Mortality of resprouting chaparral shrubs after a fire and during a record drought: physiological mechanisms and demographic consequences

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Abstract

We examined postfire regeneration of chaparral shrubs during an intense drought. This study focused on the demography and physiology of shrub species that resprout from a basal lignotuber following fire. We found significant levels of resprout mortality when intense drought occurred in the year following fire during the period of shrub recovery. Three of the seven sampled resprouting species had the greatest or near greatest levels of mortality ever recorded when compared to previous studies. Most shrub mortality occurred during the drought after individuals had resprouted (i.e. individuals survived fire, resprouted and then subsequently died). Physiological measurements of species with high mortality suggested that resprout stems were highly embolized and xylem hydraulic conductivities were close to zero during the peak of the drought. In addition, lignotubers of two of the three species experiencing high mortality were depleted of starch. Population densities of most shrub species declined after the drought compared with their prefire levels, with the exception of one drought tolerant obligate seeding species. Resprouting shrub species may deplete their carbohydrate reserves during the resprouting process, making them particularly vulnerable to drought because of the need to transpire water to acquire the CO_2 that is used to supply energy to a large respiring root system. Drought appears to interact with fire by altering postfire shrub recovery and altering species abundances and composition of chaparral communities.

Introduction

Plants face many disturbances such as herbivore damage or crown fire that leads to partial or complete crown removal. A common response to such a disturbance is to resprout new shoots. Although resprouting is a trait shared by many species that inhabit fire-prone ecosystems, it is debatable if resprouting is an adaptation to fire for many species (Bradshaw *et al.*, 2011); however, it is clear that resprouting is adaptive in fire-prone ecosystems and that fire has shaped many plant traits (Cowan & Ackerly, 2010; Keeley *et al.*, 2011, 2012). Resprouting ability is important at many scales and can, for example, influence population and community dynamics and structure (Malanson & O'leary, 1982; Clarke, 2002; Clarke & Dorji, 2008; Clarke *et al.*, 2013). Resprouting species dominate large areas of the globe and improving our understanding of resprouting will enhance our understanding of plant evolution and our ability to predict the response of communities and species to environmental change (Pausas *et al.*, 2006; Keeley *et al.*, 2012; Clarke *et al.*, 2013).

Factors related to fire regime affect resprouting and have been well studied (Clarke *et al.*, 2013). For example, there is good evidence that resprout success is partially determined by the intensity of a fire (Rundel *et al.*, 1987; Moreno & Oechel, 1993; Borchert & Odion, 1995; Odion & Davis, 2000; Keeley, 2006b; Wright & Clarke, 2007). Moreover, fire frequency and seasonal timing of fire are important factors affecting resprouting for some species (Zedler *et al.*, 1983; Rundel *et al.*, 1987; Haidinger & Keeley, 1993; Franklin *et al.*, 2001; Lloret *et al.*, 2003; Wright & Clarke, 2007; Enright *et al.*, 2011). Beyond fire regime, there are plant life history and functional traits that influence the success of resprouts (Moreira *et al.*, 2012).

Successful resprouting after crown fire requires that a plant survive and compete to reclaim the space lost in the fire. This requires buds that can rapidly form new

shoots (Zammit, 1988; Vesk & Westoby, 2004), stored belowground resources that fuel initial aboveground growth (Canadell & López-Soria, 1998), and vigorous stem elongation and leaf expansion that compete for space and acquire new carbon to fuel further growth (Malanson & Trabaud, 1988; Moreira *et al.*, 2012; Marais *et al.*, 2014). In this context, successful resprouting has three components: first, surviving the fire; second, sprouting vigor; and third, postresprouting survival and final re-establishment (Le Maitre *et al.*, 1992; Moreira *et al.*, 2012). Moreira *et al.* (2012) found that each of these three factors vary in importance for a given species.

There are life history differences that are associated with resprouting success. After fire, some species resprout (R+) without seedling establishment (S−), others resprout and establish seedlings (R+S+), and still others do not resprout and only reestablish by seedling recruitment (R−S+). Among resprouters, there is wide variability in resprouting ability, especially in the R+S+ group (Le Maitre *et al.*, 1992). For example, some species regularly experience >50% mortality after a fire, while other species generally have no mortality (Thomas & Davis, 1989; Keeley, 2006b; Marais *et al.*, 2014).

Drought is an additional factor that may affect resprout success (Van Nieuwstadt & Sheil, 2005; Granzow-De La Cerda *et al.*, 2012; Clarke *et al.*, 2013). Resprouts often experience favorable water status in the months immediately after crown fire (Desouza *et al.*, 1986; Saruwatari & Davis, 1989; Clemente *et al.*, 2005; Ramirez *et al.*, 2012). This is likely due to the reduction of the leaf area of the community, which leaves more water available in the soil (Silva *et al.*, 2006). Moreover, at the individual plant level, the root to shoot ratio is elevated after crown fire leading to elevated water supply relative to the demand. However, there is also evidence that resprouts are more sensitive to water stress than co-occurring unburned plants. For example, compared with unburned plants, resprouts typically lose turgor of leaf tissues at less negative water potentials (Saruwatari & Davis, 1989), and stem xylem cavitation resistance is reduced in resprouts (Ramirez *et al.*, 2012). In fire-prone ecosystems that are seasonally dry, such as Mediterranean-type ecosystems, a drought may lead to reduced water status in resprouts, and that, coupled with their heightened vulnerability to water stress, could lead to greater resprout mortality.

The physiological factors associated with mortality during water stress are complex and much debated (Sala *et al.*, 2010; Anderegg & Callaway, 2012). Two leading hypotheses regarding the causes of mortality of woody plants are loss of hydraulic function due to drought-induced cavitation (Pratt *et al.*, 2008; Kursar *et al.*, 2009; Anderegg *et al.*, 2012), and complications arising from protracted stomatal closure and declining carbohydrate reserves (Breshears *et al.*, 2008; Mcdowell *et al.*, 2008; Anderegg *et al.*, 2012). This latter cause is hypothesized to be important over long periods such as multiyear or decade long droughts (Mcdowell *et al.*, 2008; Galiano *et al.*, 2012). However, carbohydrate stores can be depleted on the short-term when they are mobilized to fuel resprouting of new shoots following crown fire. If a drought occurs during this resprouting period, carbohydrates could plummet to harmful levels due to restriction of water loss and CO_2 uptake by stomata.

In the context of climate change, understanding the physiological causes of mortality is needed for predictive modeling of vegetation changes (Allen *et al.*, 2010; Mcdowell *et al.*, 2011; West *et al.*, 2012). One of the challenges of understanding and predicting vegetation dynamics is that stresses often occur simultaneously leading to complex and poorly understood responses (Niinemets, 2010; Anderson-Teixeira *et al.*, 2013). In Mediterranean-type ecosystems, soil moisture depletion during a typical summer rainless season often places plants under considerable water stress (Kolb & Davis, 1994; Beveridge & Simmons, 2006; Jacobsen *et al.*, 2007a). Predicted hotter and dryer summer conditions in Mediterranean-type shrublands may increase both droughts and fires (Field *et al.*, 1999). Thus, it is increasingly important to understand how these two forces interact to affect shrub survival.

We investigated how drought effects postfire resprout success using a natural postfire experiment in a mixed species chaparral stand that had experienced a fire and was followed by a record drought. Our measurements included resprouting success, water status, xylem cavitation resistance, and tissue carbohydrate concentration. We also monitored resprout survival and seedling recruitment to determine the demographic consequences of a fire followed by a drought. Gaps created by resprout mortality may create sites for seedling recruitment (Keeley *et al.*, 2012), thus resprout mortality could be offset by seedling recruitment (Le Maitre *et al.*, 1992). We compared the physiology of resprouts to co-occurring unburned plants, and for plant survival, we compared our results to a database that we compiled of previous studies.

