

Desert wildfire impacts on plant community function

Kevin J. Horn · Joseph Wilkinson ·
Steven White · Samuel B. St. Clair

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Abstract Dramatic increases are occurring in the size and frequency of wildfires in arid ecosystems. The objective of this study was to characterize the composition of plant communities after desert wildfires and evaluate plant functional responses to post-fire environments. Plant community characteristics and functional traits were assessed from 2009 to 2011 along paired burned–unburned transects of multiple independent fires that occurred in the Mojave Desert in 2005. We measured plant community composition and diversity; xylem water potential; and foliar nitrogen, phosphorus, and non-structural carbohydrates of *Yucca brevifolia* and *Larrea tridentata*. Fire effects on the plant community remained evident on burned landscapes 6 years post-fire with 81, 86, and 42 % less shrub abundance, cover, and diversity. Plant functional traits had neutral to positive responses to burned landscapes that varied by species and season. Plants on burned and unburned landscapes had similar xylem

water potentials following wetter periods but were significantly better in burned landscapes during dry periods and were more pronounced for *L. tridentata* than *Y. brevifolia*. Both species tended to maintain higher foliar nitrogen and phosphorus concentrations in burned areas across seasons. Post-fire conditions increased non-structural carbohydrates in *L. tridentata* leaves in summer and fall periods. *L. tridentata* had 50 % greater canopy leaf area index in burned landscapes compared to unburned areas. Improvements in water and nutrient relations of surviving desert shrubs in burned landscapes may be associated with competitive release from neighboring plants or altered root-shoot ratios and may enhance reproductive capacity that could facilitate the post-fire recovery of woody shrubs.

Keywords Creosote bush · Invasion · Joshua tree · Mojave Desert · Ecophysiology · Red brome · Water potential

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K. J. Horn
Department of Forest Resources and Environmental
Conservation, Virginia Polytechnic Institute and State
University, 311A Cheatham Hall, Blacksburg, VA 24061,
USA

J. Wilkinson · S. White · S. B. St. Clair (✉)
Department of Plant and Wildlife Sciences, Brigham
Young University, 4124 LSB, Provo, UT 84602, USA
e-mail: stclair@byu.edu

Introduction

Human activities are increasing the size, frequency, and severity of wildfires at a global scale (Bowman et al. 2009). In fire-adapted systems, the effects of fire on plant communities are well documented but we know far less about its effects in non-fire-adapted systems. Deserts generally experience less fire than other biomes because water deficits and nutrient

limitations to plant growth result in low and spatially discontinuous plant fuels (Humphrey 1974; Brooks and Chambers 2011). However, introduction of exotic grasses in deserts of North America has increased the connectivity and quantity of plant fuels resulting in larger more intense fires (D'Antonio and Vitousek 1992; Brooks et al. 2004; Brooks and Matchett 2006; Bukowski and Baker 2012). Also, it is estimated that fire return intervals that occurred on multi-century time scales historically can now have a periodicity of a decade or less (Haubensak et al. 2009; Bukowski and Baker 2012). Large-scale fires appear to be unprecedented or extremely rare in these deserts over the last several millennia (Brown and Minnich 1986) suggesting that the biological community may exhibit limited resilience.

Plant community response to disturbance varies markedly across ecosystems. In fire-adapted systems, plant cover and plant community diversity often increase drastically following fire through vegetative regeneration and stimulation of seed bank germination (Keeley et al. 2005). Desert flora often demonstrates limited capacity for vegetative regeneration and sensitivity to fire (Callison et al. 1985; Lei 1999; Webb et al. 2009). This suggests that desert plant communities may generally be poorly adapted to fire and raises questions about the long-term impacts of increased wildfire frequency on desert plant communities and their potential for recovery (Engel and Abella 2011). Recent studies suggest that re-establishment of the structure and diversity of desert plant communities following wildfire is possible but post-fire communities do not resemble pre-fire communities or adjacent unburned areas (Abella 2010; Vamstad and Rotenberry 2010). The ecological interactions and functional relationships that shape post-disturbance plant community assembly in arid ecosystems remain poorly understood.

High-intensity desert wildfires can limit plant community regeneration by scorching root crowns and reducing the viability of native seed banks near the soil surface (Brooks 2002; Esque et al. 2010). These effects of fire can limit plant community regeneration in the short term. However, desert wildfires can be patchy resulting in a mosaic of surviving plants in burned desert landscapes (Steers and Allen 2011a, b; Brooks 2012). Post-fire recovery of the native perennial community is at least partially dependent on the survivorship and the functional responses of those

survivors to burned landscapes and how their response translates to reproductive success and recruitment.

Surviving plants on burned landscapes experience drastic shifts in environmental conditions. Many desert plants have been shown to be sensitive to small differences in soil characteristics, particularly in surface geology (Hamerlynck et al. 2002; Stevenson et al. 2009). Fire induces change in physical soil characteristics and in soil nutrient availability through loss of plant cover, shifts in soil microbial activity and increased wind and water erosion (Webb et al. 2009). Fire can decrease soil pore space, water holding capacity, and soil organic matter while increasing pH and surface temperature (Lei 1999). Fire has been shown to affect soil nitrogen by altering the structure and activity of biogenic soil crusts (Lei 1999; Belnap and Lange 2001). These alterations to soil structure and chemistry will likely affect plant access to water and nutrients. Additionally, plant competition for soil water and nutrient resources may be altered with the reduction in plant density following fire (Mahall and Callaway 1992; Brisson and Reynolds 1994; Holzappel and Mahall 1999) that may affect plant water potential (a measure of water acquisition and maintenance in plant tissues). While recent studies have shed light on the structural effects of desert fire on plant communities (Abella et al. 2009; Abella 2010), plant functional responses in post-fire desert ecosystems have not been reported.

With the emergence of large-scale fires in deserts and predicted expansion of fire under future climate change (Lenihan et al. 2003; IPCC 2007), there is a critical need to better understand fire effects on plant function in fire-altered plant communities and landscapes. Herein, we characterize plant functional responses to fire-altered plant communities and landscapes in the Mojave Desert several years after the occurrence of fire. The following questions were addressed: (1) How is the function of surviving plants modified in post-fire desert landscapes? (2) Do plant functional responses to fire-altered landscapes vary by species with different resource acquisition strategies? (3) How do functional responses to fire-altered landscapes change across seasons?

