of precipitation at 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 one data point. Rolling averages were calculated to smooth variation in annual precipitation in Figure 6; the arithmetic mean of 7 years, including a given year and the 6 previous years, were used.

From 1963 to 2003, the average annual rainfall at the site was estimated to be 236 mm. The average annual rainfall for the 5 year period from 1998 to 2003 was estimated as only 103 mm. This is less than 44% of the site's average. During the year from July 2002 to June 2003 it is estimated that only 73 mm of rain (31% of average) fell on the study site (Figure 6). During the year from July 2003 to June 2004 the drought eased some; it is estimated that 143 mm of rain fell on the site.

DISCUSSION

Species Effects

Mortality of adult shrubs did occur, and it was more frequent among some species than others, but the pattern was opposite to that we had expected; the highest proportions of mortality were observed in the species that exhibited the greatest resistance to xylem cavitation (lowest Ψ_{50}) and the greatest sclerophylly (lowest SLA). This resulted in a relationship between life history type and mortality that was opposite to our prediction as well. The nonsprouting species had higher proportions of mortality than the sprouting species. Finally, we correctly predicted that the water stress experienced by the various species would not be a good predictor of dieback or mortality, but the relationship between life history strategy and the water stress experienced was not as expected.

Since it was expected that species with low Ψ_{50} and low SLA should be resistant to water stress, we predicted that these species would experience less mortality during the drought. Sclerophylly has classically been considered a measure of water stress tolerance (Schimper, 1903; Oppenheimer, 1960; Fahn and Cutler, 1992). Also, species with high resistance to cavitation are less likely to have their water conduction compromised during water limitation (Tyree and Sperry, 1989; Pockman and Sperry, 2000). Species with low SLA are considered to be more conservative in water use (Oppenheimer, 1960; Fahn and Cutler, 1992). Since more xeric sites tend to contain species with low xylem vulnerability (Davis et al., 1999; Kolb and Sperry, 1999; Pockman and Sperry, 2000) and more sclerophyllous leaves (Ackerly et al., 2002) it has generally been assumed that these traits are advantageous for drought survival.

Species with more vulnerable xylem should be the first to experience cavitation and eventually catastrophic failure of water conduction (Tyree and Sperry, 1989; Hacke and Sperry, 2001). Species with more sclerophyllous leaves should be more resistant to desiccation (Fahn and Cutler, 1992). Our conclusion that more resistant species were less successful at surviving drought conditions suggests that water stress resistance alone cannot predict success during a prolonged and severe drought. Specifically, the stress a species experiences must be known to make predictions about the extent of dysfunction caused. Since the data show that the more resistant species were actually more likely to experience dieback and mortality it seems that co-occurring species were not experiencing water stress in the same way.

Our quantification of water stress showed much variability and, as expected, little relationship between water stress and mortality. One reason to expect differences in water stress among species would be if different water stress coping strategies were being utilized by each species. The various strategies for resisting water stress have been reviewed thoroughly by Oppenheimer (1960) and later by Fahn and Cutler (1992). For woody shrubs, the two available strategies are: 1) to avoid tissue dehydration and 2) to tolerate tissue dehydration (Fahn and Cutler, 1992). These strategies have characterized by suites of characteristics that enable species to either avoid or tolerate water limitation (Oppenheimer, 1960; Fahn and Cutler, 1992).

Reviews of xerophytism by Oppenheimer (1960) and Fahn and Cutler (1992) have listed of dozens of strategies for success in xeric environments. One method of avoiding tissue dehydration is to have deep roots with large root mass relative to shoot mass, thus reducing the need to conserve water (Fahn and Cutler, 1992). Oppenheimer

(1960) asserts that since these species "spend much water" they should not be considered xerophytes at all because they survive in arid environments by accessing ground water available year-round. He points out that these species have few anatomical, morphological, or physiological characters typically associated with xerophytes. Davis (1989) also described this suite of characteristics, suited for avoidance of tissue dehydration, in resprouting chaparral species. This avoidance strategy is plausible at this site given that measurements of ground water depth from wells less than five km from the study site show ground water to fluctuates between 6 m and 15 m below the surface (California Department of Water Resources, 2006). Considering rooting depths observed in some chaparral species by Hellmers et al. (1955) and Thomas and Davis (1989) it is reasonable to hypothesize that species could be accessing ground water.

Alternatively, species that resist water limitation by tolerating tissue dehydration have relatively shallow roots; therefore, these species utilize xeromorphic adaptations such as reduction in leaf area per mass (i.e. low SLA) and reduced stomatal conductance (Fahn and Cutler, 1992). Davis (1989) described this suite of characteristics as being associated with the nonsprouting chaparral species. Davis (1989) further suggests that there are species in the chaparral that have an intermediate strategy (e.g. *A. fasciculatum*) with intermediate rooting depth and intermediate stomatal conductances.

Another strategy to avoid tissue dehydration is the succulent habit as characterized by members of the Cactaceae, Agavaceae, and Euphorbiaceae families (Oppenheimer, 1960; Fahn and Cutler, 1992). This strategy is not found in chaparral but is found in desert communities adjacent to the study site. This strategy is particularly effective when rain is especially unpredictable and scarce (Oppenheimer, 1960).