This study provides an important snapshot of how fire and intense drought interact to affect postfire regeneration of chaparral shrubs. Moreover, the physiological mechanisms driving mortality of resprouts during drought are not clear, which motivated this study. The focus on physiological mechanisms required time-consuming measurements, which is why we focused our efforts on intensively sampling at one field site.

Materials and methods

The Sherwood Lake Fire occurred on July 6, 2006. We established a field site in a chaparral shrub community in an area burned by the fire (N34°7.950′, W118°51.560′) at about 400 m elevation. An adjacent unburned stand was used as a comparison group for many of our physiological measurements. The site experiences a Mediterranean-type climate characterized by hot dry summers, cool rainy winters, and a predictable summer rainless period that typically lasts 5–7 months. The year following the fire was the driest year in recorded history for Los Angeles County (82 mm compared with the hundred year mean of 380 mm). A remote automated weather station located about 24 km from the field site in Cheesebro Canyon recorded about 116 mm of rain from July 2006–July 2007. The average rainfall from this weather station from 1995–2011 was 348 mm. The site burned 30 years prior to July 6, 2006 on 4 July 1976, and thus, the fire we studied fell within the natural fire regime for chaparral in this region (Keeley, 2006a).

The seven dominant resprouting shrub species that occurred at the site were all studied. These species represented two different life history types (Table 1), including five species that resprout from a lignotuber and recruit new seedlings postfire (R+S+), and two species that only regenerate after fire by resprouting (R+S−). We also sampled seedlings of an eighth species, *Ceanothus crassifolius* Torr., from a third life history type, obligate seeders (R−S+), but made no other measurements on this life history type. Although we tracked shrub survival for seven resprouting species, the study design was focused on intensively sampling three of the most abundant and dominant species at the site: *Adenostoma fasciculatum* Hook. and Arn., *Cenothus spinosus* Nutt., and *Heteromeles arbutifolia* (Lindl.) M. Roem. (Table 1). The focus on these species was aimed at identifying the physiological mechanisms linked to postfire resprout success.

Beginning June 25, 2007, individuals (root crowns and resprouts) were tagged and tracked through time. Burnt plants that had not resprouted were identified by their burned branch and root crown characteristics. By counting burned plants, we determined prefire stand density for our sampled species. Plants that had resprouted and subsequently died before our initial survey were easily identified because the dead resprouted shoots were still attached to plants. We tagged every individual of a species, and we could find in our study area except for Af. For this species, 200 individuals were tagged (about 33% facing west, 33% facing east, and 33% on a ridge top). Time limitations precluded us from tagging all of the species at the same time. Individuals of Af were tagged on June 25, 2007, Cs (*n* = 64), Ha (*n* = 27), and *Rhamnus ilicifolia* Kellogg (*n* = 12) on August 14, 2007, *Adenostoma sparsifolium* Torr. (*n* = 11) on December 11, 2007, and *Malosma laurina* (Nutt.) Nutt. ex Abrams (*n* = 26) and *Rhus ovata* S. Watson (*n* = 16) on February 9, 2008 (see Table 1 for species abbreviations). At the time of tagging, root crown (lignotuber) diameter was measured for all individuals as an estimate of plant size. Survival of all shrubs was followed every two or three months until October 2008, then less frequently until the last sample date in January 2013. At each sampling time, we also visually estimated the percentage of the crown of each plant that was alive, measured plant height, and noted if plants had been browsed or otherwise damaged by animals. Browsing and damage was minimal for the duration of the experiment.

As a comparison group, we surveyed the literature for resprouting mortality. We found 19 studies (Table 2), including our own unpublished data that contained quantitative information on resprouting mortality after fire. Many of these studies included data from multiple sites, and each site was treated as an independent estimate of resprout survival. Rundel *et al.* (1987) sampled low-, moderate-, and high-intensity subplots within their study plots, and we had no way to weight the subplots so we only included data reported from moderate intensity burn subplots. One report mentioned 100% mortality of 'patches' of Af adults after a prescribed fire in May 1986 (White *et al.*, 1995). This reference provided no additional data and the observation of 100% mortality in patches is presumably not a random sample, and thus, it was not analyzed. To compare to our data, we used total survival, that is, those plants that resprouted after fire and the resprouts that survived. We used total survival because most studies only

Table 1 Species included in study, survival of plants burned in fire, and the ratio of seedlings to parents in plots

Species	Abbreviation	Life History Type	*n*	Resprouted (%)	Resprout Survival (%)*	Total Survival (%)†	Seedling: Parent
A. fasciculatum	Af	(R+S+)	200	62	44	27	1.81
A. sparsifolium	As	(R+S+)	12	100	100	100	N/A‡
C. crassifolius	Ccr	(R−S+)	56	0	0	0	6.15
C. spinosus	Cs	(R+S+)	64	95	38	36	1.10
H. arbutifolia	Ha	(R+S−)	30	100	73	73	0
M. laurina	Ml	(R+S+)	26	100	100	100	0.81
R. ilicifolia	Ri	(R+S−)	12	100	100	100	0
R. ovata	Ro	(R+S+)	16	100	100	100	0.17

*This is individual resprout survival of the drought period that ended January 2008.

†This is total survival that includes plants that resprouted and those resprouts that survived up to January 2008. There was some additional mortality of few individuals after this sampling date.

‡As individuals were located downslope from all other sampled species, thus there were no seedlings in the sampled plots.

Table 2 Total resprout survival from current study compared with mean ± 95% confidence limits (*n* = number of independent reports), maximum, and minimum resprout survival reported in the literature

Species	Total resprout survival (%)*	Mean resprout survival (%)†	*n*	Max resprout survival (%)	Minimum resprout survival (%)	References§
A. fasciculatum	20	64.5 (57.9–71.1)	47	100	12.0	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 15, 16, 18, 19
C. spinosus	25	59 (23.8–93.6)	4	86	40	6, 7, 14, 17
H. arbutifolia	57	84.5 (74.3–94.6)	10	100	60‡	6, 7, 8, 11, 12, 13, 16, 19

*Total resprout survival recorded after 5 years of sampling.
†Mean resprout survival sampled from published and unpublished sources. Published reports generally did not separate the numbers of individuals that resprouted from those that resprouted and then died, and thus, the numbers reported represent total resprout survival. Most mortality typically occurs in the first year after fire (e.g., Fig. 1a); however, reported values are often reported at time points >1 year after the fire, which is why we report our five-year resprout survival for comparison.
‡This value may underestimate survival because it comes from sampling in December at a high elevation site (1250 m) after a July fire, and it is typical for some individuals of this species to sprout later in the winter and spring.
§1. Barton (1995)2. Beyers and Wakeman (2000); 3. Dodge (1975); 4. Hedrick (1951); 5. Horton and Kraebel (1955); 6. Keeley (1998); 7. Keeley *et al.* (2006); 8. Kinucan (1965); 9. Moreno and Oechel (1991); 10. Odion and Davis (2000); 11. Plumb (1961); 12. Pratt *et al.* unpublished data; 13. Ramirez *et al.* (2012); 14. Rowan (2008); 15. Rundel *et al.* (1987); 16. Safford and Harrison (2004); 17. Thomas and Davis (1989); 18. Tyler and D'antonio (1995); 19. Zedler *et al.* (1983).

report total survival making it impossible to separate out mortality due to fire vs. resprout mortality.