To examine the range of potential functional responses of perennial desert plants to burned landscapes, we studied *Y. brevifolia* Engelm. and *L. tridentata* D.C. Cov. two dominant, perennial, and non-deciduous species that vary markedly in their

functional traits and resource acquisition strategies. *Y. brevifolia* is an arborescent species with an extensive but shallow root system that acquires water and nutrients from near-surface soil and stores reserves in its stem and semi-succulent leaves. In contrast, *L. tridentata*, a large woody shrub, has deep roots (up to 5 m) and depends on deeper water sources to maintain year-round function (Smith et al. 1983; Schwinning and Hooten 2009; Stevenson et al. 2009). Both can resprout following disturbance but mortality and post-fire regeneration failure are common with high fire severity (Humphrey 1974; Brown and Smith 2000; Loik et al. 2000; Gibson et al. 2004). Both species are evergreen which allowed repeated measurements to look at seasonal changes in functional response over time.

Materials and methods

The study area was located in the Beaver Dam Wash in northeastern region of the Mojave Desert. The vegetation present is typical of mid-elevation (850–1080 m) Mojave Desert shrubland dominated by *Coleogyne ramosissima* (Torr.), *L. tridentata*, *Ambrosia dumosa* (A. Gray Payne), and *Y. brevifolia*. Much of the area is covered with exotic plant species including *Erodium cicutarium* (L. L'Hér. ex Aiton) and the winter annual *Bromus rubens* (L.). The soil is a young alluvium with a sandy-loam texture.

The study area experienced extensive fires in 2005 and 2006. Six study sites were established along burn boundaries of four separate fires that occurred in the summer of 2005: *Westside* (ignition: June 23–23,782 ha), *Duzak* (ignition: June 22–132,395 ha), *Burgess 1* (ignition: July–60 ha), and *Burgess 2* (ignition: July 23–543 ha). Fires were identified from Monitoring Trends in Burn Severity (MTBS) (Eidenshink et al. 2007) and assessed personally in the field. Each of the six study sites consisted of a pair of transect lines (1 km in length) with one line in the burned area and one line in the adjacent unburned area. Each transect line was positioned approximately 200 m inside or outside the burn boundary to keep physiographic conditions between transect pairs similar (e.g., aspect and slope). Burn conditions were classified as severe based on plot level mortality and reduction in shrub cover (see results). Climate data were obtained from Badger Springs meteorological station located

within Beaver Dam Wash study area (37.1506°N, 113.9539°W, elevation: 1216 m) through University of Utah MesoWest Station Interface (mesowest.utah.edu). The sum of precipitation received across the 90 days previous to sampling times was used to assess precipitation history.

In May of 2011, vegetation surveys were conducted in circular plots (5 m radius) at 100-m intervals along each 1 km transect line. Shrubs rooted within plots were counted by species to calculate species density, and measurements of the major and minor axes of perennial shrubs were used to calculate shrub cover. We used species richness and Shannon's Diversity Index ($H = -\sum p_i \ln(p_i)$ where p_i is the proportion of the i th species) to estimate changes in plant community composition.

Canopy dimensions and leaf area index of shrub canopy (LAI_{canopy}) of *L. tridentata* were characterized in October 2011. Canopy dimensions were measured horizontally along major and minor axes and vertically at the highest branch point on the same shrubs used for physiological measurements. Leaf area index of shrub canopy (LAI_{canopy}) was taken as an average from ten measurements on each *L. tridentata* shrub using an AccuPAR LP-80 ceptometer (Decagon Devices Pullman, WA) placed at various angles horizontally at the base of the shrub canopy. Beneath canopy PAR and outside canopy PAR were measured simultaneously with the use of an external PAR sensor to eliminate the need for cloud cover and time of day correction. The χ (chi) value for leaf angle was set to 1.

To assess functional responses of plants to fire-altered landscapes, five *Y. brevifolia* and five *L. tridentata* plants were measured along each transect line of the six transect pairs for a total of 120 plants. Xylem water potential measurements, and leaf sample collections for foliar nutrient (nitrogen and phosphorus) and carbohydrate analysis occurred the weeks of February 9th, May 3rd, August 16th, and October 29th of 2010. Xylem water potential measurements were also made in August 2009 and August 2011. Measurement times were randomized across sites to avoid any diurnal bias.

Xylem water potential measurements

To determine plant access to water, pre-dawn xylem water potentials (Ψ_{pd}) were measured between 00:00 and 06:00 using a pressure chamber (PMS Instrument

Company, Albany, OR, USA). We plotted water potential values against the time the measurement occurred and found no significant time drift from midnight to 6 AM within each sampling period for either species (data not shown). Mid-day (Ψ_{md}) water potential measurements taken in August 2011 occurred between the hours of 11:30 and 16:00. For *Y. brevifolia*, fully expanded leaves were cut near the point of attachment on rosettes approximately 1.5 m from the ground. Terminal *L. tridentata* stems were sampled from the mid-upper canopy. Two measurements were obtained from every plant during each sampling period and the two values were averaged prior to analysis.

Foliar nutrient analysis

To examine effects of post-fire landscapes on foliar nutrient status (nitrogen and phosphorus), leaf tissue from *Y. brevifolia* and *L. tridentata* used in the pre-dawn water potential measurement was retained for laboratory analysis. Leaf tissue was dried at 60 °C for approximately 72 h. Samples were then ground using a Wiley Mini-Mill (Thomas Scientific, Swedesboro, NJ, USA). Dried leaf tissue was analyzed with a nitrogen analyzer (TruSpec, CN Determinator, LECO Cooperation, St. Joseph, MI) using the combustion method (Campbell 1991). For phosphorus analysis, dried leaf tissue was ashed in glass scintillation vials in a muffle furnace for 12 h at 495 °C, dissolved in hydrochloric acid, and analyzed on a spectrophotometer (SpectraMax Plus 384, MDS, Toronto, Canada) according to the methods of Murphy and Riley (1962).