The species examined in this study seem to represent a continuum from drought evading to drought tolerating. Rooting depth may be the primary characteristic that allows us to predict which strategies species will employ. *Rhus ovata* and *Q. Cornelius-mulleri* are perhaps the most avoidance oriented species of the group. Both are likely to be very deep rooted and so apparently can have higher transpiration and still experience high xylem pressure potentials, thus they do not require highly resistant xylem to survive the extreme drought. We are not aware of any published data from root excavation of these species but closely related congeners of each have been observed to be some of the deepest rooted species ever excavated in the chaparral (Hellmers et al., 1955; Thomas and Davis, 1989). Regarding stomatal conductance and transpiration, our data show that these two species had values among the highest, but they both maintained xylem pressure potentials that were among the least negative. Since Poole and Miller (1975) showed that stomatal closure occurred quickly in *R. ovata,* before xylem pressure potentials reach low values (i.e., -3 MPa), the relatively high conductance and transpiration rates maintained in the individuals we sampled is further evidence that the plants were not water stressed. The fact that these plants did not experience great stress at the end of the summer drought in 2004 suggests that the plants would not need highly resistant xylem in order to be successful during drought. Therefore, it is not surprising that *R. ovata* and *Q. Cornelius-mulleri* had the most vulnerable xylem but were still among the group of species with extremely low dieback and mortality. In the case of *R. ovata* it has also been demonstrated that the species has very low minimum transpiration rates; when individuals are water stressed they are particularly effective at minimizing water loss (Pratt et al., 2005).

Adenostoma sparsifolium appears to be next on the continuum from drought avoidance to drought tolerance. Hanes (1965) measured the rooting depth of *A. sparsifolium* and its congener *A. fasciculatum* to be just over 2 m deep. However, physiological evidence collected from co-occurring individuals of the two species suggests that *A. sparsifolium* has deeper roots than *A. fasciculatum* (Redtfeldt and Davis, 1996). Since *A. sparsifolium* has more shallow roots than *R. ovata* or *Q. Cornelius-mulleri* it is advantageous for the species to reduce stomatal conductance and conserve water. In this way *A. sparsifolium* can maintain xylem pressure potentials similar to those of the two deep rooted species and can survive severe drought even with fairly vulnerable xylem.

Further along the continuum from drought avoidance to drought tolerance is *A. fasciculatum.* Two studies have excavated roots of this species. When Hellmers et al. (1955) excavated roots of *A. fasciculatum* they found roots penetrating rock 8 meters below the surface. At another location, Hanes (1965) measured the rooting depth of *A. fasciculatum* to be just over 2 m deep. Direct measures of rooting depth are few in number and therefore somewhat anecdotal, but as stated above, physiological evidence suggests that this species has shallower roots than *A. sparsifolium* (Redtfeldt and Davis, 1996). Since we measured similar transpiration rates in the two species we would expect *A. fasciculatum* to experience lower xylem pressure potentials. This too was observed in the present study. *Adenostoma fasciculatum* was still able to survive the extreme drought because, compared to all the other low-mortality species, it has the most cavitation resistant xylem.

Since *A. glauca* is a much shallower rooted species [less than 1 m deep (Hellmers et al., 1955), or 0.3 m deep (Miller and Ng, 2005)] it has less access to deeper water resources and is likely to experience low xylem pressure potentials during drought. This did not seem to be the case when we measured minimum seasonal xylem pressure potential at the end of the summer of 2004. At this time *A. glauca* maintained high stomatal conductance while also keeping xylem pressure potential high. Poole and Miller (1975) also observed that *A. glauca* maintains high conductance even while xylem pressure potential gets quite low (i.e., to -5.5 MPa). Our xylem vulnerability curves (Figure 3) show that this potential is not sufficient to cause much dysfunction in water conduction. However, since the species has shallow roots, the situation must have been different following the prolonged and severe drought from 1998 to 2003. During such a dry time it appears that even though *A. glauca* had the most cavitation resistant xylem of all species, there was not enough water available at such shallow soil depths, thus it experienced a high frequency of mortality following the drought.

Like *A. glauca, C. greggii* is a shallow rooted species with roots growing less that 1 m deep (Hellmers et al., 1955; Miller and Ng, 2005). Lateral root growth is much less than *A. glauca* (Hellmers et al., 1955; Kummerow et al., 1977). It too has less access to water resources during drought; however, our data suggest that it compensates for this with low stomatal conductance. Poole and Miller (1975) demonstrated that *C. greggii* only reduced stomatal conductance when experiencing very low xylem pressure potentials. This is consistent with our observation that *C. greggii* experienced the lowest pressure potentials of all species in August of 2004. This species appeared to be the most water stressed of all 7 co-dominant shrubs at the study site; it is not surprising that, even though its xylem is resistant, it failed to function adequately during the prolonged drought.