The water status of resprouting shrubs and of unburned shrubs in an immediately adjacent stand was sampled using a pressure chamber (PMS Instrument Company, Albany, OR, USA) starting 16 August 2007, as the dry season was peaking. We made these measurements on our three focal species: Af, Cs, and Ha. Water potentials were sampled approximately monthly during the dry season and every two or three months after that. Samples were collected at predawn when plants were at their most hydrated and at midday on the same day when their tissues would be maximally dehydrated.

Plant physiological measures were also made on resprouting and unburned plants of the three focal species. To estimate the effect of the drought on stem cavitation, we measured the vulnerability to cavitation using a centrifuge method that we have thoroughly tested (Jacobsen & Pratt, 2012; Tobin *et al.*, 2013). Vulnerability curves for Ha were measured from individuals at the field site. Due to time constraints, we used unpublished vulnerability curves collected in previous studies taken from nearby field sites in the San Gabriel Mountains and the Santa Monica Mountains. Vulnerability to cavitation curves were used in conjunction with water potential data (mean between predawn and mid-day to approximate midday stem xylem water potential) to estimate the percentage loss of conductivity (PLC) and the xylem-specific conductivity of stems due to cavitation during the summer 2007 dry season.

Net carbon assimilation and stomatal conductance were measured 23 September 2007 using a Li-Cor 6200 (Li-Cor Corporation, Lincoln, NB, USA). Measurements were made in the morning hours (*n* = 4–6 per species and treatment). Measured leaves were collected, and the area was measured using a leaf area meter (Li-3000, Li-Cor Corporation, Lincoln, NB, USA). For the needle-like leaves of chamise, projected area was multiplied by PI to get total leaf surface area. Leaf Area Index of shrubs (*n* = 3–4 for unburned plants and *n* = 6–8 for resprouts) was estimated by measuring interception of light by individual plant canopies using a commercial quantum sensor array (AccuPAR LP-80; Decagon Devices, Pullman, WA, USA).

The carbohydrate content of lignotubers was measured using an enzymatic/colorimetric assay. Lignotuber tissue was harvested using an increment borer in the field (5 mm diameter bore; *n* = 6 individuals per species, treatment, and sampling time). The tissue was kept on ice for transport to a laboratory the same day where it was heated in an oven at 100 °C for 1 h and then dried at 60 °C for >3 days. When dry, the tissue was ground and stored in a desiccation chamber. To extract carbohydrates, 100 mg of dried samples were boiled for three minutes in a pH 4.8 75 µM sodium acetate buffer solution and then autoclaved for 20 min. The extraction was concluded by centrifuging samples at 770 *g* to remove solids. Aliquots of the extract were assayed for glucose using a standard assay kit (Glucose Hexokinase Assay; Sigma-Aldrich Co., St. Louis, MO, USA). Starch was analyzed by digesting starch to glucose using amyloglucosidase (Product number 10115, Sigma-Aldrich Co.), analyzing for glucose using the above kit, and calculating starch content by subtraction of predigestion glucose. The starch content of lignotuber tissue was expressed as a percentage of the dry mass.

Seedlings were surveyed December 1, 2007, October 11, 2008, and January 12, 2013. To sample the seedlings, three large rectangular plots (areas = 7000, 5000, and 5000 m^2) were established in the areas where we sampled resprouts. Each plot was 50 m wide and ≥100 m long. In the first survey, we recorded 489 seedlings. All of the seedlings in the plots were sampled by at least six people walking parallel transects the full length of the plots. The density of resprouts in these sample plots was also surveyed.

Carbohydrate, water potential, stomatal conductance, net carbon assimilation, and percentage loss of conductivity data

Table 3 ANOVA table for percentage loss of conductivity analysis

Factor	df	SS	F	P
Treatment*	1	0.056	8.781	0.003
Spp	2	1.003	78.301	<0.001
Date	1	0.128	10.027	<0.001
Treatment × Spp	2	0.197	15.402	<0.001
Spp × Date	2	0.069	2.729	0.033
Date × Treatment	1	0.039	3.089	0.05
Spp × Date × Treatment	2	0.018	0.709	0.587
Error	93	0.595		

*Treatment refers to unburned and resprouts.

Table 4 ANOVA table for xylem-specific conductivity analysis

Factor	df	SS	F	P
Treatment*	1	0.365	196.214	<0.001
Spp	2	1.635	438.607	<0.001
Date	2	0.024	6.567	0.002
Treatment × Spp	2	0.604	162.041	<0.001
Spp × Date	4	0.014	1.941	0.109
Date × Treatment	2	0.013	3.745	0.027
Spp × Date × Treatment	4	0.003	0.448	0.773
Error	97	0.180		

*Treatment refers to unburned and burned resprouts.

were analyzed using ANOVA (Tables 3 and 4). Independent variables included in the models were species, treatment (unburned and resprouts), and time where appropriate. Contrasts were used to compare specific differences between treatments. The relationship between survival (response) and the independent variables of plant size and species was analyzed using general linear models with binomial errors. Individuals of species were sampled randomly. All analyses were performed using JMP software (JMP v9.0; SAS Institute Inc., Cary, NC, USA). Assumptions of statistical models were checked, and transformations were used when necessary.

Results

Most species survived the fire. All of the species (except the obligate seeder) approached 100% survival of the fire except for Af (Table 1). Plant size (lignotuber diameter) was not different between the Af individuals that survived the fire and the ones that did not survive (χ^2 = 0.58, P = 0.446; the mean ± 1 SE of Af survivors was 279 ± 17 mm and 258 ± 21 mm for nonsurvivors).

There was wide variability among the species in resprout survival during the drought (Table 1). Four species had 100% survival; however, three other species, Af, Cs, and Ha, suffered significant mortality of resprouting individuals (Table 1). For Af, Cs, and Ha,

the plants that survived the drought had larger lignotuber diameters than individuals that did not survive (χ^2 = 6.08, P = 0.013) and species did not interact with lignotuber size (χ^2 = 2.66, P = 0.264). The mean ± 1SE lignotuber diameter of survivors was 336 ± 23 mm, and for nonsurvivors, it was 245 ± 16.

The timing of the mortality and dieback suggested that it was drought-induced (Fig. 1a and b). The survival among resprouts had its sharpest decline during the peak of the drought, which occurred shortly after we began sampling in July 2007 (Fig. 1a). At this time, plants were already at peak water stress (a seasonal low in water potential; Fig. 2), and Af and Cs had considerable dieback (Fig. 1b). Some rain fell in November and December 2007 (Fig. 1); however, this rain had little impact in alleviating water stress (Fig. 2), and the drought did not fully end until large rainstorms occurred in January 2008 (Fig. 1a). After these storms, the predawn and mid-day water potentials increased in all species (Fig. 2a and b). *Ceanothus spinosus* and Ha may have had some mortality after the January rains, but we did not immediately sample before the rains, thus we do not know if the mortality occurred during the drought or after (Fig. 1). Mortality ceased during the rainy season, suggesting that water stress was a driver of the observed mortality (Fig. 1a).

For resprouts, initial dieback of shoots was predictive of later death. Upon initial sampling, if plants had a percentage crown alive of <90%, they had a lower percentage of survival during the drought period (23% for Af, 11% for Cs, and 0% for Ha). By contrast, those plants that had >90% of the crown alive had much higher drought survival (78% for Af, 73% of Cs, and 81% for Ha).

Height of plants was unrelated to mortality; however, our sample size for height was small (n = 12) for each species, which precluded a robust analysis. Height of shrubs closely followed seasonal rainfall patterns (Fig. 1c). The three species that we intensively sampled grew to 20–40 cm tall in their first winter and spring after fire (Fig. 1c). The other species are omitted from Fig. 1c for clarity and their heights in summer 2007 were as follows: As = 78.5; Ml = 83.5; Ri = 28.3; and Ro = 52.3 cm. During the dry season, height remained about constant except for Cs where the average height declined due to mortality of some plants (Fig. 1c).