Foliar sucrose and starch

Sucrose and starch concentrations were examined from *Y. brevifolia* and *L. tridentata* leaf tissue retained from pre-dawn water potential measurements and according to the methods of St. Clair et al. (2009) using a Megazyme total starch kit (Wicklow, Ireland). Non-structural carbohydrates (glucose, sucrose, and starch) were extracted from 20 mg of ground leaf tissue in three volumes of 0.67 ml of 80 % ethanol (final extraction volume of 2 ml) in a shaking incubator at 80 °C. Between extractions, samples were spun at 16,000×g for 60 s in a microcentrifuge. Aliquots of sample extract (20 µl) were placed in

micro-plate wells in triplicate for both glucose and sucrose analysis then evaporated in a drying oven for 20 min at 55 °C. A volume of 200 µl GOPOD reagent (Megazyme kit) was added to each well. Invertase was added to the wells being analyzed for sucrose. Absorbance was read at 510 nm. Sucrose values were determined from the differences in absorbance between samples before and after the addition of invertase. Standard curves were prepared using pure glucose and sucrose standards (Sigma Aldrich).

Starch was extracted from tissue samples left after the ethanol extractions described above. Deionized water (2 ml) was added, and the samples were then autoclaved at 135 °C for 1 h. Aliquots of 40 µl of sample were hydrolyzed in an alpha-amylase solution and placed in a shaking incubator for 20 min at 100 °C. Samples were cooled at room temperature for 10 min and further hydrolyzed with the addition of amyloglucosidase and incubation with gentle shaking at 50 °C for 45 min. Megazyme GOPOD reagent was added to the samples, and the reaction was allowed to develop for 15 min. Samples were read at a wavelength of 510 nm in the spectrophotometer. Starch standard curves were developed from purified corn starch (Sigma Aldrich) serially diluted in water. All standards and unknown samples were run in triplicate.

Soil nitrogen and phosphorus analysis

To examine fire effects on soil nutrient status, soil samples were collected from two paired transects along the Westside and Duzak fire burn boundaries (37.098°N, 113.975°W and 37.143°N, 114.030°W, respectively). Samples were taken from beneath current and former *L. tridentata* canopies to a depth of 10 cm. Five soil samples were collected from each transect for a total of 20 samples. Gravel and larger rocks were removed from soils prior to analysis. Total nitrogen and phosphorus was assessed by Brigham Young University's Environmental Analytical Lab (Provo, UT eal.byu.edu). Total soil nitrogen was determined with a nitrogen analyzer (TruSpec, CN Determinator, LECO Cooperation, St. Joseph, MI) using the combustion method (Campbell 1991). Bioavailable phosphorus was extracted using 0.5 M NaHCO₃, and concentration was determined using the molybdenum blue method using a spectrophotometer (Olsen and Watanabe 1957).

Statistical analysis

Fire effects on xylem water potential, foliar nutrients, and carbohydrates were analyzed using Proc Mixed Repeated Measures ANOVA with burn conditions as a fixed effect, sampling period as a repeated measure, and site as a random effect. Effects of burned landscapes during each sampling period were tested using a student’s *t* test paired by site. Pearson’s correlation coefficient was used to determine relationships between xylem water potential, foliar nutrients, and foliar carbohydrates. Two-way ANOVA models with burn conditions as a fixed effect and site as a random effect were used to assess the effects of burned landscapes on plant density, cover, diversity and canopy architecture, and LAI_{canopy} of *L. tridentata*. Statistical analyses were conducted in SAS (version 9.2) and JMP (version 10.0) statistical software (SAS Institute, Cary North Carolina). Differences in soil nitrogen and phosphorus content due to burn condition were statistically tested via a one-way ANOVA with a within factor analysis (site-Duzak and Westside fires) using Program R (v2.14.1 Vienna, Austria; R Core Team).

Results

Plant community structure and diversity

Burned transects had drastically altered plant community composition and structure from unburned reference transects 6 years post-fire. Density of common shrubs was reduced by more than 80 % in burned areas (Table 1). Burned landscapes (6 years post-fire) had 86 % less shrub cover than adjacent unburned areas (Table 1). *C. ramosissima* experienced the greatest reduction in cover (97 %) followed by several other species that had greater than 80 % cover reduction (Table 1). Post-fire landscapes were reduced in species diversity (H) and richness by 42 % ($F_{1,113} = 61, P < 0.001$) and by 56 % ($F_{1,113} = 125, P < 0.001$), respectively.

Larrea tridentata canopy structure

Larrea tridentata canopies were structurally different in burned and unburned locations. In burned areas, *L. tridentata* shrubs were on average 18 % shorter ($F_{1,57} = 13, P < 0.001$) with 50 % greater LAI_{canopy}

Table 1 Density and cover of 12 shrub species in burned and unburned transects (mean ± SE)

Species	Plant density (m ⁻²)				Plant cover (%)			
	Unburned plot	Burned plot	Change (%)	<i>P</i> value	Unburned plot	Burned plot	Change (%)	<i>P</i> value
<i>C. ramosissima</i>	0.161 ±0.011	0.005 ±0.011	-97	<0.01	7.42 ±0.51	0.22 ±0.51	-97	<0.01
<i>A. dumosa</i>	0.073 ±0.01	0.02 ±0.01	-73	<0.01	1.82 ±0.25	0.4 ±0.25	-78	<0.01
<i>L. tridentata</i>	0.038 ±0.003	0.008 ±0.003	-79	<0.01	4.98 ±0.48	0.61 ±0.48	-88	<0.01
<i>Krameria spp.</i>	0.036 ±0.003	0.005 ±0.003	-87	<0.01	1.45 ±0.13	0.13 ±0.13	-91	<0.01
<i>Yucca baccata</i>	0.03 ±0.009	0.009 ±0.009	-69	0.12	0.85 ±0.24	0.3 ±0.24	-65	0.1
<i>Thamnosma montana</i>	0.034 ±0.004	0.005 ±0.004	-85	<0.01	1.12 ±0.13	0.14 ±0.13	-88	<0.01
<i>Y. brevifolia</i>	0.022 ±0.003	0.002 ±0.003	-90	<0.01	1.93 ±0.3	0.31 ±0.3	-84	<0.01
<i>Ephedra nevadensis</i>	0.021 ±0.004	0.001 ±0.004	-93	<0.01	0.29 ±0.05	0.02 ±0.05	-93	<0.01
<i>Encelia farinosa</i>	0.007 ±0.003	0.011 ±0.003	54	0.36	0.33 ±0.11	0.37 ±0.11	11	0.81
<i>Acamptopappus sphaerocephalus</i>	0.013 ±0.003	0.004 ±0.003	-66	0.02	0.23 ±0.05	0.05 ±0.05	-77	<0.01
<i>Lycium andersonii</i>	0.006 ±0.002	0.011 ±0.002	93	0.04	0.12 ±0.03	0.12 ±0.03	0.00	1
<i>Cylindropuntia acanthocarpa</i>	0.013 ±0.002	0.003 ±0.002	-81	<0.01	0.84 ±0.13	0.17 ±0.13	-80	<0.01
Total	0.454 ±0.019	0.084 ±0.019	-81	<0.01	21.4 ±0.58	2.84 ±0.58	-86	<0.01