The fact that the seven co-existing species are utilizing different strategies along the continuum from drought avoidance to drought tolerance suggests all of the strategies are successful in this water-limited system. Hacke et al. (2000) described a similar variety of strategies used by species in the Great Basin desert of Utah. On the other hand, the extreme drought that occurred from 1998 to 2003 shows that drought avoidance may be more effective when conditions get very dry. It appears that during this extreme event the tolerance of *A. glauca* and *C. greggii* was surpassed by the water stress they experienced, likely inducing catastrophic dysfunction of the xylem (Tyree and Sperry, 1989; Tyree and Ewers, 1991; Rood et al., 2000; Davis et al., 2002).

Site Effects

As was noted above, there was little clear relationship to measures of stress experienced by a species and mortality thereof. However, there appears to be a relationship between the four measures of drought stress and the site where the physiological data was collected. As stated above, it was not possible to locate all seven species at one site; therefore, physiological data was collected from individuals at sites 4 and 7. Inspection of the data shows that the plants at site 7 appear to have been more water stressed at the end of the 2004 dry season than the plants at site 4. Figure 6 shows that *B. incana*, *Q. cornelius-mulleri*, *R. ovata*, and *A. glauca* which occur at site 4 all had greater mean stomatal conductance and transpiration rates than the species at site 7, *A. fasciculatum*, *A. sparsifolium*, and *C. greggii*. In almost all cases these differences were significant, with the exception of *R. ovata* which was not different from two of the species at site 7. A similar pattern is seen in xylem pressure potential, but the differences between site 4 and 7 are less distinct (figure 6c and 6d).

It appears that site differences are best correlate with our measures of water stress. It is know that soil moisture can have dramatic effects on transpiration rates (Pereira and Chaves, 1993). Therefore, it is likely that there were differences in water availability at site 4 and site 7. Still, it was surprising that site 7 contained the more stressed species because appears to be the more mesic site; it is farther from the desert and has more dense vegetation. It may be that in dry years the denser vegetation results in more transpirational water loss from the soil.

Morphology

The inverse relationship between crown size and mortality in the two high-mortality species is intriguing. One explanation for this pattern could be microsite differences. An individual growing in a dry microsite would be more water limited, resulting in reduced size (Stocker, 1960). Although increased root allocation can be a response to drought (Stocker, 1960), root: shoot biomass allocation appears to be relatively consistent within a species (Miller and Ng, 2005) so we would expect smaller individuals to have shorter, perhaps shallower, roots than conspecific neighbors. Thus, the higher mortality of small individuals could be due to small-crown individuals having more shallow roots and/or to the smaller individuals occurring at drier microsites.

Future implications

It is notable that, although the site where this morality was observed has experienced drought in recent years, the western United States has been wetter in this century than it has been historically (Smith et al., 2001). The western United States has also increased in temperature by 2-5°C this century (Smith et al., 2001). Smith et al. (2001) examine two climate models, the Hadley and Canadian models, and make a number of predictions for the next century: temperature is likely to increase by 8-11°C; precipitation will likely increase (although the Canadian model suggests some chance that the area will be drier); and there will likely be more extremes of wet and dry years. The fact that the mortality observed in this study follows a five year dry period suggests that the predictability of rainfall may be of particular importance to chaparral species.

For plants living in water-limited environments changes in temperature and precipitation will have important implications for survival and recruitment. If the Hadley model is correct, species that can take advantage of increased moisture may out-compete the species that are currently present. If the Canadian model is correct and the area does become drier, drought adaptations will be increasingly important for survival. Our data suggests that the strategy plants use to cope with water limitation in the chaparral system may affect their success as the climate changes.

Based on these climate models, it is possible, if not likely, that the climate in the CA chaparral will become drier, and it is likely that rainfall will become more unpredictable (Smith et al., 2001). Our results allow us to make several predictions for chaparral systems at ecotones with more xeric ecosystems, assuming climate change fits the predictions of the models (Smith et al., 2001). First of all, there will be effects on species composition. Drought-tolerating, nonsprouting species will likely experience widespread mortality and potentially be lost from these communities. Secondly, seedlings of the drought-avoiding, sprouting species, which have more vulnerable xylem and less sclerophyllous foliage, have a high frequency of mortality when water limited (Davis, 1989). Therefore, recruitment will be very difficult, even for sprouting species. The mortality in drought-tolerating, nonsprouting species and lack of recruitment in drought-avoiding, sprouting species could result in desertification of chaparral stands that grow at ecotones with desert communities.

However, if rainfall increases and occurs with the annual regularity that is typical of the chaparral then our data would lead us to predict the opposite trend. With the absence of drought-induced mortality there would be no regression of chaparral stands. In addition, increased rainfall would support recruitment of sprouting species during fire free periods and non-sprouting species after fire events. The increased rainfall would likely allow chaparral species to recruit in areas currently dominated by desert communities.