This study was a natural experiment, and we did not have a nondrought control. Thus, to determine whether the observed survival for our intensively studied species was out of the normal range, we surveyed the literature and used previous studies that had examined resprout survival (Table 2). For Cs and Ha, the survival that we recorded was the lowest ever observed, and for Af, the survival was substantially
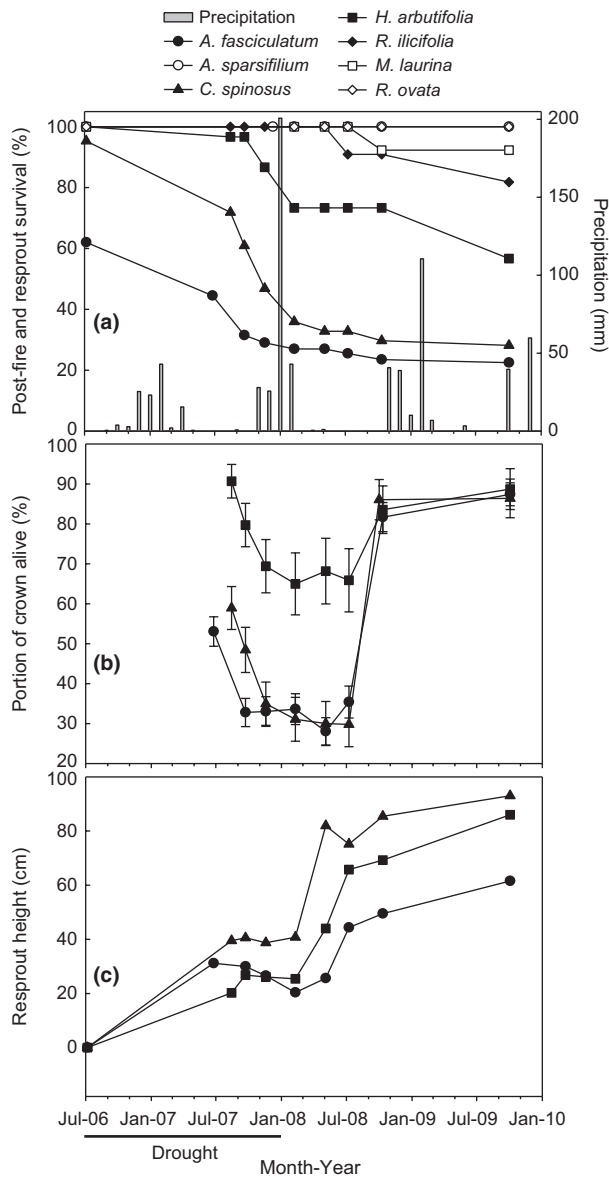
Fig. 1 Plants that survived a fire (the first data point in panel a) and the subsequent survival of resprouts for seven chaparral shrub species (a). Panel (b) shows the percentage of crown that was alive at each sampling period. The resprout height of three chaparral species in the first 2 years following fire (c). This figure was truncated to highlight the time period during and immediately following the drought (the drought period is labeled on the x-axis). Heights of only the three focal species are shown for clarity.

below the lower 95% CL of the mean of previously reported studies and was close to the lowest survival ever reported (Table 2).

During the summer and fall, drought months of August–November 2007 water potential at both predawn and mid-day were generally more negative than the same months of the following year (Fig. 2a and b).
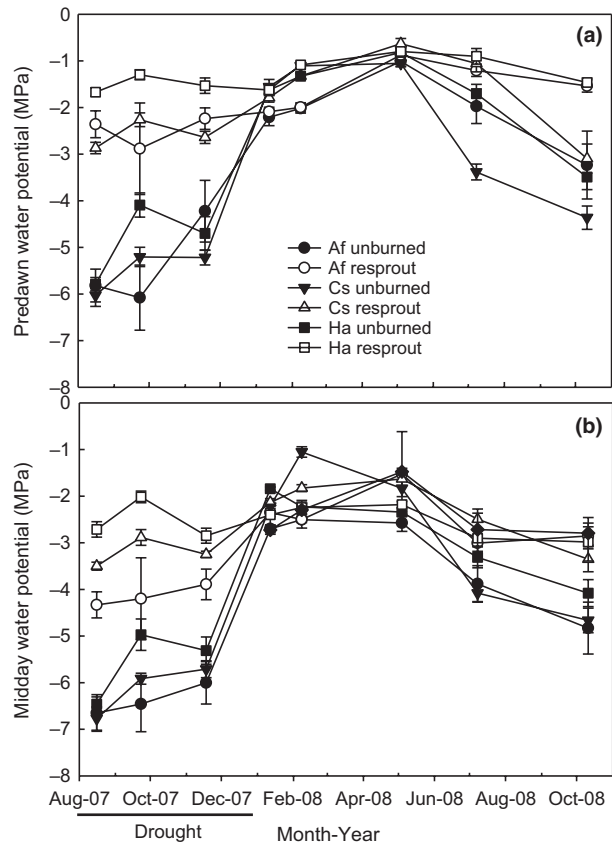

Fig. 2 The mean $\pm$ 1 SE ($n = 6$) of predawn (a) and mid-day (b) water potential for unburned plants and postfire resprouts. The months corresponding to the drought period are highlighted on the x-axis.

This indicates that both unburned plants and resprouts experienced heightened water stress during the drought.

During the drought months of August–November 2007, resprouts had significantly less negative Ψ_w than unburned plants at both predawn and mid-day ($F_{1,122.6} = 238.73$, $P < 0.001$; Fig. 2a and b). Predawn Ψ_w approximates the functional rooting depth for a species and, among the unburned plants, the three species did not markedly differ (Fig. 2a). The difference between unburned plants and resprouts was probably not due to differences in rooting depth. Instead, this difference was likely due to reduced water use by resprouts because of an increased root to shoot ratio, leading to greater available soil moisture during the dry season months (Fig. 2a).

Among resprouts, Af and Cs had more negative predawn Ψ_w during the drought than Ha (Fig. 2a). This could indicate differences in rooting depth if the deeper roots of Af and Cs were pruned or inactive during the drought. Alternatively, it could indicate that Ha had a more extensive root system occupying a greater volume

of soil giving it a larger root to shoot ratio than the other resprouts. In support of this possibility, Ha lignotuber diameters were generally larger than the other species (mean $\pm$ 1 SE for Af = 271.6 $\pm$ 13.6 mm; Cs = 224.1 $\pm$ 12.5 mm; Ha = 505.5 $\pm$ 60.1 mm) suggesting a greater belowground biomass. Aboveground, the height of the Ha shoots were not taller than the other two species (Fig. 1c); however, the Leaf Area Index (m^2 m^{-2}) was greatest for Ha resprouts (LAI mean $\pm$ 1 SE = 2.55 $\pm$ 0.17 for Ha; 1.17 $\pm$ 0.07 for Cs; and 0.87 $\pm$ 0.14 for Af).

Midday Ψ_w provides an estimate of maximum leaf tissue dehydration. As with predawn Ψ_w, the resprouts had less negative Ψ_w than the unburned plants during the drought months (Fig. 2b). The Ψ_w of resprouting species differed more from one another at midday than at predawn, and Af consistently had more negative Ψ_w than the other two species (Fig. 2b). This could be due to Af having greater rates of transpiration or a lower soil to plant hydraulic conductance than the other two species. Leaf gas exchange data suggest that Af had

very low stomatal conductance during the dry season and thus would be expected to have lower transpiration than the other two species (Fig. 3b). Therefore, the more negative Ψ_w for Af was probably due to lower plant and soil hydraulic conductance.