Change is the percent reduction of burned locations relative to unburned areas. Measurements were taken in May 2011, 6 years post-fire

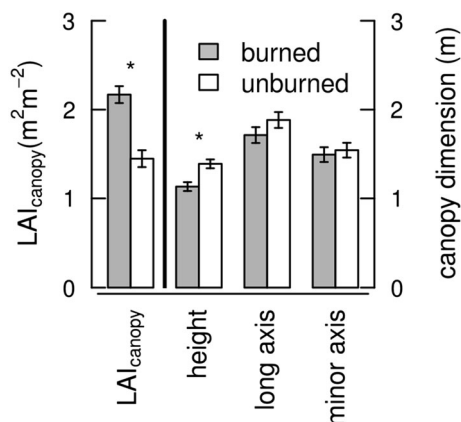


Fig. 1 *L. tridentata* canopy leaf area index (LAI_{canopy}), height, major-axis, and minor-axis (mean \pm SE) on burned and unburned landscapes. Asterisk indicates $P < .05$

($F_{1,57} = 28$, $P < 0.001$) than plants in unburned areas (Fig. 1). The major and minor horizontal axes of *L. tridentata* in burned and unburned areas did not differ ($F_{1,57} = 0.17$ and 1.6 ; $P = 0.18$ and 0.67).

Plant water potential

The effects of burned landscapes on plant water potentials were neutral to positive and differed by species (Fig. 2 and Table 2). The main effect of fire was significant for *L. tridentata* but not *Y. brevifolia*; however, both species demonstrated at least one sampling period where plant water relations differed between burned and unburned landscapes (Table 2 and Fig. 2). In May 2010, *Y. brevifolia* Ψ_{pd} was 29 % higher in burned than unburned locations but no other water potential differences with burn condition were observed in *Y. brevifolia* at other time points. *L. tridentata* Ψ_{pd} did not differ based on burn condition for Feb., May, Aug., and Oct. of 2010 a relatively wet time period, but significant differences between burned and unburned areas were observed during drier periods in 2009 and 2011 (Figs. 2, 3). The lowest average Ψ_{pd} (-4.8 ± 0.2 MPa) was observed in the August of 2009 during which time Ψ_{pd} for *L. tridentata* was 30 % higher for plants in burned transects. Positive effects of burned landscapes on *L. tridentata* Ψ_{pd} were most evident when accumulated precipitation was at its lowest (Fig. 3).

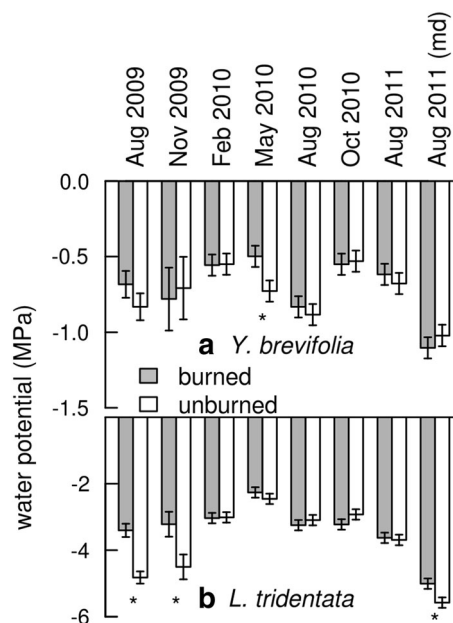


Fig. 2 a *Y. brevifolia* and b *L. tridentata* water potentials (mean \pm SE) in burned and unburned areas across various sampling periods in 2009, 2010, and 2011. All values are from pre-dawn measurements except the last set of bars that present mid-day (md) values. Asterisk indicates $P < 0.05$ for pairwise comparison

Foliar nutrients

Foliar nutrients were consistently higher in plants in burned areas. *Y. brevifolia* and *L. tridentata* plants had on average 17 and 22 % greater foliar N in burned locations compared to unburned areas when averaged across all time points (Table 2; Fig. 4a, b). In both species, responses of foliar nitrogen to fire-altered landscapes were consistent across time (Table 2) with higher levels from fall to spring and then a drop during the summer period (Fig. 4). Foliar phosphorus concentrations were significantly greater for both species in burned areas at specific sampling periods (Table 2 and Fig. 4c, d). The mean effect of burned landscapes on foliar phosphorus across all sampling periods was only significant for *L. tridentata*.

Non-structural carbohydrates

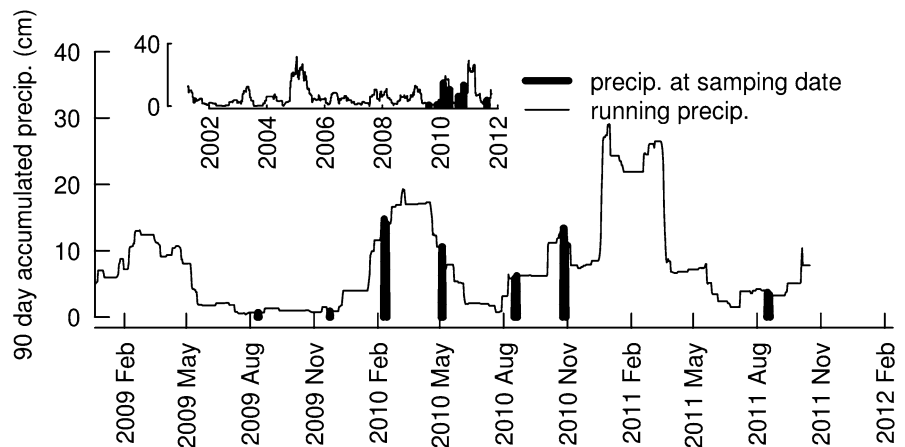
Foliar starch and sucrose levels in *Y. brevifolia* were not significantly different in burned and unburned landscapes but the accumulation of non-structural carbohydrates in *L. tridentata* tended to be higher in plants in burned areas during the summer and fall