In addition to the ecological effects there is evolutionary significance to the patterns of mortality we observed. Of the various regeneration strategies, sprouting is considered a relictual trait present in ancestors, which evolved in different ecosystems (Wells, 1969). Nonsprouting is considered to be the derived trait in the chaparral community and an adaptation to the frequent fire events in chaparral stands (Wells, 1969). Nonsprouters are most successful at recruiting new individuals after fire (Keeley and Zedler, 1978). However, since both climate models predict that rainfall is likely to be more unpredictable, severe drought events may become as frequent as fire events; if this occurs, our data suggest that sprouting species may have a strong survival advantage. Severe drought events would result in mortality in nonsprouters as reduced fire frequency restricts recruitment in those species since they require fire for germination. The reduced rainfall predicted by the Canadian model would reinforce this trend since drought conditions would reduce the density of individuals in chaparral communities, reducing the extensive spread of fire. On the contrary, if the Hadley model is correct the increased moisture would result in denser chaparral vegetation and improved fire propagation. It is interesting to note that in desert communities fire is not important in driving community structure (Brown and Minnich, 1986). If increased moisture results in more dense vegetation thus increasing the propagation of fire in areas of desert then fire could contribute to the replacement of desert with chaparral communities.

As global climate change continues, the southwestern United States will likely provide many opportunities to examine the effects on plant ecology and biogeography. Prior to this study, subleathal effects of drought have been reported in woody plant communities (Parsons et al., 1981; Rood et al., 2000; Davis et al., 2002) but there has been no documentation of widespread drought-induced mortality in chaparral communities. However, as communities respond to the changing climate and species distributions shift, it is likely that widespread mortality will be observed at ecotones and we will be provided with many opportunities to learn more about the survival value of strategies for success in the water-limited chaparral system.

FUTURE DIRECTIONS

The dramatic difference in mortality between deep rooted and shallow rooted species suggests several promising directions for research. Since there has been little direct measurement of rooting depth it would be valuable to excavate plants to learn more about variation in rooting habit both within and among species. It is also true that our real interest is not the depth of roots but rather in their ability to access water resources. If, as Oppenheimer (1960) suggests, extremely deep rooted species like *R. ovata* and *Q. cornelius-mulleri* are accessing ground water, then stable isotope analysis, which characterizes active rooting depth (Ehleringer and Dawson, 1992), should be very effective at differentiating water resources used by deep rooted and shallow rooted species. For example, Williams and Ehleringer (2000) examined hybrid *Quercus* plants and identified individuals that avoided drought by accessing deep water sources. If the active rooting depths of the species in this system are congruent with rooting depths estimated from excavations, it would provide verification of the patterns of tolerance and avoidance proposed above.

There would also be value in expanding the suite of anatomical and physiological characteristics associated with mortality in the current study by making additional measures on plants in this community. We demonstrated that high xylem resistance to cavitation and low specific leaf area, both commonly associated with drought adaptation (Oppenheimer, 1960; Fahn and Cutler, 1992), were associated with high mortality following severe drought. Measuring xylem parameters such as specific conductivity, hydraulic mean vessel diameter, vessel implosion resistance, xylem density, and the mechanical strength of stems would likely elucidate additional patterns since each has been associated with water stress resistance (Wagner et al., 1998; Hacke and Sperry, 2001; Martinez-Vilalta and Pinol, 2002; Jacobsen et al., 2005).

Finally, the sampling methods used here did not thoroughly address ecological factors that likely influenced the incidence of mortality in this community. Species identity was clearly very important in determining which individuals experienced mortality. However, ecological factors such as slope inclination, slope aspect, elevation, and various microsite differences almost certainly influenced mortality as well. Trends in global climate predict even drier times to come for the southwestern United States (Sheppard et al., 2002). If widespread mortality reoccurs it will be important to characterize ecological patterns of mortality using classical ecological methods on the local scale and remote sensing techniques to characterize patterns on the landscape scale.

TABLES

Table 1. Location, elevation, slope, and aspect of 7 sampling sites. Sites are listed in order of increasing distance from the desert ecotone. Refer to Figure 1 for a map of locations. Species are listed (see table 2 below for abbreviations) from left to right in general order of occurrence on sites with increasing distance from the desert ecotone. Species numbers indicate the quantity of individuals captured in the mortality survey. Less than 60 individuals are listed in some sites if some woody species were sampled but were too rare to be included in statistical analyses.

Site	Lat; Lon	Elevation	Slope	Aspect			Species				
	(deg N; W)	(m)	(deg)	(deg)	Bi	Ag	Ro	Qc	Cg	As	Af
3	33.604;116.422	1103	12	108	28	22	4	6			
1	33.587;116.437	1339	30	250		48	2	7			
4	33.592;116.444	1265	07	168	22	5	4	21			
5	33.568;116.444	1453	26	020		2	2	5	41	10	
2	33.577;116.460	1259	06	035			2	7	46		5
6	33.565;116.477	1502	30	008			2	4	53	1	
7	33.549;116.508	1591	11	225					13	18	29

Table 2. A list of the seven species of woody shrubs co-dominant in the study community. Abbreviations (Ab.) are defined. Authorities are according to the Jepson Manual (Hickman, 1993). Life history strategy refers to regeneration mode after fire or other disturbance that removes above-ground biomass.