Net carbon assimilation per unit area (A_{net}) and stomatal conductance (g_s) measured during the peak of the drought were both lower for unburned plants than resprouts ($F_{1,23}$ = 45.6, $P \ll 0.001$ for A_{net} and $F_{1,23}$ = 131.9, $P \ll 0.001$ for g_s; Fig. 3a and b). There was a significant interaction between treatment and species for A_{net} and g_s ($F_{2,23}$ = 8.9, P = 0.001 for A_{net} and $F_{2,23}$ = 16.9, $P \ll 0.001$ for g_s) because unburned plants were similar to resprouts for Af ($F_{1,23}$ = 0.18, P = 0.672 for A_{net} and $F_{1,23}$ = 4.49, P = 0.044 for g_s), whereas for Cs and Ha unburned and resprouts were significantly different ($P < 0.05$). Among the resprouts, Af was clearly the most stressed with low levels of g_s and A_{net} among all measured individuals (Fig. 3a and b). By contrast, Cs and Ha were more variable in A_{net} and g_s indicating that some individuals were more stressed than others (Fig. 3a and b).

Two factors were assessed that may help explain the differential mortality of resprouts: hydraulic dysfunction due to water stress-induced cavitation and depletion of carbohydrate reserves. The PLC differed among species and treatments (Table 3). The relationships were not straightforward and included numerous interactions among treatment factors (Table 3). The PLC was greatest for the two species with the greatest mortality during the drought, Af and Cs, suggesting they were experiencing the greatest degree of drought-induced embolism (Fig. 4a, c, e). Moreover, Af resprouts were consistently predicted to be more embolized than unburned comparison plants (Fig. 4a).

Another way to examine drought-induced embolism is to assess the effect of the drought on the absolute conductivity (xylem-specific conductivity; K_s) of stems. This is important to determine how close stems were to having zero conductivity, that is, how close they were to runaway cavitation. When examined this way, Af resprouts had the lowest K_s followed by Ha and Cs resprouts (Fig. 4b, d, f; Table 4). All unburned plants had relatively low K_s with the exception of Cs (Fig. 4b, d, f).

Carbohydrate reserves were analyzed as starch content of lignotubers. Lignotuber starch was different among species, and resprouts and unburned shrubs (Table 5; Fig. 5). During the first summer after the fire, Af and Ha had lower starch among resprouts than unburned plants, whereas *C. spinosus* had starch that was not different (Fig. 5c). At this time, the starch content of lignotubers for Af and Ha was quite low (<5%), and this may have contributed to the demise of some
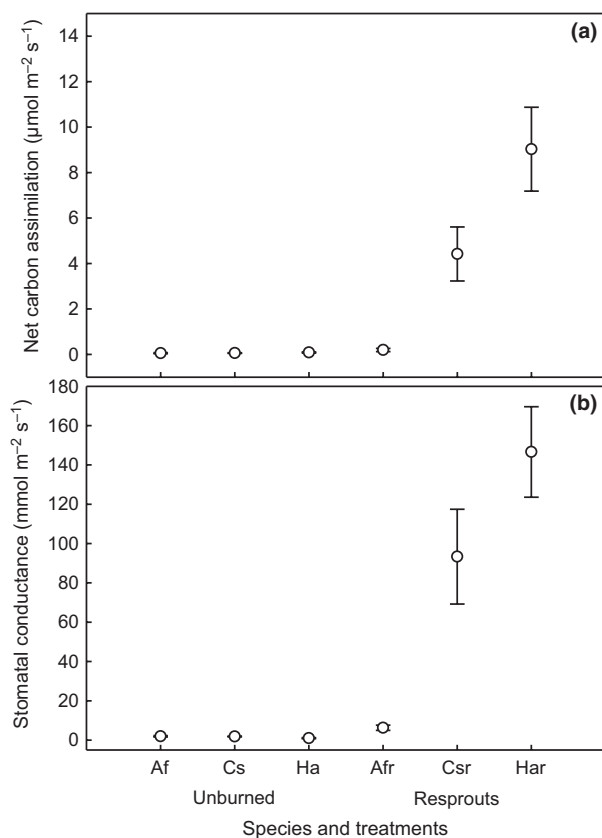

Fig. 3 Mean $\pm$ 1 SE (n = 4–6) net carbon assimilation per unit area (a) and stomatal conductance (b) for unburned shrubs and postfire resprouts. Measurements were made at mid-morning during the peak of the drought on September 23, 2007.
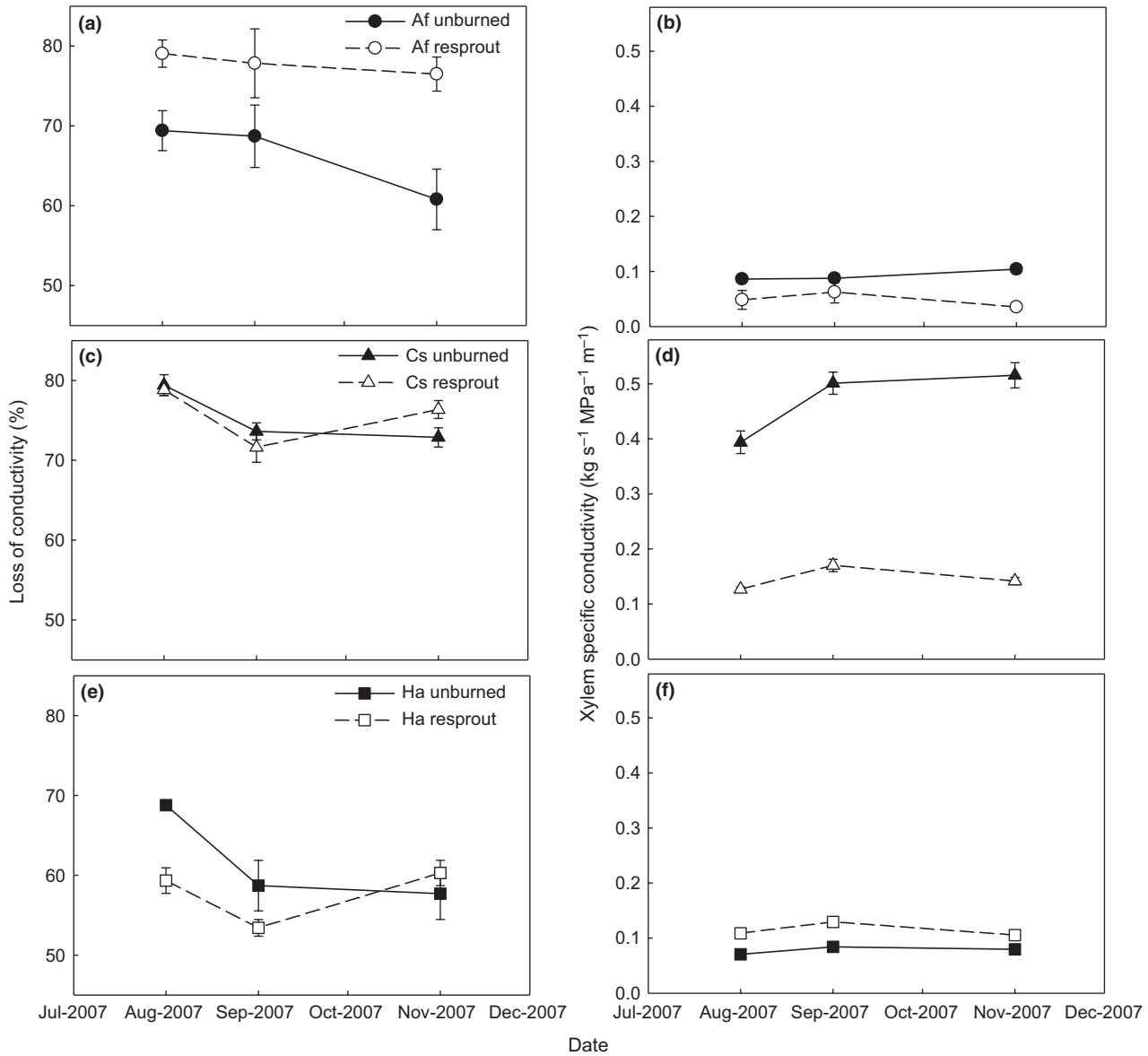
Fig. 4 Mean ± 1 SE of percentage loss of hydraulic conductivity (PLC) and xylem-specific conductivity (K_s) of stems estimated using vulnerability curves and water potentials. Estimates of PLC were made during the peak period of drought (July – December 2007). Error bars that are not visible are smaller than symbols.

