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Permalink

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Journal

Functional Ecology, 30(4)

ISSN

0269-8463

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Publication Date

2016-04-01

DOI

10.1111/1365-2435.12518

Peer reviewed

Multiple strategies for drought survival among woody plant species

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Summary

1. Drought-induced mortality and regional dieback of woody vegetation are reported from numerous locations around the world. Yet within any one site, predicting which species are most likely to survive global change-type drought is a challenge.

2. We studied the diversity of drought survival traits of a community of 15 woody plant species in a desert-chaparral ecotone. The vegetation was a mix of chaparral and desert shrubs, as well as endemic species that only occur along this margin. This vegetation boundary has large potential for drought-induced mortality because nearly all species are at the edge of their range.

3. Drought survival traits studied were vulnerability to drought-induced xylem cavitation, sapwood capacitance, deciduousness, photosynthetic stems, deep roots, photosynthetic responses to leaf water potential and hydraulic architecture. Drought survival strategies were evaluated as combinations of traits that could be effective in dealing with drought.

4. The large variation in seasonal predawn water potential of leaves and stem xylem ranged from -6.82 to -0.29 MPa and -6.92 to -0.27 MPa, respectively. The water potential at which photosynthesis ceases ranged from -9.42 to -3.44 MPa. Architecture was a determinant of hydraulic traits, with species supporting large leaf area per sapwood area exhibiting high rates of water transport, but also xylem that is vulnerable to drought-induced cavitation. Species with more negative midday leaf water potential during the growing season also showed access to deeper water sources based on hydrogen isotope analysis.

5. Drought survival mechanisms comprised of drought deciduousness, photosynthetic stems, tolerance of low minimum seasonal tissue water potential and vulnerability to drought-induced xylem cavitation thus varied orthogonally among species, and promote a diverse array of drought survival strategies in an arid ecosystem of considerable floristic complexity.

Key-words: climate change, drought-induced mortality, hydraulic conductance, Mediterranean-type ecosystems, photosynthesis, plant water potential, transpiration, xylem cavitation

Introduction

Global change-type drought occurs in conjunction with warmer temperatures due to climate change (Breshears *et al.* 2005), and is more extreme in intensity and duration than normal rainless periods experienced by vegetation annually in arid climates (Field 2014). Recent reports of drought-induced mortality of woody species are documented from locations worldwide (Allen *et al.* 2010), raising the importance of predicting future mortality risk in natural vegetation. Woody plants from a wide range of forest biomes are similar in their susceptibility to drought

induced mortality (Choat *et al.* 2012). However, within biomes, there is wide variation of drought susceptibility (Moreno-Gutierrez *et al.* 2012; West *et al.* 2012; Craine *et al.* 2013; Salgado Negret *et al.* 2013; Pivovarovff, Sack & Santiago 2014). Plant traits that facilitate survival during drought include: (1) Xylem that is highly resistant to drought-induced cavitation, (2) high sapwood capacitance that protects xylem from critically low water potentials, (3) a deciduous phenology allowing leaf loss during drought, (4) photosynthetic stems which promote carbon gain at greater water-use efficiency than leaves, (5) deep roots that increase access to water sources, (6) regulation of gas exchange to reduce leaf water loss or to maintain photosynthesis at low leaf water potential and (7) safe hydraulic

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architecture that supports low leaf area-to-sapwood area ratio (Sperry 2000; Ackerly 2004a; Meinzer *et al.* 2008; Choat *et al.* 2012; Ávila, Herrera & Tezara 2014). Drought survival strategies, like other ecological strategies, thus consist of the presence or absence of drought survival traits within species and coalesce around particular trait combinations (Chapin 1980). Because predicting differential mortality of woody plants is of special concern for projecting vegetation responses to global change, we evaluated the drought survival strategies of woody plant species growing at the intersection of two major vegetation types in southern California.

While climate-induced forest dieback is a global occurrence (Breshears *et al.* 2005; Allen *et al.* 2010), mortality mechanisms are currently under debate. A recent synthesis proposed two alternative mechanisms of woody plant mortality, providing a useful conceptual framework (McDowell *et al.* 2008). The hydraulic failure hypothesis suggests that drought reduces plant water potential such that the xylem water column undergoes catastrophic cavitation, ceasing water supply to the leaves (Sperry, Donnelly & Tyree 1988; Tyree & Sperry 1989; McDowell *et al.* 2008). The series of physiological events leading to hydraulic failure occur as plants continue low levels of photosynthesis at the expense of declining water potential, typical of anisohydric stomatal behaviour. In contrast, the carbon starvation hypothesis suggests that some plants maintain water potential above critical levels during drought by closing stomata, eventually leading to exhaustion of non-structural carbohydrate reserves, typical of isohydric stomatal behaviour (McDowell *et al.* 2008; Sevanto *et al.* 2014). Carbohydrate exhaustion may also increase vulnerability to pathogens and herbivores, which may be the ultimate cause of mortality (McDowell *et al.* 2008). Drought effects on water and carbon supply also interact in complex ways when limited water supply reduces carbon uptake, transport and utilization, or when limited carbon supply reduces xylem refilling (Salleo *et al.* 2004; McDowell 2011; McDowell *et al.* 2013).

Understanding plant responses to drought along ecotones is a critical component of global change biology (Box 1981; Woodward 1987; Allen & Breshears 1998). An ecotone is a transition zone between two biomes, serving as a seam at the edges of typically distinct vegetation types. Hence, ecotone communities are often comprised of individuals operating at the extreme of their physiological limit, making these zones more responsive to environmental or biotic disturbance and more sensitive to climate change than communities that are spatially buffered from range edges (Gitlin *et al.* 2006; Field 2014). The intersection of the biologically diverse California Floristic Province with the Mojave Desert in southern California represents an especially dynamic mixing of plant communities from contrasting evolutionary and climatic origins, that has undergone evolutionary migrations in response to climate (Minnich 1974; Raven & Axelrod 1978). Plant lineages contributing to the chaparral shrub flora have

occurred at the ecotone of drier margins of mixed evergreen forests in North America for more than 20 million years (Raven & Axelrod 1978). Their radiation into the highly endemic California Floristic Province happened in response to the development of a dry summer, wet winter Mediterranean-type climate three million years ago (Axelrod 1977). The floristic complexity and mesic-arid span of the desert-chaparral ecotone suggests high potential for responding to global change-type drought (Breshears *et al.* 2005). We utilized the desert-chaparral ecotone in southern California to evaluate the diversity of drought survival strategies among coexisting woody species. We propose that drought survival traits cluster among species, reflecting trait combinations that lead to drought survival strategies. Specifically, we hypothesized that: (1) Shallow rooted species are highly resistant to xylem cavitation; (2) Species with a hydraulic architecture supporting large leaf area per unit sapwood are vulnerable to xylem cavitation; (3) Drought deciduous species maintain photosynthetic stems and (4) Species vulnerable to xylem cavitation compensate with high sapwood capacitance.