Species	Ab.	Family	Life history strategy
Adenostoma fasciculatum Hook. & Arn.	Af	Rosaceae	Sprouting (Hanes, 1965)
Rhus ovata S. Watson	Ro	Anacardiaceae	Sprouting (Stone and Juhren, 1951)
Adenostoma sparsifolium Torrey	As	Rosaceae	Sprouting (Hanes, 1965)
Quercus cornelius-mulleri K. Nixon & K. Steele	Qc	Fagaceae	Sprouting (Nixon, 2002)
Bernardia incana C. Morton	Bi	Euphorbiaceae	unknown
Ceanothus greggii A. Gray	Cg	Rhamnaceae	Nonsprouting (Keeley and Zedler, 1978)
Arctostaphylos glauca Lindley	Ag	Ericaceae	Nonsprouting (Keeley, 1977)

FIGURES

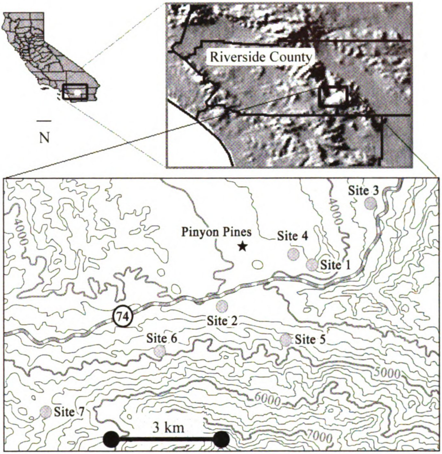

Figure 1. Location of Study Site in Riverside County, CA, USA. The inset shows the location of the seven sites used for sample collection. See Table 1 for latitude and longitude of each site.

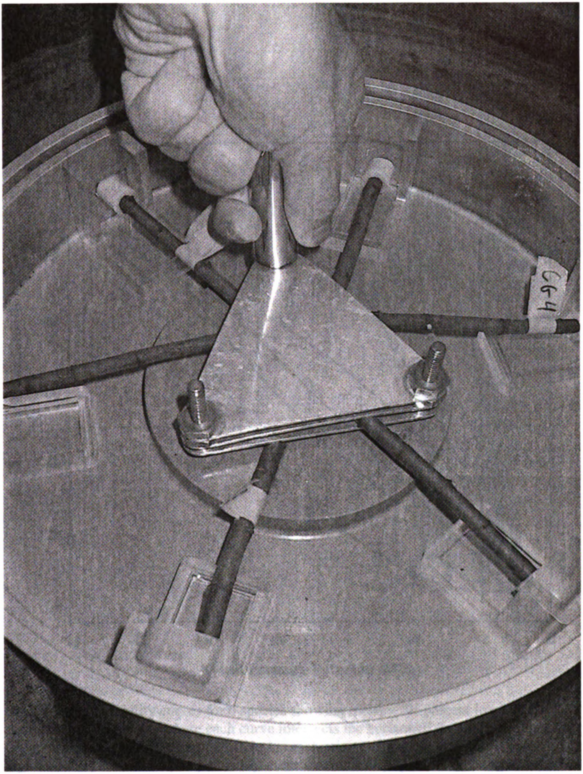

Figure 2. Specialized centrifuge rotor designed to exert tension on the xylem water column. Plastic cups at each end of each stem segment keep the ends submerged in deionized water while the rotor spins.