Table 2 F values from repeated measures ANOVA examining effects of burned landscapes and time of sampling on pre-dawn water potentials (Ψ_{pd}), foliar nitrogen (N), foliar phosphorus (P), foliar sucrose, and foliar starch of *Y. brevifolia* and *L. tridentata*

Source of variance	Ψ_{pd}	N	P	Sucrose	Starch
<i>Y. brevifolia</i>					
Fire	0.67	23***	3.55	0.71	0.4
Sampling period	14.84***	72***	2.34	38***	342***
Fire*sampling period	1.13	0.19	2.11	0.24	0.69
<i>L. tridentata</i>					
Fire	21***	70***	40***	0.43	10.1**
Sampling period	120***	19***	15***	22***	119***
Fire*sampling period	8.47***	0.83	4.07**	2.14	3.1*

Significance designated as * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fig. 3 Accumulated precipitation record for Beaver Dam Wash recorded at the Badger Springs meteorological station (37.1506°N, 113.9539°W). Ninety-day accumulated precipitation was lowest during the 2009 sampling period



periods (Fig. 5). For both species, foliar sucrose and starch levels varied significantly by sampling period (Table 2). Foliar carbohydrates in *Y. brevifolia* tended to be higher in the fall and winter sampling periods (Fig. 5). For *L. tridentata*, sucrose and starch peaked strongly during the spring and fall sampling periods (Fig. 5). Interestingly, *Y. brevifolia* had much higher levels of sucrose, while *L. tridentata* had much higher levels of starch. Non-structural carbohydrates were not significantly correlated with foliar nitrogen, foliar phosphorus, or plant water potential in either species (all r values < 0.22).

Soil nitrogen and phosphorus

Soil nitrogen and phosphorus concentrations did not differ across burned and unburned areas ($F_{1,31} = 0.001$

and 0.231, $P = 0.97$ and 0.83, respectively). Soil nitrogen averaged 1366 ± 227 mg kg⁻¹ in burned areas and 1359 ± 154 mg kg⁻¹ in unburned areas. Soil phosphorus averaged 10.3 ± 1.1 mg kg⁻¹ in burned areas and 9.7 ± 1.5 mg kg⁻¹ in unburned areas.

Discussion

The 2005 wildfires in the Mojave Desert drastically altered the native plant community as evidenced by reductions in the abundance, cover, diversity, and richness of vegetation 6 years after the fire (Table 1). Shrub cover in some Mojave Desert landscapes can return relatively quickly and are often dominated by one or two species (i.e., *A. dumosa* and *E. farinosa*)

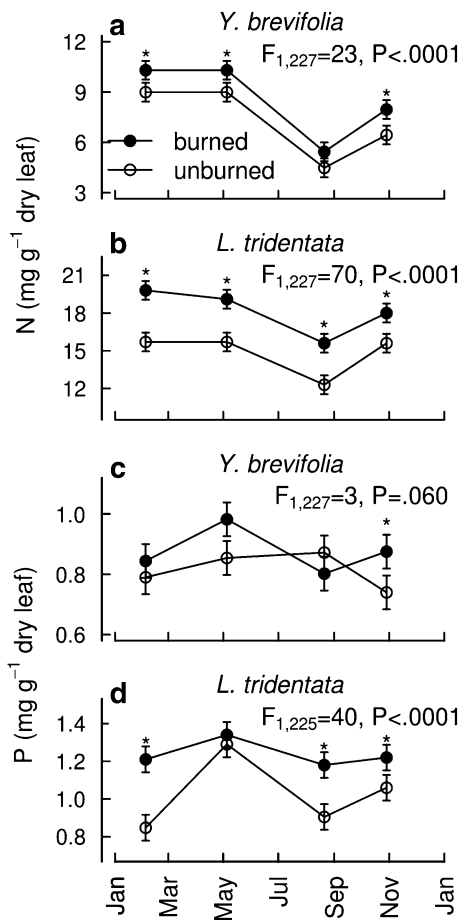


Fig. 4 a–b Foliar nitrogen, and c–d foliar phosphorus of *Y. brevifolia* and *L. tridentata* (mean \pm SE) in burned and unburned areas across 2010. *P* values for the main effect of fire across all time points are given in upper right corners of each graph. Asterisks indicate significant differences ($P \leq 0.05$) between paired comparisons

(Steers and Allen 2011a, b). Our data suggest that the return of shrub cover in the mid-elevation shrublands of the northeast Mojave where this study was conducted could take several decades. Species diversity and richness on our study sites remained significantly lower along burned versus unburned transects, which is consistent with studies showing lower plant diversity several decades after wildfires in other regions of the Mojave Desert (Vamstad and Rotenberry 2010; Engel and Abella 2011; Steers and Allen 2011a).

The loss of shrubs and their subsequent seed production due to vegetation mortality following wildfire likely slows the re-establishment of the native plant community. Additionally, the absence of nurse-

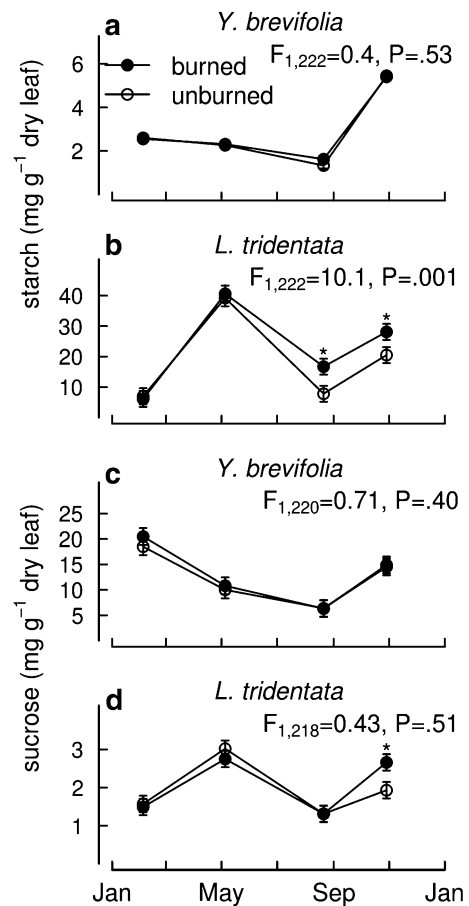


Fig. 5 a–b Foliar starch, and c–d foliar sucrose of *Y. brevifolia* and *L. tridentata* (mean \pm SE) from burned and unburned areas across the four major seasons of 2010. *P* values for the main effect of fire across all time points are given in upper corners of each graph. Asterisks indicate significant response to fire-altered landscapes ($P \leq 0.05$) within single sampling times

shrubs (shrubs that can protect establishment of plant during the seedling phase) impairs the regeneration of long-lived perennials such as the *Y. brevifolia* (Brittingham and Walker 2000; Walker et al. 2001; Drezner 2006). Long-term changes in plant community structure and diversity are likely to have cascading effects on the entire biological community as bottom-up forces alter population structure of primary and secondary consumers (Horn et al. 2012).