Materials and methods

STUDY SITE AND SPECIES

The study was conducted in Morongo Valley, California, USA (34°02'12.0"N, 116°37'24.4"W). The site occurs at *c.* 1000 m elevation and receives 283 mm of precipitation annually, with a mean annual temperature of 15.7 °C and a mean potential evapotranspiration (PET) of 4.38 mm day⁻¹ (New *et al.* 2002). Soils are alluvial and sandy and classified as Typic Torripsamments (Soil Survey Staff 2008). The vegetation type is generally known as desert chaparral and represents an ecotone between upslope chaparral shrublands and downslope Mojave Desert scrub, found mostly on east-facing slopes with desert exposure (Minnich 1974). We included all 15 woody species occurring at this site in our study (Table 1).

SEASONAL PLANT WATER STATUS AND PHENOLOGY

Predawn and midday stem and leaf water potentials were measured monthly during 2011 using pressure chambers (1000 and 1001; Plant Moisture Stress Instruments, Albany, OR, USA) to determine plant water status. The day before measurements, six branch samples on each of three individuals per species were covered with plastic bags and aluminium foil to stop transpiration and allow leaf water potential to equilibrate with stem xylem water potential. Three covered and non-covered sample pairs were collected from each individual for predawn measurements, and again for midday measurements. Upon collection, samples were sealed in plastic bags (Whirlpak 0.057 mm thick; Nasco, Fort Atkinson, WI, USA) and placed in a dark cooler before measurements. Covered samples represent stem water status (Ψ_{stem}), whereas non-covered samples represent leaf water status (Ψ_{leaf}). *Ephedra californica* has tiny ephemeral leaves and green stems; when it had no leaves, Ψ_{leaf} corresponds to uncovered green stem water potential. We also defined the most negative seasonal predawn value of stem water potential for each species as minimum water potential (Ψ_{min} ; the greatest predawn xylem tension experienced by a species during the course of a year), because we reasoned that minimum seasonal values represent the ability to recharge plant water status and

Table 1. Coexisting woody plant species from a desert-chaparral ecotone in southern California, with representative figure symbols, leaf phenology, and presence of photosynthetic stems. Evergreen species are represented by black symbols, species with photosynthetic stems are represented by grey symbols, and deciduous species are represented by white symbols in figures

Species	Code	Family	Symbol	Leaf phenology	Photosynthetic stems
<i>Ambrosia salsola</i>	AMSA	Asteraceae	●	Deciduous	+
<i>Encelia actoni</i>	ENAC	Asteraceae	○	Deciduous	–
<i>Ephedra californica</i>	EPCA	Ephedraceae	■	Deciduous	+
<i>Eriogonum fasciculatum</i>	ERFA	Polygonaceae	●	Evergreen	–
<i>Ericameria linearifolia</i>	ERLI	Asteraceae	□	Deciduous	–
<i>Juniperus californica</i>	JUCA	Cupressaceae	■	Evergreen	–
<i>Prunus fasciculata</i>	PRFA	Rosaceae	△	Deciduous	–
<i>Psoralethamnus arborescens</i>	PSAR	Fabaceae	▽	Deciduous	–
<i>Purshia tridentata</i>	PUTR	Rosaceae	◇	Deciduous	–
<i>Quercus cornelius-mulleri</i>	QUCO	Fagaceae	▲	Evergreen	–
<i>Rhus ovata</i>	RHOV	Anacardiaceae	▼	Evergreen	–
<i>Scutellaria mexicana</i>	SCME	Lamiaceae	◆	Deciduous	+
<i>Senegalia greggii</i>	SEGR	Fabaceae	○	Deciduous	–
<i>Thamnosma montana</i>	THMO	Rutaceae	△	Deciduous	+
<i>Ziziphus parryi</i>	ZIPA	Rhamnaceae	☆	Deciduous	–

should be closely related to root contact with water sources when water is most scarce (Bhaskar & Ackerly 2006). During water potential measurements each month, we also recorded leaf phenological state and scored each species as having mature leaves, no mature leaves but with the presence of photosynthetic stems, or no mature leaves and no photosynthetic stems.

GAS EXCHANGE AND WATER POTENTIAL RELATIONSHIPS

Rates of net photosynthetic CO₂ assimilation (*A*) and stomatal conductance (*g_s*) were measured with an infrared gas analyser (6400; Li-Cor Biosciences, Lincoln, NE, USA) between 0800 and 1300 h in March–April 2009, March, April and July 2010, September 2011, and June–September 2012, to obtain a wide variety of seasonal gas exchange rates. For each individual, two newly formed mature leaves per twig were measured at ambient temperature, 400 μmol mol⁻¹ CO₂ and 1500 μmol m⁻² s⁻¹ photosynthetic photon flux density (PPFD) provided by a red blue light source (6400-02B #SI-710, Li-Cor Biosciences) (Evans & Santiago 2014). Following photosynthetic measurements, the twig was excised and placed in a plastic bag before measurement of bulk leaf water potential (Ψ_{leaf}) with a pressure chamber (1001; Plant Moisture Stress Instruments). Gas exchange leaves were stored in plastic bags and a cooler until returning to the laboratory for measurement of leaf area (Li-Cor 3000C; Li-Cor Biosciences). Maximum rates of photosynthesis (*A_{max}*) and stomatal conductance (*g_{s-max}*) were determined between 0800 and 1030 h on the youngest fully mature leaves during June and July (2010 and 2012), when leaves for all species were physiologically active and ambient conditions were 34.9–42.1 °C, 13–65% RH and 654–2226 μmol m⁻² s⁻¹ PPFD.