individuals (Fig. 5). By contrast, Cs had lignotuber starch contents that were significantly greater than resprouts of Af and Ha ($F_{1,109} = 27.1$, $P \ll 0.001$), and it seems unlikely that low starch was related to the mortality observed for Cs. Following the drought, starch content of lignotubers among resprouts showed steady recovery for Af and Ha (Fig. 5a and c).

To assess whether this fire and drought led to a decline in population density, we surveyed plots for seedlings and surviving resprouts. For six of the seven sampled species, the combination of fire and drought led to a decline in population density compared with the prefire density (Fig. 6). The one species that has had a population increase is Ccr, which is a non-resprouter and obligate seeder after fire (R−S+). The population density averaged across all the shrubs prefire was 0.044 shrubs m^{-2}, and 5 years after the fire, the density was 0.047 shrubs m^{-2}. Thus, the 60.9% increase in the Ccr population density more than offset the average decline in shrub density due to resprout mortality, which was about 21.5%. There appears to be a significant trade-off between the number of seedlings produced (seeding : parent ratio) and postfire survival (Fig. 7).

Table 5 ANOVA table for starch analysis

Factor	df	SS	F	P
Treatment	1	4.122	83.269	<0.001
Spp	2	1.991	20.111	<0.001
Date	1	0.052	1.060	0.305
Treatment × Spp	2	0.678	6.853	0.001
Spp × Date	2	0.549	5.549	0.004
Date × Treatment	1	0.238	4.822	0.030
Spp × Date × Treatment	2	1.044	10.546	<0.001
Error	109	4.833		

Treatment refers to unburned and burned resprouts.

Discussion

Differential resprout mortality due to drought

We found that resprouting shrub species differed in postfire survival during a record drought in southern California. Six of the seven sampled species had 95–100% resprout success after the fire suggesting that fire damage to lignotubers and buds was not a direct cause of the observed mortality for these species. In addition, the site had last burned 30 years prior, which is within the normal range of the fire return interval precluding a short fire return interval effect as a cause of the mortality (Zedler *et al.*, 1983; Syphard *et al.*, 2006). Most mortality occurred among resprouts and during an intense drought that occurred in the year after the fire. When compared to previous reports of postfire survival values, the observed survival was the lowest or close to the lowest ever reported for the studied species. Further supporting drought as a causal factor in resprout mortality, measurements of water relations of shrubs suggested they were under considerable water stress. Water stress from drought or even the water stress that attends a typical summer rainless season can be a potent agent of mortality for postfire seedlings in California's Mediterranean-type climate region (Frazer & Davis, 1988; Thomas & Davis, 1989), but this is the first study to link high levels of resprout mortality to intense drought. These results suggest that drought may interact with fire and lead to a decline in resprouting shrub survival as has been found in some tropical forest systems (Van Nieuwstadt & Sheil, 2005; Granzow-De La Cerda *et al.*, 2012).

The unburned shrubs, that inhabited large stands adjacent to our resprout study area, did not suffer the same mortality as the resprouts. This is not because these shrubs avoided water stress as the water potentials we recorded for the unburned plants were among the lowest ever recorded for these taxa (cf. Miller & Poole, 1979; Poole & Miller, 1981; Baker *et al.*, 1982; Pratt *et al.*, 2007b). We did not tag large numbers of
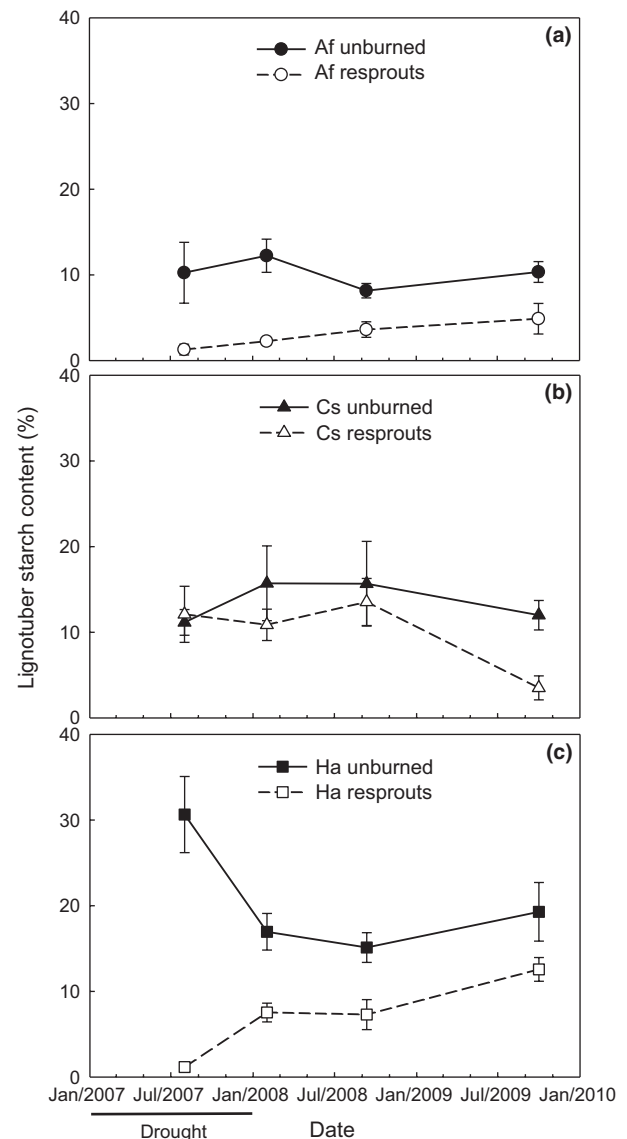

Fig. 5 Mean ± 1SE ($n = 6$) of lignotuber starch content (percentage of dry mass) measured for unburned plants and postfire resrprouts. The months corresponding to the drought period are highlighted on the x-axis.