Loss of native seed bank with high burn intensity (Brooks 2002) and excessive cost and frequent failure of re-seeding efforts are constraints to plant community re-establishment in burned desert landscapes (Zouhar et al. 2008; Weigand and Rogers 2009).

There is, however, an intact (albeit modified) native shrub community that survived the 2005 fires (Table 1). How these surviving and regenerating native shrubs function and reproduce in burned landscapes is likely an important determinant of the recovery potential and assembly of the native plant community. However, the functional responses of surviving or regenerating shrubs in burned desert landscapes are not well studied.

Growth patterns in some desert plants have been strongly linked to soil structure and hydrology (Runyon 1934; Stevenson et al. 2009). Whether fire positively or negatively influences soil moisture availability to plants in deserts remains ambiguous (Allen et al. 2011). Lei (1999) suggested that fire effects on soil hydrology tended to be negative. However, we found that post-fire conditions can positively affect plant water potential and that the effect can persist several years after the fire (Fig. 2). Positive effects of fire on plant water potential were limited to drier periods for *L. tridentata* indicating interactions between burn condition and water availability (Table 2 and Figs. 2, 3). Similarly, resprouting shrubs in a *Eucalyptus populnea* woodland were shown to have higher pre-dawn water potentials and increased stomatal conductance up to 5 years following fire under drought stress (Hodgkinson 1992). When moisture is limited, plant competition can have a greater influence on plant water relations than soil characteristics; however, soil characteristics dominate under conditions of high moisture availability (Hamerlynck et al. 2002). Fonteyn and Mahall (1981) and Schlesinger et al. (1989) found that reduction of neighboring vegetation improved water relations in *L. tridentata*. This suggests that competition release stemming from reduced plant density may be a primary reason for more favorable water potentials observed on burned landscapes under conditions of water deficit (Fig. 2).

Hydraulic responses to burn conditions and seasonality were species-specific and likely a result of the different water acquisition strategies. *Yucca brevifolia* acquires water from near-surface soils and stores water in its semi-succulent leaves. This water storage strategy enables *Y. brevifolia* to be less dependent than *L. tridentata* on available soil moisture, especially during dry periods (Smith et al. 1983; Schwinning and Hooten 2009). High water potentials measured on the leaves of *Y. brevifolia* reflected their

function as water storage structures (Fig. 2) and appear to mitigate competition for soil moisture in unburned areas during drought (Schwinning and Ehleringer 2001).

Fire can strongly alter soil nutrient status and nutrient acquisition by plants. In arid systems, a significant amount of biological nitrogen is found in plant tissues (Esque et al. 2010; Allen et al. 2011). Much of this nitrogen is returned to the soil in the form of NH_4 and NO_3 along with other mineral nutrients following fire (Esque et al. 2010). However, soil nutrient pulses following fire can dissipate rather quickly (1–2 years) in desert systems (Allen et al. 2011), and we did not observe significant differences in soil N and P 6 years post-fire. This may be related to nutrient export via wind erosion and/or heavy leaching due to the poor nutrient holding capacity of desert soils (Steers and Allen 2011a; Allen et al. 2011). However, our results demonstrate that both *Y. brevifolia* and *L. tridentata* in burned areas tended to have higher foliar nitrogen and phosphorus than plants in unburned locations six years post-fire (Fig. 4) indicating that factors other than a nutrient pulse immediately after fire are involved.

Post-fire conditions could promote shifts in soil microbial community composition or activity that alters N-fixation rates in desert soil crusts. However, in the Colorado Plateau, N-fixation rates of soil crusts were observed to dramatically decrease with disturbance (grazing and fire) resulting in reduction in soil nitrogen availability (Evans and Belnap 1999). Within the Mojave Desert, soil nitrogen is tightly cycled between soil microbes and plants within “fertile islands” that develop beneath shrub canopies (Ewing et al. 2007). High burn intensities within these fertile islands (Table 1) reduce microbial activity and N-fixation rates in the short term (Bahr et al. unpubl. data). Much less is known about long-term (>2 years) soil microbial responses to fire.

Competition release likely contributes to better nutrient relations as the tight nutrient cycling within fertile islands is disrupted, making those nutrients available to surviving plants. Death of competitors may also allow root expansion of surviving plants into rooting zones of burned plants (Fonteyn and Mahall 1981; Brisson and Reynolds 1994). While we see a clear signal of greater foliar nutrient content of surviving perennial plants in burned desert landscapes, the underlying mechanisms are still poorly understood.

The legacy effects of burned landscapes on plant carbon metabolism are largely uncharacterized in deserts, and we hypothesized these would be strongly linked with increased foliar nutrients. Our data indicate that burned desert environments had neutral to positive effects on leaf carbohydrates and that these effects varied strongly across seasons (Fig. 5). Foliar starch and sucrose concentrations were influenced more by seasonality than by burn condition however. The highest carbohydrate accumulations for *L. tridentata* were observed in spring and fall, which is consistent with other studies (Strain 1969; Oechel et al. 1972), and may be related to less stressful temperature and moisture conditions. Increases in nutrients and plant-available water affect carbon metabolism (Lajtha and Whitford 1989; Hooper and Johnson 1999) and may have contributed to the positive effects that burned landscapes had on non-structural carbohydrates. However, we saw no correlation between foliar starch accumulation and foliar nutrient (nitrogen and phosphorus) concentrations across burn conditions.