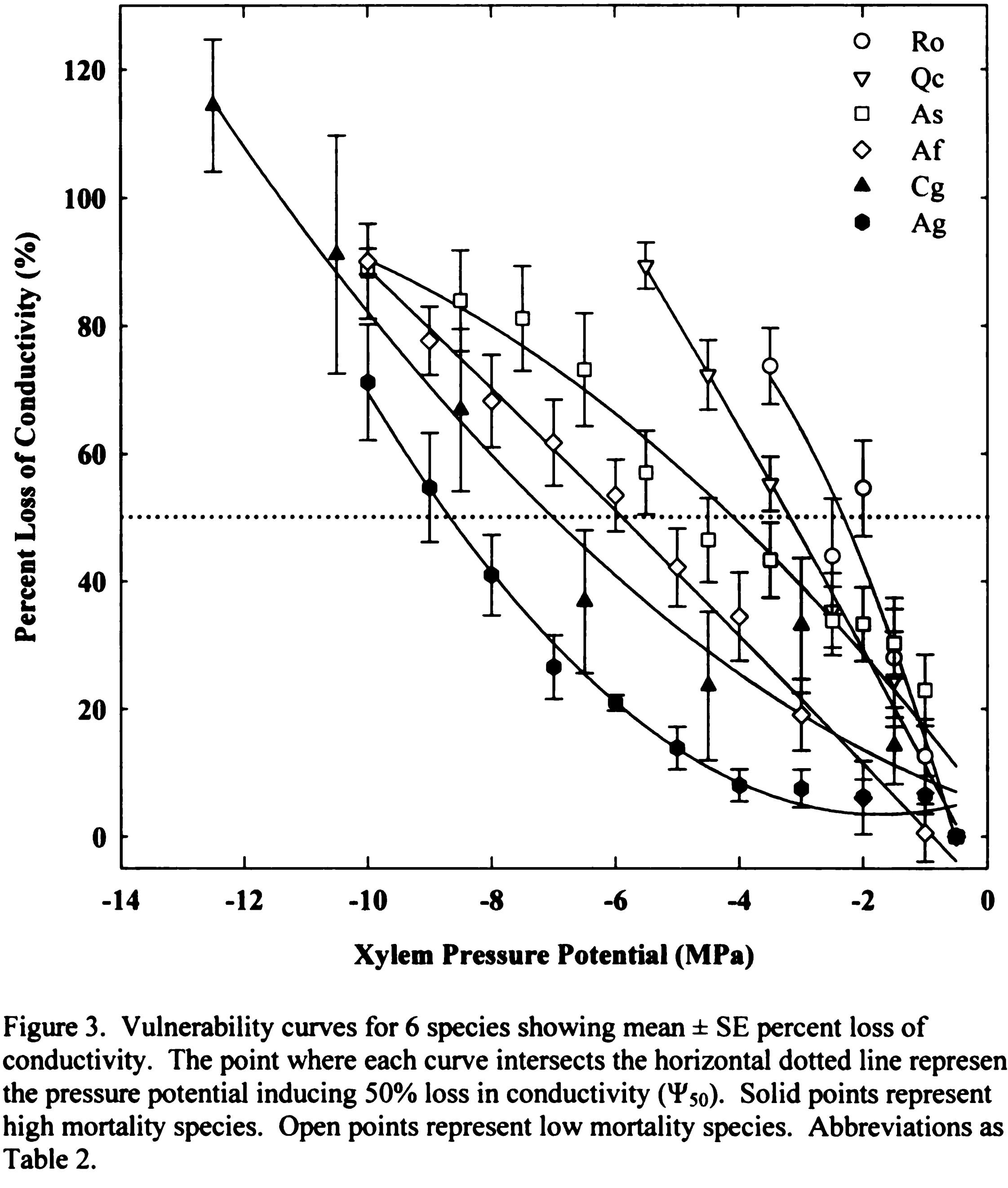

Figure 3. Vulnerability curves for 6 species showing mean ± SE percent loss of conductivity. The point where each curve intersects the horizontal dotted line represents the pressure potential inducing 50% loss in conductivity (Ψ_{50}). Solid points represent high mortality species. Open points represent low mortality species. Abbreviations as in Table 2.