individuals to systematically sample this population for mortality, but we did carefully examine them on numerous occasions anticipating the possibility of mortality during the drought. We observed some dieback of branch tips of tagged branches that we were following for growth and the plants appeared visibly stressed, that is, leaves were curled (for Cs and Ha) and had yellowed. It appears that resprouts are more vulnerable to intense drought than undisturbed mature plants. The site we sampled is within a region dominated by chaparral shrubs and on the arid margins of the chaparral distribution is where established mature plants may be
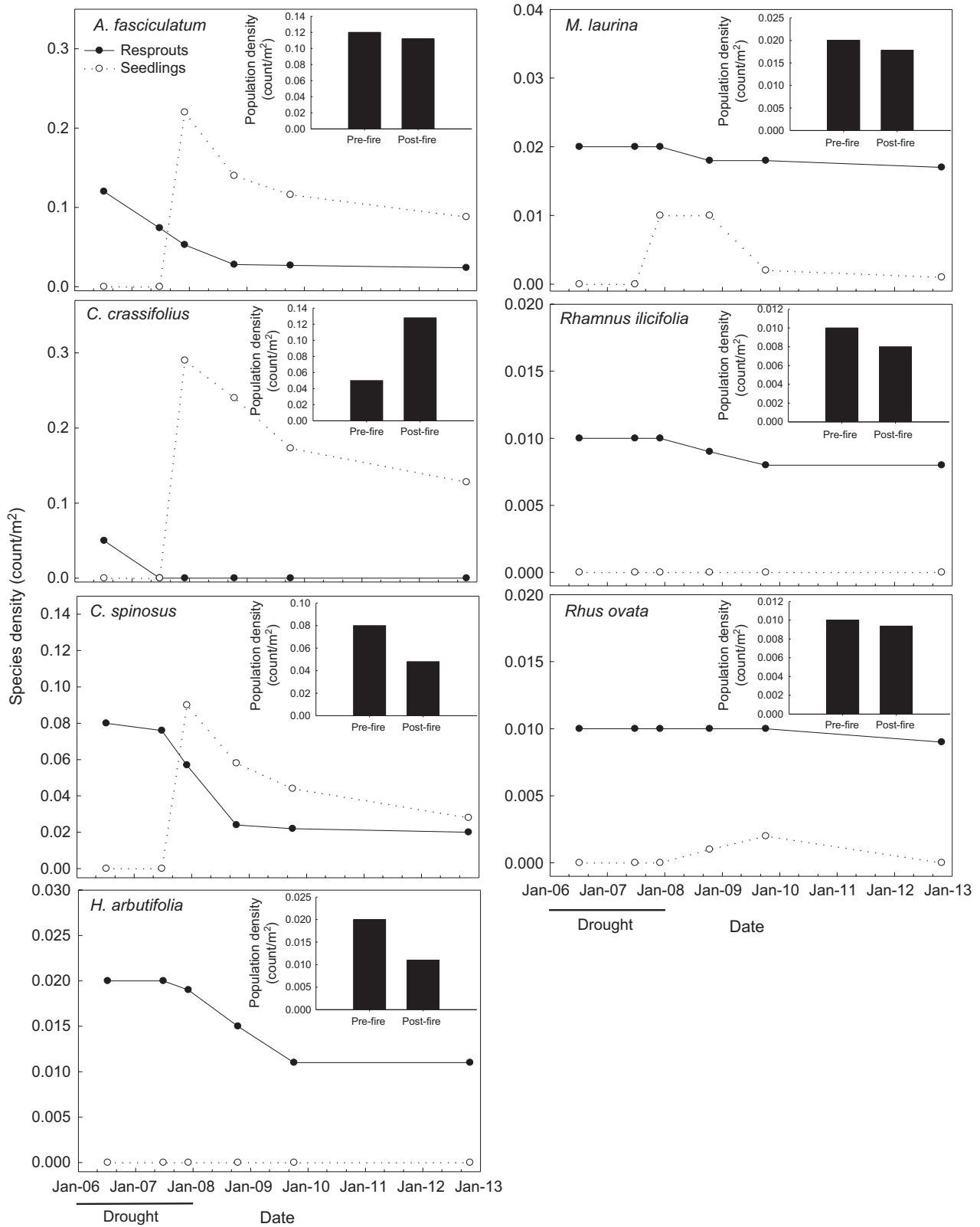
Fig. 6 Population density of adult shrubs and seedlings before and after a fire. Insets show the prefire density compared with the post-fire density about 5 years after the fire. The months corresponding to the drought period are highlighted on the x-axis. Note that each species is plotted on a different scale for the y-axis.
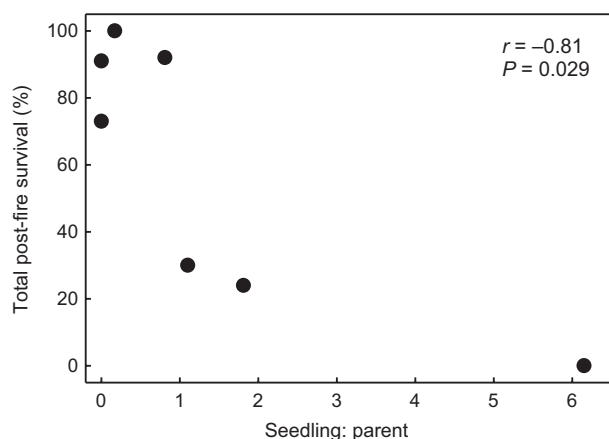
Fig. 7 The total postfire survival of adults plotted in relation to seedilng to parent ratio for the first year after fire. Statistics reported are from a correlation analysis.

more vulnerable to mortality during drought (Paddock et al., 2013).

The fire that burned our study site occurred in July, and the timing of this fire may have contributed to the high mortality and also the low starch content of lignotubers observed for Af and Ha (Cs had high mortality, but did not have low starch stores). Early season fires (April-July) have been hypothesized to lead to high levels of mortality because plants have low levels of carbohydrate stores after spending reserves during the winter and spring growth period (Blanford, 1960; Jones & Laude, 1960; Dodge, 1975; Beyers & Wakeman, 2000). Jones & Laude (1961)found that the roots of unburned adult Af plants had a seasonal low in starch and low tissue water contents in late spring and early summer. They suggested that both of these factors reduced vigor of resprout growth following a clipping experiment (Jones & Laude, 1960). Fires early in the season are unlikely in normal rainfall years with typical winter/spring rains because fuel moisture is high. During drought, low rainfall may lead to earlier drying of fuel and increase the chances of ignitions. This effect would be exacerbated by warmer temperatures associated with regional climate change (Westerling et al., 2006). Thus, one way that drought may lead to greater resprout mortality is to alter the timing of fires so that they occur at a time when plants are physiologically vulnerable (Drewa et al., 2002).

We recorded the lowest percentage of resprout survival for Cs and Ha and near the lowest ever recorded values for Af, and it is informative to consider in greater detail the few reported lower values for Af. Of the 47 reports that we compiled for Af, only three of them are below 36% survival. Zedler et al. (1983) reported values of 15 and 21% survival and attributed

these low values to dry conditions on equatorial facing slopes compared with the higher survival they observed on less arid slopes; however, the authors did not report mortality due to fire vs. resprout mortality, and thus, it is difficult to separate fire intensity effects from other causes of mortality. The lowest survival reported for Af was 12% (Dodge, 1975). This value was recorded after a fire that occurred July 1962 following what was the lowest yearly rainfall ever recorded at that time (123 mm) at the Los Angeles Civic Center where the long-term average is 380 mm (Civic Center data are an index of rainfall patterns for the region; National Oceanographic and Atmospheric Administration of the United States). This record has since been broken twice, once in 2001–2002 when 112 mm was recorded, and again during our study when 82 mm fell in 2006–2007. Dodge (1975) notes that 61% of the burned plants resprouted (similar to our 62%), but that by 27 November 1962 only 40% of those resprouts were alive, and by the following August of 1963 only 20% of the resprouts were alive. From April–December 1962, a period of 9 months, virtually no rain fell. Although Dodge (1975) did not consider drought as an agent of mortality, the timing of resprout mortality reported by Dodge (1975) is suggestive that acute drought may have been a factor leading to the very low resprout survival values they reported and is consistent with our findings.