The different shoot architecture (LAI_{canopy}) of *L. tridentata* in burned versus unburned transects suggests that post-fire environments can drastically alter both the structure and function of plants (Fig. 1). Similar enhancements of shoot growth occur when *L. tridentata* is grown on favorable soils and after reductions in above ground biomass (Hamerlynck et al. 2002; Gibson et al. 2004) and are likely driven by better water and nutrient relations (Runyon 1934; Lajtha and Whitford 1989). A denser canopy structure is associated with improved water relations and may be due to any combination of increased root:shoot ratio, alterations in surface soil structure, and reduced resource competition (Jones 1984; Brisson and Reynolds 1994; Hamerlynck et al. 2002). Hamerlynck et al. (2004) found that *L. tridentata* growing in hydrologically favorable soils had greater leaf N and growth responses. Later these same plants were subject to greater die-back during drought (Hamerlynck and McAuliffe 2008) suggesting that positive growth responses on burned landscapes may increase susceptibility to die-back under drought conditions likely due to the greater shoot biomass. However, this may also be counterbalanced by better water relations in burned areas during drier periods as suggested by our data (Fig. 2).

Fire-altered desert environments may contribute to the possibility of autogenic recovery through enhanced

plant function. However, complete mechanisms for recovery are unclear and non-uniform due to the variability in revegetation times and pre- and post-fire plant community composition throughout the Mojave Desert (Abella et al. 2009; Webb et al. 2009; Vamstad and Rotenberry 2010; Steers and Allen 2011a). Recent assessments of plant reproduction along the same paired transects used in our study demonstrated that burned environments strongly stimulate flower and fruit production of surviving plants suggesting a link between fire, greater soil resource acquisition by surviving plants, and higher reproductive capacity (Lybbert and St. Clair, unpubl. data). However, other aspects crucial to consider when assessing revegetation potential are pollination dynamics (Ashworth et al. 2004; Lybbert and St. Clair, unpubl. data) and trophic influences on seed and seedling fate by primary consumers (Vander Wall et al. 2005; Beck and Vander Wall 2010; Horn et al. 2012).

None of the above examples of autogenic recovery, nor our findings, consider multiple burns which would continue to reduce the number of surviving shrubs and may alter plant functional responses differently than single burns (Brooks 2012). Repeat fires on short time scales are occurring as the same exotic grasses that carried the initial fire are among the first to re-colonize the burned landscape (Brooks 2002, 2012) and are responding positively to changes in precipitation patterns (Horn et al. 2015). Grass invasion and shorter fire cycles alter nutrient availability in desert systems through erosion, volatilization, and nutrient homogenization (Ravi and D'Odorico 2009; Allen et al. 2011). These changes could constrain native shrub recruitment and preclude re-establishment of native shrub communities.

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References

- Abella SR (2010) Disturbance and plant succession in the Mojave and Sonoran Deserts of the American Southwest. *IJERPH* 7:1248–1284. doi:10.3390/ijerph7041248