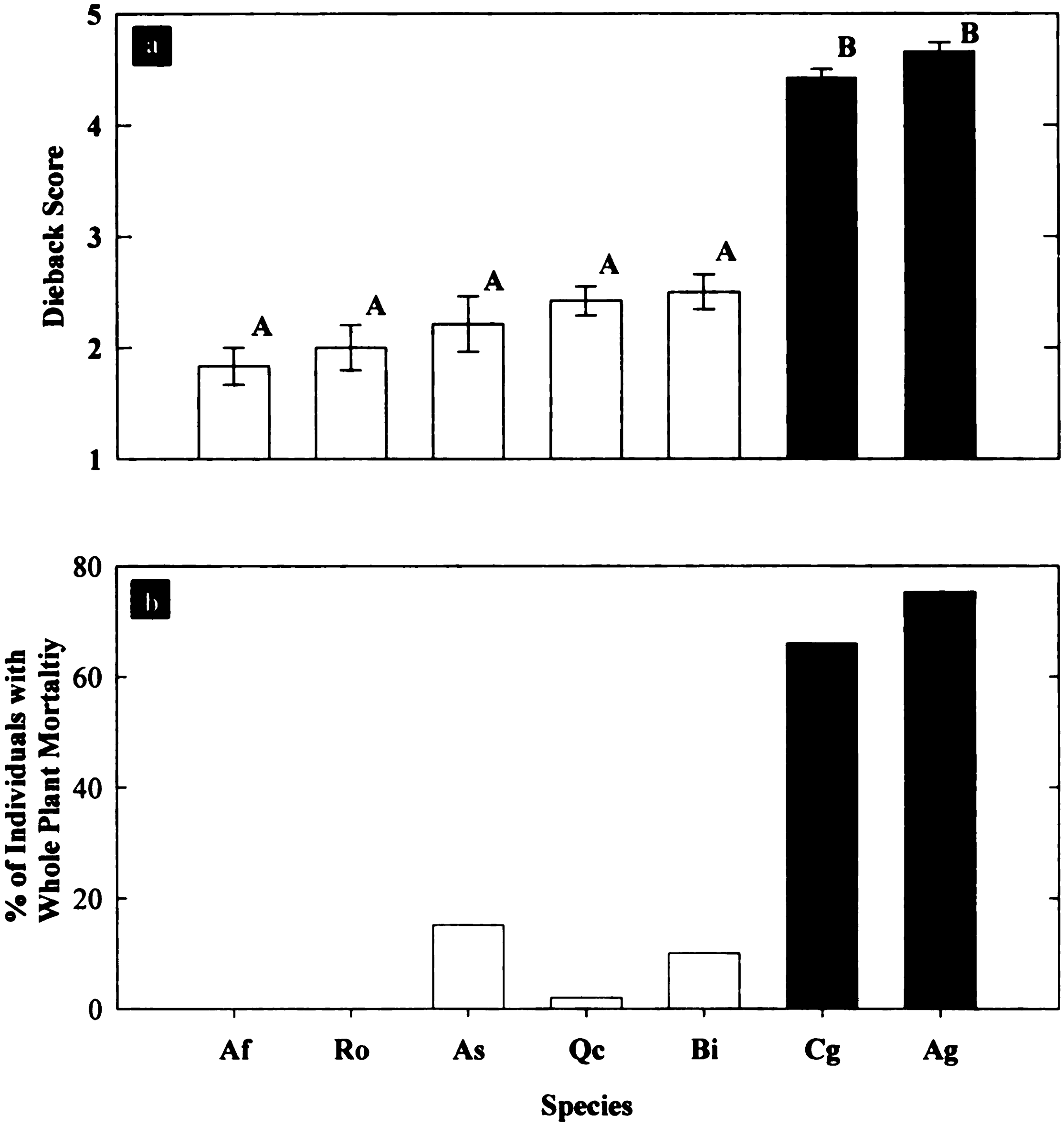

Figure 4. Measures of dieback recorded in 2003. Figure a shows mean ± SE dieback score for seven species (scale of 1-no dead foliage, to 5-all foliage dead). A and B denote significantly different dieback ($p<0.0001$). Figure b shows the frequency of death within each of the 7 species. Abbreviations as in Table 2.