LEAF AND STEM MORPHOLOGY AND STRUCTURE

Leaf area-to-sapwood area ratio (LA:SA) was measured in 2010 on three twigs on each of three individuals per species as an index of hydraulic architecture to determine the relationship between total transpiring leaf area and the area of sapwood supplying water to those leaves (Martínez-Vilalta & PrometheusWIKI contributors 2011). Cross-sectional sapwood area of excised shoot samples taken at the first terminal branching point was determined by removing bark and measuring sapwood diameter with digital callipers to calculate cross-sectional area. If pith was present, its cross-sectional area was subtracted from total sapwood area. All

leaves distal to the first terminal branching point were removed from the sample segment and their total area was measured (LI-3100; Li-Cor Biosciences). We calculated specific leaf area (SLA) as fresh leaf area divided by leaf dry mass on three leaves from each of three individuals after drying at 65 °C for 48 h.

HYDRAULIC CONDUCTIVITY AND VULNERABILITY CURVES

Hydraulic trait measurements were conducted in fall (September–December) from 2009–2012. Large branch samples *c.* 1 m in length were collected from 4–8 individuals of each species in the field. Cut ends were covered with Parafilm and samples were placed in opaque plastic bags with wet paper towels to minimize water loss until transported to the lab. Once in the lab, stem samples were cut under water to a length of *c.* 16 cm. Emboli were removed from stems by vacuum infiltration under filtered (0.2 μm) degassed water for 8 h. Stem ends were then re-cut under water with a fresh razor blade for a final sample length of 14.2 cm.

Maximum stem hydraulic conductivity (*K_{max}*) was determined by connecting stems to tubing filled with filtered (0.2 μm) water flowing gravimetrically from an elevated source, through the stem, and into a reservoir on an analytical balance interfaced with a computer to record the flow rate (*F*; kg s⁻¹) (Sperry, Donnelly & Tyree 1988). Stem hydraulic conductivity (*K_H*; kg m s⁻¹ MPa⁻¹) was calculated as:

$$K_H = F \times L / \Delta P, \quad \text{eqn 1}$$

where *L* is the stem length (*m*), and ΔP is the hydraulic head (MPa). Stem hydraulic conductivity was also divided by sapwood area (SA; m²) to determine stem sapwood-specific hydraulic conductivity (*K_S*; kg m⁻¹ s⁻¹ MPa⁻¹) and distal leaf area (LA; m²) for calculating leaf specific hydraulic conductivity (*K_L*; kg m⁻¹ s⁻¹ MPa⁻¹).

Stem xylem vulnerability to cavitation was determined with vulnerability curves using the 'static' centrifuge method (Alder *et al.*, 1997; Sperry *et al.*, 2012; Jacobsen & Pratt, 2012). After determining *K_{max}*, stems were spun using a custom-built 14.2-cm diameter rotor in a refrigerated centrifuge (Sorvall RC-5C+; Thermo Scientific, Waltham, MA, USA) to induce negative pressure in the stem. After spinning, stems were removed and conductivity was measured as explained above. This process was repeated at progressively more negative pressures until conductivity approached zero. Per cent loss

of conductivity (PLC) was calculated at each water potential step as:

$$\text{PLC} = 100 \times (1 - (K/K_{\text{max}})). \quad \text{eqn 2}$$

Vulnerability curves were constructed by plotting water potential vs. PLC and fitting a Weibull model (Pammenter & Wiligen, 1998) to determine the water potential at which 50% of conductivity was lost (Ψ_{50}) for each species. Maximum xylem vessel lengths among our study species varied from 36–124 cm (L. Santiago, unpublished data). Vulnerability curves were validated by measurement of native midday water potential and native PLC and comparing them to the vulnerability curve.

CAPACITANCE

Terminal stem samples 5 mm in diameter were collected from 3–5 individuals per species in the early morning in November–December of 2011. Samples were sealed for transport to the lab, where they were cut to 10 mm in length, followed by removal of bark and pith. Fresh mass and volume were determined before xylem samples were rehydrated by vacuum infiltration. Xylem water potential (Ψ_x) was measured with a thermocouple psychrometer (PST-55-15; Wescor, Inc., Logan, UT, USA) connected to a data logger (Psypro; Wescor, Inc.), and placed inside an insulated water bath at 20 °C. Values were logged every 0.5 h and Ψ_x was recorded when stable readings were achieved (8–12 h), alternated with measurements of fresh mass until a Ψ_x of -7 MPa. Finally, samples were dried in an oven at 65 °C for 48 h and weighed to calculate water released. Capacitance was calculated as the linear regression slope fitted to the initial phase of the moisture release curve plotted as cumulative mass of water released against Ψ_x (Barnard *et al.* 2011).

TRANSPIRATION

Transpiration was measured as stem sap flow using thermal dissipation probes (TDP-15 or TDP-30; Dynamax Inc., Houston, TX, USA) or stem collar sensors (SGA2, SGA3 or SGA5; Dynamax Inc.), on three individuals of the 11 woody species with large enough stems to accommodate sensors (stem diameter ≥ 3 cm). These species represent 91.4% of stand basal area, based on two circular 0.125 ha study plots, in which diameter of the main stem of each individual was determined at 1.5 m height. Measurement of temperature difference between the heated upper probe and the unheated lower probe were recorded every minute and averaged every 10 min with a micrologger (CR1000; Campbell Scientific, Logan, UT, USA) and multiplexor (AM16/32; Campbell Scientific). We assumed that all sapwood was conducting for stems with a diameter < 6 cm. For stems > 6 cm in diameter, conducting sapwood area was determined by dye injection and the difference in wood color 2 cm above the point of insertion after 2 h (Santiago *et al.* 2000), and multiplied by sap flow velocity to determine transpiration rates. Total daily transpiration (E) and E normalized by basal area (E_{BA}) were averaged among the three individuals of each species. Relative humidity and temperature were quantified between shrubs at 1.5 m height with a shielded sensor (HMP 45AC; Viasala, Helsinki, Finland), in synchrony with transpiration measurements with a micrologger (CR1000; Campbell Scientific). All transpiration and environmental measurements were conducted during a 4-week study period in August 2010, at the earliest occurrences of peak midday temperatures (36–40 °C) that year.