There are three important elements to the resprout process: (i) surviving the fire; (ii)resprouting vigor; and (iii) resprout survival (Noble, 1984; Le Maitre et al., 1992; Moreira et al., 2012). For only one species, Af, surviving the fire was an important limit to resprout success. We did not design this experiment to determine whether resprouting vigor was a key factor linked to mortality, but we did find that vigor (estimated as plant height over time) during the first growing season was greater (about twice as great) for species with highest resprout success (As, Ml, and Ro, but not Ri). Because of limited sample size for plant height, we did not test if intraspecific differences in vigor were linked to resprout success as was performed by Moreira et al. (2012). We found that resprout mortality during drought was the key step-controlling success for three species (Af, Cs, and Ha).

Physiological causes of mortality during drought: cavitation vs. carbohydrate depletion

The three resprouting species that had high mortality during the drought also suffered high levels of cavitation and embolism, in contrast to the low levels of resprout embolism found in a previous study during a nondrought year (Williams et al., 1997). Moreover,

stomatal conductance was very low for all sampled Af individuals and was low for some Cs and Ha individuals, suggesting acute drought stress. Low stomatal conductance may have been a response to avoid harmful levels of cavitation, but even with stomata maximally closed transpiration is not zero (Burghardt & Riederer, 2003; Pratt *et al.*, 2005). Under these conditions, the xylem supply of water may not have been sufficient to replace the water lost due to transpiration, which may have led to an uncontrolled decline in water potential and xylem cavitation, that is, runaway cavitation (Tyree & Sperry, 1989). For Af, Cs, and Ha resprouting shrubs, the high levels of embolism suggest that runaway cavitation could have caused mortality for some individuals as has been found for chaparral seedlings (Williams *et al.*, 1997; Pratt *et al.*, 2008).

During a typical summer dry season, unburned adult chaparral shrubs have PLC of about 50% (Jacobsen *et al.*, 2007b; Pratt *et al.*, 2007a). Among unburned plants studied here, PLC was well above 50%. An additional sign of their stress was that their stomata were uniformly closed. Unburned plants had dieback of some distal branchlets, but there was no observed mortality of unburned individuals. Limiting dieback to distal branches may be part of a drought survival strategy whereby such branches are sacrificed to protect the whole (Rood *et al.*, 2000; Davis *et al.*, 2002). For the resprouts, there were no distal branches, but resprouts generally have many more shoots than unburned plants. As a rule, resprouts had shoot dieback prior to death, and like unburned plants, this may be part of a strategy where some shoots are sacrificed for the survival of the whole; however, we found that plants that developed dieback were far less likely to survive the drought than those that avoided substantial dieback. It is possible that shoot dieback of resprouts prolonged survival, but sacrificing shoots was ultimately not an effective survival strategy. This may be because resprouts deplete their carbohydrate stores during the resprouting phase, and loss of shoots leads to an unsustainable carbohydrate budget. The presence of dieback in resprouts is a good indicator that foreshadows mortality.

Resprouts may be uniquely vulnerable to water stress. Resprouts have an elevated root to shoot ratio, assuming that most roots survive the fire. This leads to resprouts having less negative water potentials, greater stomatal conductance, and carbon assimilation compared with co-occurring unburned plants (Desouza *et al.*, 1986; Hastings *et al.*, 1989; Goorman *et al.*, 2011; Ramirez *et al.*, 2012). This is important for successful resprouting because after a crown fire carbohydrate reserves are deployed to resprout new shoots (Jones & Laude, 1960; Cruz *et al.*, 2002). During drought, this

may make them more susceptible to mortality because of the need to close stomata to preserve their water status may lead to a shortage of carbohydrates and an inability to sustain the metabolic demands of the heterotrophic root system. If the water stress is not alleviated and the carbon budget remains negative, roots may be pruned in an attempt to balance carbon supply to demand (roots could also dieback in an uncontrolled fashion). At a critical point, root loss will lead to decreased water supply that cannot support demand leading to a decline in water potential and increased cavitation. A viscous cycle ensues that leads to even greater decline in water potential and more cavitation until the xylem is completely occluded by emboli (i.e. runaway cavitation). Alternatively, resprouts may have weak stomatal control that leads to soil water depletion and runaway cavitation. Leaves of resprouts are typically different from unburned plants in having higher specific leaf area (less sclerophyllous), and in some species, they revert to a juvenile form (e.g., Af), and they are generally less tolerant of water stress than leaves from unburned plants (Saruwatari & Davis, 1989).

Runaway cavitation and carbohydrate depletion are interdependent and difficult to separate because carbon acquisition is necessarily linked to water loss (Sala *et al.*, 2010; Mcdowell *et al.*, 2011; West *et al.*, 2012). Because of this, we predicted that resprout mortality during drought would be associated with both high levels of xylem embolism and low levels of carbohydrate stores. This was clearly the case for Af and Ha, both of which had very low hydraulic conductivities and lignotuber starch contents close to zero. For Cs resprouts, lignotuber starch content was greater than the other resprout species and was not different from unburned plants during the drought. This suggests that it is unlikely that carbohydrate limitation was a proximate cause of the observed mortality for this species. This species has green photosynthetic stems that may reduce the carbon costs of maintaining shoots. Thus, Cs mortality seems likely to have occurred due to poor stomatal control of water loss leading to runaway cavitation. Lignotubers may be an organ that expands the buds available for resprouting in some species and not important in storing carbohydrates to fuel resprouting (Cruz *et al.*, 2003; Clarke *et al.*, 2013); however, this is unlikely for Cs because it had stored starch in its lignotuber, and presumably, it would have mobilized this starch if it was needed.

Life history types and populations of chaparral shrubs

Shrubs with different life history types exhibit a trade-off between recruitment of seedlings vs. persistence by resprouting. At one extreme, obligate seeders (R−S+)

are killed by fire but persist through successful recruitment of seedlings. At the other extreme, obligate resprouters (R+S−) produce fire-sensitive seeds but have high resprout success (Marais *et al.*, 2014). Species that produce refractory seeds and resprout (R+S+) fall along a continuum between the obligate seeders and obligate resprouters in both the numbers of seedlings they produce and the percentage of resprouts that survive (Keeley & Zedler, 1978).

We found that after an intense drought concurrent with postfire recovery, the population density of most of the sampled shrub species declined with the strongest declines in Cs and Ha. For Af, there was considerable resprout mortality; however, seeding recruitment offset most of the losses. In contrast to the resprouters, the obligate seeder Ccr had an approximate tripling of population density following the fire. Our results are consistent with the model that obligate seeders do well in gaps that are opened up after fire (Keeley & Zedler, 1978; Keeley *et al.*, 2012). *Ceanothus crassifolius* is a highly water stress tolerant species (Pratt *et al.*, 2008) and populations of Ccr and other functionally similar species may expand their populations during droughts at the expense of some resprouting species.

Summary and Conclusions

Fires and drought have become more frequent in the western United States (Westerling *et al.*, 2006). Our study suggests that drought can interact with fire and lead to a decline in abundance of some resprouting species and an increase in drought tolerant obligate seeder populations. Droughts lasting many years may lead to reduced carbon assimilation, and depletion of stored carbohydrates, which may be a causal factor in large-scale tree and shrub die offs in the western United States (Mcdowell *et al.*, 2008). After a crown fire, carbohydrate reserves can be rapidly depleted to support resprouting of new shoots. If a drought follows a fire, drought-induced stomatal closure may make it impossible for individuals to acquire enough carbohydrates to meet their metabolic demands. This may exacerbate drought-stress as roots die that cannot be maintained metabolically. Alternatively, if stomata are left open to acquire carbon, this may lead to shoot death due to runaway cavitation. The combined and interacting stresses of drought and fire have the potential to significantly alter the composition of chaparral stands.

Acknowledgments

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