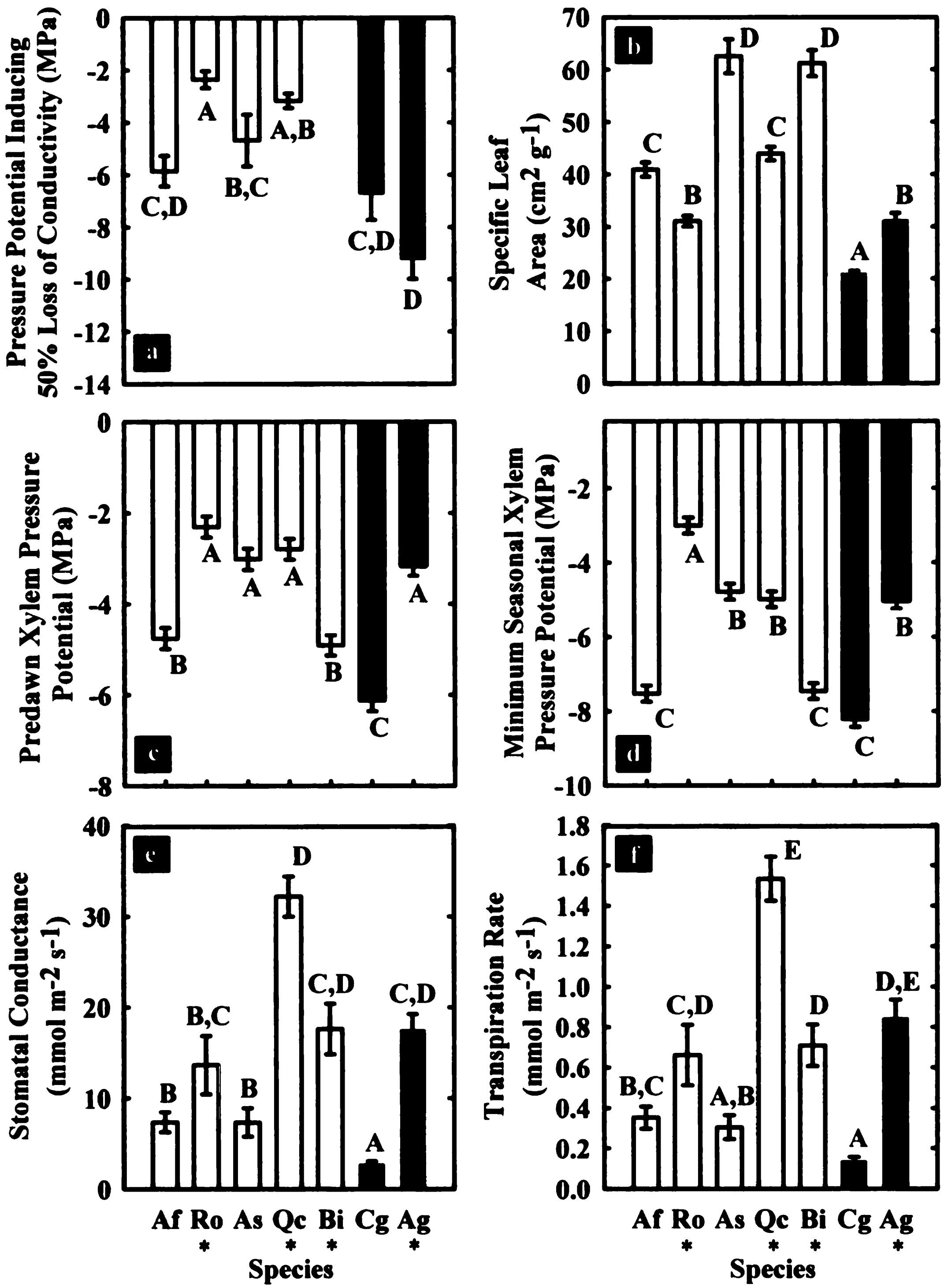

Figure 5. Comparison of physiological measures for the 7 species. Figures a + b represent water stress resistance; Figures c-f represent water stress experienced. Bars represent means ± SE for the seven co-dominant species (abbreviations as in Table 2). Letters adjacent to bars denote significantly different groups ($p<0.05$). Closed bars indicate high-mortality species, open bars represent low-mortality species. * Denotes species for which physiological data was collected at site 4; such data for the other species was collected at site 7.

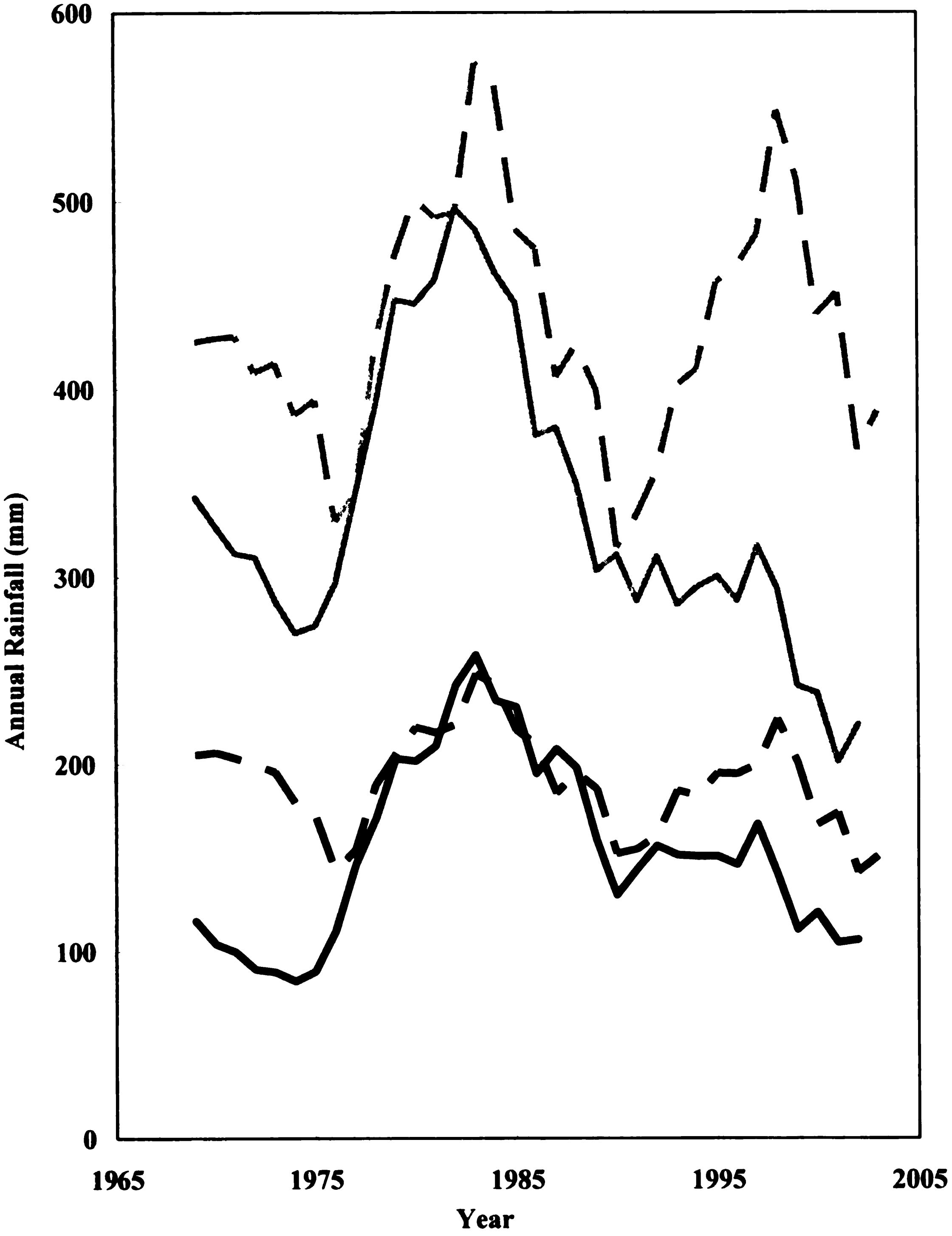

Figure 6. Lines indicate a 7 year rolling average of annual rainfall for the area surrounding the study site. Solid lines represent the 2 individual rain stations nearest to the study site (Anza in grey; Deep Canyon in black). Dashed lines represent the climate division in which each station is located (South Coast Drainage Climate Division in grey; Southeast Basin Climate Division in black). Original data from NOAA (2005).

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