DEPTH OF WATER EXTRACTION

We compared hydrogen stable isotopic composition (δD), which represents the amount of the rare heavy isotope of hydrogen ^2H (Deuterium, D) relative to the common light isotope of hydrogen ^1H , in plant sap and water in the vertical soil profile to assess the

depth water sources used by plants (Allison 1982; Ehleringer & Dawson 1992; Hasselquist, Allen & Santiago 2010). Three 2-m deep soil cores randomly located within the two study plots were collected in April 2010, c. 1 week after the last rain of the spring season that year. We separated core samples into a total of 14 depths at 0, 5, 15, 20 cm depths and further 20-cm increments down to 2 m. Within each core, two subsamples at each depth were immediately sealed into glass vials. On the same day as soil sampling, we collected samples of terminal twigs from three individuals per species. We only collected stem samples with no green material to ensure that they were not transpiring. We were unable to collect stem samples for three of the woody species because they exhibited little non-green material above-ground. One set of soil samples was measured for gravimetric water content by weighing, drying at 105 °C, and weighing again, whereas we stored the remaining soil and stem samples in a freezer at -20 °C until water was extracted using cryogenic vacuum distillation (Ehleringer & Osmond 1989). We determined δD of soil water and plant sap with a high temperature conversion elemental analyser (TC/EA; Thermo Scientific, Bremen, Germany) interfaced with a continuous flow isotope ratio mass spectrometer (DeltaV Advantage; Thermo Scientific) at the University of California Facility for Isotope Ratio Mass Spectrometry (FIRMS), Riverside, CA, USA.

STATISTICAL ANALYSIS

All variables were evaluated for normality and were \log_{10} -transformed if they were not normally distributed. We used a one-way ANOVA to compare trait values of species with photosynthetic stems and deciduous phenology vs. species that lacked of these features. Pearson's correlation coefficients were used to analyse relationships between measured traits. The relationship between A and Ψ_{leaf} was evaluated with linear regression to predict Ψ_{leaf} values at which A reaches $0 \mu\text{mol m}^{-2} \text{s}^{-1}$. We compared values of δD with the vertical pattern of isotopic composition of the soil profile for an estimate of integrated depth of water uptake using the Isosource Model (Phillips & Gregg 2003), which calculates ranges of isotopic source proportional contributions to a mixture when the number of sources is too large to permit a unique solution. The model generates a frequency distribution of feasible contributions from each source (soil depth) for each unique mixture (mean plant sap δD value for each species).

Results

Four of the 15 study species had photosynthetic stems and 11 of the 15 study species were deciduous (Table 1). Species with photosynthetic stems had significantly lower LA:SA than species without photosynthetic stems ($F = 9.43$; $P = 0.0089$), and all species with photosynthetic stems were deciduous, but the presence of photosynthetic stems was not related to any other physiological variable. The presence of deciduous phenology was only significantly related to SLA ($F = 8.93$; $P = 0.01$), with deciduous species showing a higher SLA than evergreen species.

All species shared similarly high predawn and midday stem and leaf water potential between January–May, the months receiving intermittent precipitation, and especially during March, the wettest month (Fig. 1). Species began to diverge in June with the onset of the summer heat (> 35 °C) until October, the driest month, when leaf water potential varied vastly between -6.82 and -0.89 MPa at predawn and between -8.27 and -1.93 MPa at midday (Fig. 1).

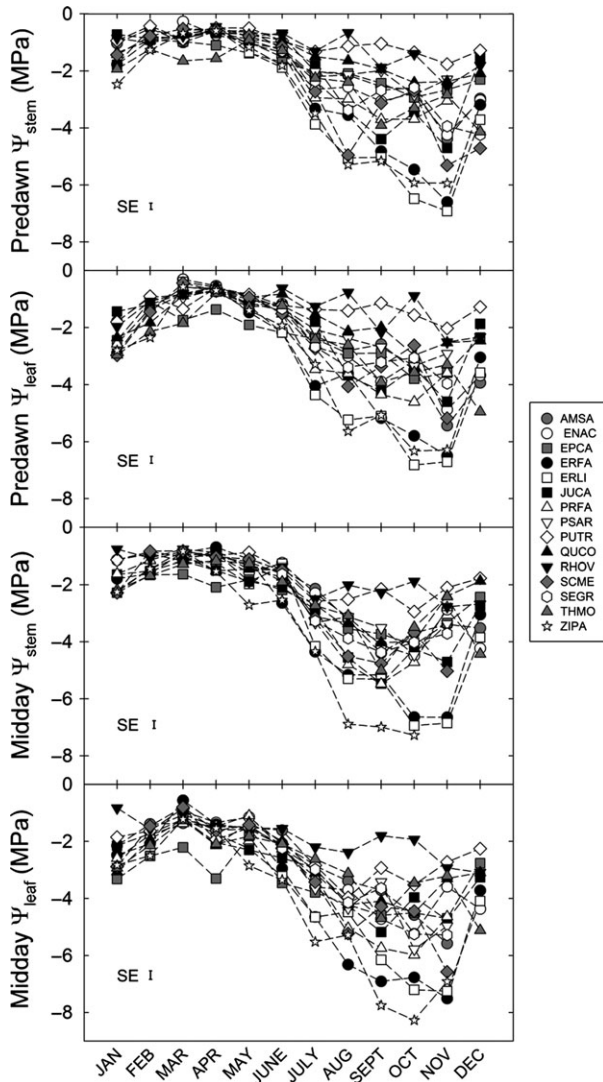


Fig. 1. Predawn and midday stem and leaf water potentials (Ψ) for 15 co-existing woody plant species from a desert-chaparral ecotone in southern California, measured each month for one calendar year. Standard error (SE) for each data set is shown. Corresponding species and symbols are found in Table 1.

Values for A_{\max} measured during the hot and dry summer season varied from $2.2 \pm 0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *S. mexicana* to $18.0 \pm 0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *S. greggi*, whereas $g_s\text{-max}$ varied from $33 \pm 11 \text{mmol m}^{-2} \text{s}^{-1}$ in *T. montana* to $281 \pm 34 \text{mmol m}^{-2} \text{s}^{-1}$ in *S. greggi* (Table 2). The regression used to predict the critical Ψ_{leaf} at which A is expected to reach $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ was only significant for seven of 15 species, but predicted values varied greatly among species (-9.42 to -3.44 MPa), and were always more negative than Ψ_{50} (Table 2, Fig. 2).

Midday Ψ_{stem} during the wettest month was the water potential parameter that was related to physiological and morphological traits. March midday Ψ_{stem} was significantly correlated with LA:SA (Fig. 2a) indicating that only species with low evaporative display per sapwood area allowed water potential to drop to low levels. March

midday Ψ_{stem} was also significantly correlated with SLA (Fig. 2b) and K_h (Fig. 2c). The correlation between March midday Ψ_{stem} and Ψ_{50} indicates that species with more resistant xylem achieved lower stem water potentials at midday during the growing season (Fig. 2d). The minimum seasonal water potential experienced by each species occurred between October and December (Fig. 1). The water potential at which A is expected to reach $0 \mu\text{mol m}^{-2} \text{s}^{-1}$ was the only variable correlated with both Ψ_{\min} ($R = 0.58$, $P = 0.02$) and minimum seasonal predawn Ψ_{leaf} ($R = 0.54$, $P = 0.04$).

Values for K_S increased with increasing LA:SA, demonstrating that enhanced water transport capacity is associated with greater evaporative surface area per sapwood area (Fig. 3a). Species with high LA:SA were also more vulnerable to xylem cavitation based on less negative values of Ψ_{50} (Fig. 3b). However, there was no significant correlation between K_S and Ψ_{50} ($R = -0.26$, $P = 0.35$). Species with high SLA also showed high K_S ($R = 0.62$, $P = 0.02$) and K_L ($R = 0.64$, $P = 0.02$), indicating that species with larger, thinner leaves support their evaporative area with enhanced water transport capacity. Among our study species, sapwood capacitance was related to sapwood density ($R = -0.81$; $P < 0.001$), but was not related to Ψ_{50} ($R = 0.30$; $P = 0.27$).

Species fell into two groups with regards to transpiration rates. The five profligate water using species transpired 8.10 to 14.40L day^{-1} , whereas the six species that showed relatively conservative water use transpired only 0.03 – 1.56L day^{-1} (Table 3). With the exception of *P. arborescens*, which has no leaves in the summer dry season when transpiration measurements were conducted, and *A. salsola*, which has photosynthetic stems and is also deciduous, the difference in water use corresponded to size, with large diameter species transpiring much more water than narrow diameter species ($R = 0.89$, $P = 0.0005$). When transpiration was normalized by the basal area of the transpiring stem, all of the profligate water users except *R. ovata* still use much more water than all of the conservative water users except *A. salsola*, indicating that beyond size, species specific regulation of water use does indeed lead to large differences in transpiration, even when the proper normalizing factor is applied.

Gravimetric soil water content varied from 2.6% at 5 cm depth to 9.2% at 160 cm depth. The δD of soil water showed a sinuous pattern of comparatively high values of -46‰ at the soil surface, a region of depleted values of -86‰ at 40 cm, and a curve back towards values around -75‰ at 200 cm depth (Fig. 4a). Compared to soil δD , stem xylem water δD occupied the relatively narrow range of -72 to -63‰ . The IsoSource model revealed that a variety of mixtures from the 14 depths were possible for each species. Per cent contribution from each depth ranged from 0–70% and no depth was ruled out as contributing to the mixture in xylem water for any species. Due to the curvature in δD with depth, five species (*E. linearifolia*, *Q. cornelius-mulleri*, *S. greggi*, *T. montana*, *Z. parryi*)

Table 2. Mean maximum rate of photosynthetic CO₂ assimilation (A_{\max}), mean maximum stomatal conductance (g_s -max), the predicted leaf water potential (Ψ_{leaf}) at which photosynthetic CO₂ assimilation (A) equals 0, based on linear regression of A as a function of Ψ_{leaf} , regression coefficient (r^2) and significance (P -value), of study species from a desert-chaparral ecotone in southern California

Species	A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	g_s -max ($\text{mmol m}^{-2} \text{s}^{-1}$)	Ψ at $A = 0$ (MPa)	r^2	P -value
<i>A. salsola</i>	9.5 ± 1.5	112 ± 18	-4.57	0.58	0.002
<i>E. actoni</i>	12.8 ± 6.1	172 ± 76	-7.18	0.96	<0.001
<i>E. californica</i>	5.9 ± 0.8	135 ± 50	-	-	NS
<i>E. fasciculatum</i>	7.7 ± 1.0	266 ± 36	-	-	NS
<i>E. linearifolia</i>	7.3 ± 2.0	51 ± 11	-	-	NS
<i>J. californica</i>	5.1 ± 1.5	69 ± 5	-	-	NS
<i>P. fasciculata</i>	7.5 ± 1.2	127 ± 36	-9.42	0.51	<0.001
<i>P. arborescens</i>	15.7 ± 2.9	184 ± 43	-4.83	0.60	0.008
<i>P. tridentata</i>	7.8 ± 2.7	153 ± 13	-	-	NS
<i>Q. cornelius-mulleri</i>	12.7 ± 3.6	141 ± 36	-	-	NS
<i>R. ovata</i>	3.3 ± 0.7	55 ± 16	-3.44	0.13	0.05
<i>S. mexicana</i>	2.2 ± 0.6	49 ± 22	-	-	NS
<i>S. greggii</i>	18.0 ± 0.6	281 ± 34	-5.1	0.89	0.004
<i>T. montana</i>	5.5 ± 0.7	33 ± 11	-	-	NS
<i>Z. parryi</i>	6.0 ± 1.9	84 ± 11	-7.37	0.21	0.02

showed δD values that overlapped with soil water δD values at 10–20 cm depth and 100–120 cm depth, making it impossible to pinpoint the most probable depth of water extraction (Fig. 4a). However, contributions from one of the sources in the top 20 cm are necessary to produce the isotopic mixtures of stem water measured in the rest of the species. The most negative March midday Ψ_{leaf} values were associated with relatively depleted δD values for xylem water, suggesting deeper water sources (Fig. 4b).

Discussion

We examined the diversity of drought survival traits among 15 co-existing woody species at a woodland ecotone site between chaparral shrublands and Mojave Desert vegetation in southern California. Our results show the existence of numerous drought survival traits, including cavitation-resistant xylem, deciduousness, photosynthetic stems and a broad range of plant water potential, water uptake depth and gas exchange behaviour. Species resistant to xylem cavitation showed more negative midday March Ψ_{stem} , but neither Ψ_{min} nor the depth of water extraction were related to Ψ_{50} , complicating the evaluation of whether a resistant xylem is associated with shallow rooting. All species with photosynthetic stems were drought deciduous, but there were also seven deciduous species without photosynthetic stems (Table S1, supporting information). We found no evidence that high sapwood capacitance buffered species with vulnerable xylem from reaching low water potentials, as capacitance was not related to Ψ_{50} . In contrast, LA:SA was a major determinant of hydraulic traits, with species supporting a large leaf area per sapwood area associated with high rates of water transport, but also associated with xylem that is vulnerable to cavitation, forming a trade-off between hydraulic safety and efficiency mediated through hydraulic architecture. The large seasonal range in water potential

among species was related to the predicted operational limits of photosynthetic gas exchange, demonstrating that the ability to withstand low water potential and maintain carbon gain at low water potential are related. Therefore, although some strategies are evident as trait combinations, many other traits are orthogonal and may promote a diversity of drought survival strategies at this ecotone.

The most dramatic evidence of diverse drought survival strategies at our site was the high variability in water potentials, both between species and within species across seasons (Fig. 1). Minimum seasonal water potentials reflect a balance between the maximum water deficit that leaves and xylem must tolerate to maintain physiological activity and access to soil water (Bhaskar & Ackerly 2006). Interestingly, there were evergreen (*E. fasciculatum*) and deciduous (*Z. parryi*) species among those with the most negative Ψ_{min} values and there were evergreen (*R. ovata*) and deciduous (*P. tridentata*) species among those with the least negative Ψ_{min} values. Photosynthetic stems were also scattered among the range of Ψ_{min} values with no apparent tendency to occur in species with high or low Ψ_{min} values. The tendency for major plant drought survival traits to occur independently among species is consistent with diverse origins of the taxa and may promote the co-existence of multiple trait combinations, and therefore strategies, at this ecotone site. The large range in minimum seasonal predawn Ψ_{leaf} values between -3.09 in MPa in *R. ovata* and -8.27 MPa in *Z. parryi*, which grow as neighbours in an area with no obvious variation in the moisture of microsites, strongly suggest that variation in rooting depth is a major determinant of operational water potential ranges and therefore contributes to drought survival strategies. Our isotopic analysis of the depth of water extraction revealed that deeper water sources are important for allowing midday Ψ_{leaf} to achieve more negative values during the growing season. However, the depth of water extraction by plants is dynamic and species may tap deeper waters sources as

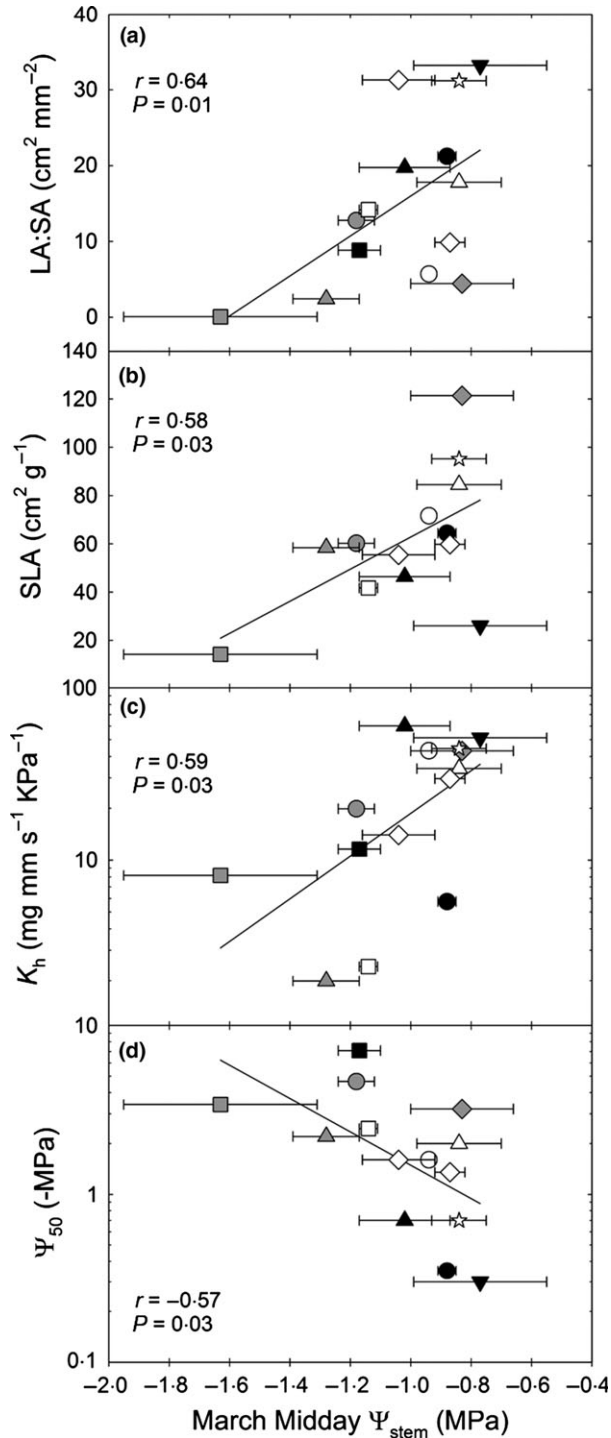


Fig. 2. (a) Leaf area-to-sapwood area ratio (LA:SA), (b) specific leaf area (SLA), (c) hydraulic conductivity (K_h), and (d) xylem water potential at 50% loss of hydraulic conductivity (Ψ_{50}) as a function of stem midday water potential (Ψ_{stem}) during the wettest month (March) for co-existing woody plant species from a desert-chaparral ecotone in southern California. Data for 14 of the 15 study species is shown because *S. greggii* had no leaves in March. Each symbol represents a species mean. Corresponding species and symbols are found in Table 1.

drought progresses (Meinzer *et al.* 1999), and ultimately access to water sources may be the strongest determinant of mortality. Data on dieback during the 2007 drought in

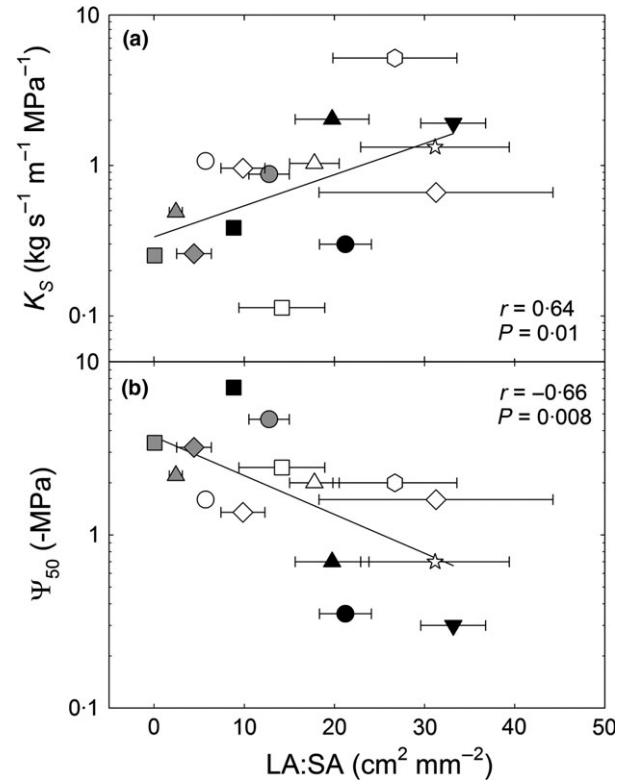


Fig. 3. (a) Stem sapwood-specific hydraulic conductivity (K_s) and (b) xylem water potential at 50% loss of hydraulic conductivity (Ψ_{50}) as a function of leaf area-to-sapwood area ratio (LA:SA) for 15 co-existing woody plant species from a desert-chaparral ecotone in southern California. Each symbol represents a species mean. Corresponding species and symbols are found in Table 1.

Table 3. Mean diameter, daily transpiration rates (E) and daily transpiration rates normalized by basal area (E_{BA}) of study individuals measured for sap flow in a desert-chaparral ecotone in southern California. Species are separated into two groups based on total amount of water use (E)

Species	Diameter (cm)	E (L day ⁻¹)	E_{BA} (g day ⁻¹ cm ⁻²)
Profligate water users			
<i>J. californica</i>	45.6 ± 24.3	11.93 ± 1.00	7.31 ± 0.87
<i>P. tridentata</i>	21.8 ± 0.7	11.91 ± 0.66	31.91 ± 2.49
<i>Q. cornelius-mulleri</i>	33.4 ± 1.4	8.10 ± 0.89	9.24 ± 1.43
<i>R. ovata</i>	52.3 ± 17.4	14.40 ± 2.26	6.70 ± 1.49
<i>Z. parryi</i>	34.9 ± 1.9	11.18 ± 0.89	11.68 ± 1.31
Conservative water users			
<i>A. salsola</i>	4.7 ± 1.2	0.64 ± 0.06	36.69 ± 4.49
<i>E. californica</i>	9.5 ± 5.1	0.36 ± 0.11	5.07 ± 2.23
<i>E. fasciculatum</i>	4.8 ± 1.0	0.03 ± 0.01	1.53 ± 0.48
<i>P. fasciculata</i>	16.6 ± 5.2	0.35 ± 0.03	1.63 ± 0.23
<i>P. arborescens</i>	29.9 ± 0.8	0.01 ± 0.01	0.01 ± 0.02
<i>S. greggii</i>	17.00 ± 8.3	1.56 ± 0.25	6.83 ± 1.58

the region showed that *E. fasciculatum*, a shallow-rooted, evergreen species with a vulnerable Ψ_{50} had 71% dead cover, whereas *R. ovata*, a species with deep enough roots

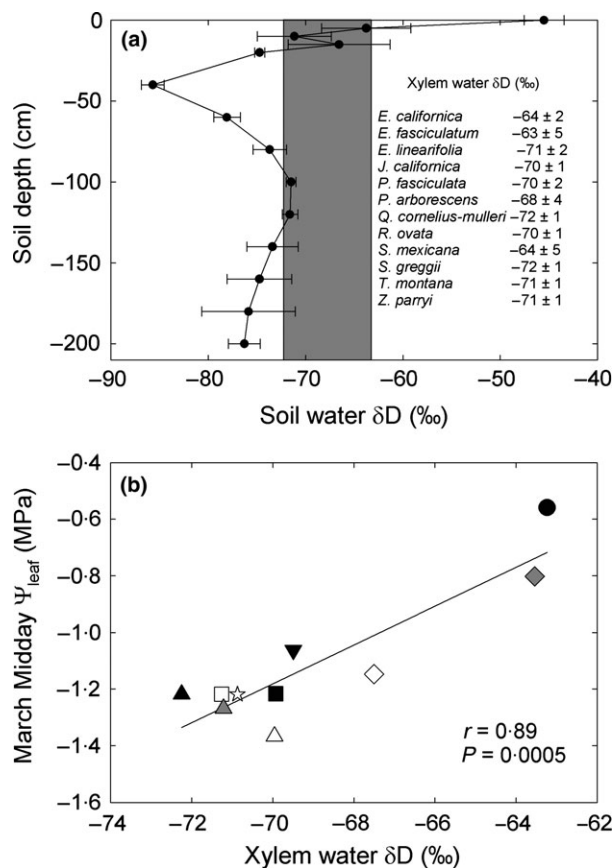


Fig. 4. (a) Hydrogen isotopic composition of soil water (δD) throughout the soil profile during the end of the wet season in April 2010. Points represent the mean of three 2-m deep profiles from a desert-chaparral ecotone in southern California. The grey region in panel (a) represents the range of stem water δD values. Numerical values in panel (a) represent the mean ± 1 SE of xylem water δD for three individuals of each species collected on the same day as soil profile samples. (b) Midday leaf water potential (Ψ_{leaf}) as a function of xylem δD during the wettest month (March) for co-existing woody plant species from a desert-chaparral ecotone in southern California. Data for 14 of the 15 study species is shown because *S. greggii* had no leaves in March. Each symbol represents a species mean. Corresponding species and symbols are found in Table 1.

to maintain Ψ_{leaf} near -3 MPa throughout the year, had only 24% dead cover (Steers 2008).

Based on our measurements of photosynthesis in relation to Ψ_{leaf} , seasonal plant water status is a key regulator of photosynthetic gas exchange and plant hydraulic traits related to mortality mechanisms by hydraulic failure or carbon starvation (McDowell *et al.* 2008). Mean maximum stomatal conductance varied from 33 to 281 $\text{mmol m}^{-2} \text{s}^{-1}$ and maximum photosynthetic CO_2 assimilation varied from 2.2 to 18.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$. However, not all species maintained these maximal rates. For example, some species had conservative, or relatively isohydric, strategies, closing their stomata at less negative Ψ_{leaf} , such as -3.44 MPa for *R. ovata*, -4.57 MPa for *A. salsola*, and -4.83 MPa for *P. arborescens*. Other species are predicted to continue carbon assimilation in an

aniso-hydric fashion, and instead tolerate the water stress until much more negative Ψ_{leaf} values, such as -9.42 in *P. fasciculatum*. However, because minimum seasonal pre-dawn Ψ_{leaf} was related to the Ψ_{leaf} at which photosynthesis is predicted to cease, different species appear to have the ability, through rooting, regulation of water loss or low Ψ_{50} , to maintain their water potential above the point at which photosynthesis ceases. Therefore, although isohydry has emerged as one important axis of ecological variation with respect to drought responses (Skelton, West & Dawson 2015), it is only one of several that appear important when a comprehensive array of drought survival traits are evaluated. During extreme drought, many of these species likely lose their leaves and thus the water potential at which leaves drop may be more indicative of the propensity for carbon starvation than degree of isohydry. Furthermore, plants with photosynthetic stems can maintain carbon gain following leaf loss, often at greater water use efficiency than photosynthesis by leaves (Ávila, Herrera & Tezara 2014), but whether these species incur a greater water loss than species with non-photosynthetic stems may be key for determining the balance of carbon gain and water loss and the mechanism of mortality.

Including the current study, there is now evidence from all five Mediterranean-type climates that a diverse range of drought survival strategies co-exist (Mitchell *et al.* 2008; Moreno-Gutierrez *et al.* 2012; West *et al.* 2012; Salgado Negret *et al.* 2013). This may be the case because plant communities in Mediterranean-type climates are composed of a combination of species derived from arid geofloras that were in place as the Mediterranean-type climate developed and species that evolved since the emergence of Mediterranean-type climates (Peñuelas, Lloret & Montoya 2001; Ackerly 2004b). There is also evidence that hydraulic trait variation is lowest in sites with lower water availability, illustrating a convergence of water-use behaviour at sites where plants experience the largest seasonal water deficits (Mitchell *et al.* 2008). The current study represents a site with a large seasonal water deficit, but also large variation in hydraulic traits and likely differs from the study sites of Mitchell *et al.* (2008) because the site of the current study occurs at an ecotone. Whereas previous studies have found ecotones to be particularly susceptible to global climate change (Allen & Breshears 1998), they were dominated by only a few woody species. The site of the current study may be more resilient than less diverse vegetation types due to a mosaic of species from different botanical origins. Thus while some species may experience increased mortality due to climate change-type drought, the intensity and duration of drought may favour other species with contrasting drought survival strategies.

Drought survival mechanisms comprised of resistant xylem, deciduousness, photosynthetic stems, soil water access and regulation of water loss varied widely among our species, and promote a diverse array of drought survival strategies in an arid ecosystem of considerable floristic complexity. Whereas ecotones may show negative signs

of environmental change before spatially buffered interior sites are affected (Gitlin *et al.* 2006), sites with diverse drought survival strategies among species should be more resistant to drought-induced mortality than sites with low species or functional richness. Overall, which species yield and which species persist during extreme drought will be a product of the type of drought, combined with the drought survival strategies of species determined by multiple trait associations.

Acknowledgements

We graciously acknowledge Jeffrey Ambriz, Hailey Buckingham, Tiffany Chu, Liz Diaz, Maria Claudia Diaz, Obaid Khan, Fortino Morales, Cara Stripe, Sisouphanh Traymany, Melody Tsoi, Dwight Williams and Larissa Yates for dependable assistance in the field and lab; David Ackerly, Brandon Pratt, Rich Minnich and Edie Allen for riveting discussions on desert chaparral vegetation; Greg Hill of the Bureau of Land Management for research permits and support; Perry and Kathy DeRouen for use of their private road to access study sites; the University of California provided logistical support. Funding was provided by the University of California Agricultural Experiment Station, the USDA National Institute for Food and Agriculture, and National Science Foundation awards IOS-0817212 and DEB-0706813 to L.S.S.

Data accessibility

All data used in this manuscript are present in the manuscript and its supporting information.

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Received 18 December 2014; accepted 11 July 2015

Handling Editor: Katie Field

Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Materials and methods.

Fig. S1. Representative vulnerability curve replicate for each species.

Fig. S2. (a) Leaf area-to-sapwood area ratio (LA:SA), (b) specific leaf area (SLA), (c) unlogged hydraulic conductivity (K_h), and (d) unlogged xylem water potential at 50% loss of hydraulic conductivity (Ψ_{50}) as a function of stem midday water potential (Ψ_{stem}) during the wettest month (March) for co-existing woody plant species from a desert-chaparral ecotone in southern California. Data for 14 of the 15 study species is shown because *S. greggii* had no leaves in March. Each symbol represents a species mean. Corresponding species and symbols are found in Table 1. Logged plots are shown in Fig. 2.

Fig. S3. (a) Unlogged stem sapwood-specific hydraulic conductivity (K_s) and (b) unlogged xylem water potential at 50% loss of hydraulic conductivity (Ψ_{50}) as a function of leaf area-to-sapwood area ratio (LA:SA) for 15 co-existing woody plant species from a desert-chaparral ecotone in southern California. Each symbols represents a species mean. Corresponding species and symbols are found in Table 1. Logged plots are shown in Fig. 3.

Table S1. Phenological chart of 15 study species from a desert-chaparral ecotone in southern California during 2011.

Table S2. Species names, code, family, phenology, morphological and physiological characteristics of study species encountered in desert chaparral ecotone at Morongo Valley, California, USA.