- Abella SR, Engel EC, Lund CL, Spencer JE (2009) Early post-fire plant establishment on a Mojave Desert Burn. *Madroño* 56:137–148. doi:[10.3120/0024-9637-56.3.137](https://doi.org/10.3120/0024-9637-56.3.137)
- Allen EB, Steers RJ, Dickens SJ (2011) Impacts of fire and invasive species on desert soil ecology. *Rangel Ecol Manag* 64:450–462. doi:[10.2111/REM-D-09-00159.1](https://doi.org/10.2111/REM-D-09-00159.1)
- Ashworth L, Aguilar R, Galetto L, Aizen MA (2004) Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *J Ecol* 92:717–719. doi:[10.1111/j.0022-0477.2004.00910.x](https://doi.org/10.1111/j.0022-0477.2004.00910.x)
- Beck MJ, Vander Wall SB (2010) Seed dispersal by scatterhoarding rodents in arid environments. *J Ecol* 98:1300–1309
- Belnap J, Lange OL (2001) Biological soil crusts: structure, function, and management. Springer, New York
- Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM, DeFries RS, Doyle JC, Harrison SP, Johnston FH, Keeley JE, Krawchuk MA, Kull CA, Marston JB, Moritz MA, Prentice IC, Roos CI, Scott AC, Swetnam TW, van der Werf GR, Pyne SJ (2009) Fire in the earth system. *Science* 324:481–484. doi:[10.1126/science.1163886](https://doi.org/10.1126/science.1163886)
- Brisson J, Reynolds JF (1994) The effect of neighbors on root distribution in a Creosotebush (*Larrea tridentata*) population. *Ecology* 75:1693–1702. doi:[10.2307/1939629](https://doi.org/10.2307/1939629)
- Brittingham S, Walker RL (2000) Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. *West North Am Nat* 60:374–383
- Brooks ML (2002) Peak fire temperatures and effects on annual plants in the Mojave Desert. *Ecol Appl* 12:1088–1102
- Brooks ML (2012) Effects of high fire frequency in creosote bush scrub vegetation of the Mojave Desert. *Int J Wildl Fire* 21:61–68
- Brooks ML, Chambers JC (2011) Resistance to invasion and resilience to fire in Desert Shrublands of North America. *Rangel Ecol Manag* 64:431–438. doi:[10.2111/REM-D-09-00165.1](https://doi.org/10.2111/REM-D-09-00165.1)
- Brooks ML, Matchett JR (2006) Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *J Arid Environ* 67:148–164
- Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. *Bioscience* 54:677
- Brown DE, Minnich RA (1986) Fire and changes in creosote bush scrub of the western Sonoran Desert, California. *Am Midl Nat* 116:411–422
- Brown JK, Smith JK (2000) Wildland fire in ecosystems: effects of fire on flora. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden
- Bukowski BE, Baker WL (2012) Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes. *Ecol Appl* 23:546–564. doi:[10.1890/12-0844.1](https://doi.org/10.1890/12-0844.1)
- Callison J, Brotherson JD, Bowns JE (1985) The effects of fire on the Blackbrush [*Coleogyne ramosissima*] community of southwestern Utah. *J Range Manag* 38:535–538
- Campbell CR (1991) Determination of total nitrogen in plant tissue by combustion. In: Plank CO (ed) Plant analysis reference procedures for the southern region of the United States. University of Georgia, Athens, pp 21–23
- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87. doi:[10.2307/2097282](https://doi.org/10.2307/2097282)
- Drezner T (2006) Plant facilitation in extreme environments: the non-random distribution of saguaro cacti (*Carnegiea gigantea*) under their nurse associates and the relationship to nurse architecture. *J Arid Environ* 65:46–61
- Eidenshink J, Schwind B, Brewer K, Zhu Z-L, Quayle B, Howard S (2007) A project for monitoring trends in burn severity. *J Assoc Fire Ecol* 3:3
- Engel EC, Abella SR (2011) Vegetation recovery in a desert landscape after wildfires: influences of community type, time since fire and contingency effects. *J Appl Ecol* 48:1401–1410. doi:[10.1111/j.1365-2664.2011.02057.x](https://doi.org/10.1111/j.1365-2664.2011.02057.x)
- Esque TC, Young JA, Tracy CR (2010) Short-term effects of experimental fires on a Mojave Desert seed bank. *J Arid Environ* 74:1302–1308. doi:[10.1016/j.jaridenv.2010.04.011](https://doi.org/10.1016/j.jaridenv.2010.04.011)
- Evans RD, Belnap J (1999) Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. *Ecology* 80:150–160
- Ewing SA, Southard RJ, Macalady JL, Hartshorn AS, Johnson MJ (2007) Soil microbial fingerprints, carbon, and nitrogen in a Mojave Desert creosote-bush ecosystem. *Soil Sci Soc Am J* 71:469–475
- Fonteyn PJ, Mahall BE (1981) An experimental analysis of structure in a desert plant community. *J Ecol* 69:883–896. doi:[10.2307/2259643](https://doi.org/10.2307/2259643)
- Gibson AC, Rasoul Sharifi M, Rundel PW (2004) Resprout characteristics of creosote bush (*Larrea tridentata*) when subjected to repeated vehicle damage. *J Arid Environ* 57:411–429. doi:[10.1016/S0140-1963\(03\)00120-4](https://doi.org/10.1016/S0140-1963(03)00120-4)
- Hamerlynck EP, McAuliffe JR (2008) Soil-dependent canopy die-back and plant mortality in two Mojave Desert shrubs. *J Arid Environ* 72:1793–1802. doi:[10.1016/j.jaridenv.2008.05.002](https://doi.org/10.1016/j.jaridenv.2008.05.002)
- Hamerlynck EP, McAuliffe JR, McDonald EV, Smith SD (2002) Ecological responses of two Mojave Desert shrubs to soil horizon development and soil water dynamics. *Ecology* 83:768–779
- Hamerlynck EP, Smith SD, Huxman TE, McAuliffe JR (2004) Carbon isotope discrimination and foliar nutrient status of *Larrea tridentata* (creosote bush) in contrasting Mojave Desert soils. *Oecologia* 138:210–215. doi:[10.1007/s00442-003-1437-7](https://doi.org/10.1007/s00442-003-1437-7)
- Haubensak K, D'Antonio C, Wixon D (2009) Effects of fire and environmental variables on plant structure and composition in grazed salt desert shrublands of the Great Basin (USA). *J Arid Environ* 73:643–650. doi:[10.1016/j.jaridenv.2008.12.020](https://doi.org/10.1016/j.jaridenv.2008.12.020)
- Hodgkinson KC (1992) Water relations and growth of shrubs before and after fire in a semi-arid woodland. *Oecologia* 90:467–473. doi:[10.1007/BF01875439](https://doi.org/10.1007/BF01875439)
- Holzappel C, Mahall BE (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology* 80:1747–1761
- Hooper DU, Johnson L (1999) Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry* 46:247–293
- Horn KJ, McMillan BR, St. Clair SB (2012) Expansive fire in Mojave Desert shrubland reduces abundance and species diversity of small mammals. *J Arid Environ* 77:54–58. doi:[10.1016/j.jaridenv.2011.10.003](https://doi.org/10.1016/j.jaridenv.2011.10.003)

- Horn KJ, Nettles R, St. Clair SB (2015) Germination response to temperature and moisture to predict distributions of the invasive grass red brome and wildfire. *Biol Invasions* 1–9:1849–1857. doi:[10.1007/s10530-015-0841-3](https://doi.org/10.1007/s10530-015-0841-3)
- Humphrey RR (1974) Fire in the deserts and desert grasslands of North America. In: Kozlowski TT, Ahlgren CE (eds) *Fire and ecosystems*. USA Academic Press, New York, pp 365–401
- IPCC (2007) *Climate Change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge
- Jones CS (1984) The effect of axis splitting on xylem pressure potentials and water movement in the desert shrub *Ambrosia dumosa* (Gray) Payne (Asteraceae). *Bot Gaz* 145:125–131
- Keeley JE, Fotheringham CJ, Baer-Keeley M (2005) Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. *Ecol Appl* 15:1515–1534. doi:[10.1890/04-1005](https://doi.org/10.1890/04-1005)
- Lajtha K, Whitford WG (1989) The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. *Oecologia* 80:341–348. doi:[10.1007/BF00379035](https://doi.org/10.1007/BF00379035)
- Lei SA (1999) Postfire woody vegetation recovery and soil properties in blackbrush (*Coleogyne ramosissima* Torr.) shrubland ecotones. *J Ariz-Nev Acad Sci* 32:105–115
- Lenihan JM, Drapek R, Bachelet D, Neilson RP (2003) Climate change effect on vegetation distribution, carbon, and fire in California. *Ecol Appl* 13:1667–1681. doi:[10.1890/025295](https://doi.org/10.1890/025295)
- Loik ME, St. Onge CD, Rogers J (2000) Post-fire recruitment of *Yucca brevifolia* and *Yucca schidigera* in Joshua Tree National Park, California. 2nd Interface Between Ecology and Land Development in California US Geological Survey OpenFile Report 0062 79–85
- Mahall BE, Callaway RM (1992) Root communication mechanisms and intercommunity distributions of two Mojave desert shrubs. *Ecology* 73:2145–2151. doi:[10.2307/1941462](https://doi.org/10.2307/1941462)
- Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. *Anal Chim Acta* 27:31–36. doi:[10.1016/S0003-2670\(00\)88444-5](https://doi.org/10.1016/S0003-2670(00)88444-5)
- Oechel WC, Strain BR, Odening WR (1972) Tissue water potential, photosynthesis, C-labeled photosynthate utilization, and growth in the desert shrub *Larrea divaricata* Cav. *Ecol Monogr* 42:128–141. doi:[10.2307/1942260](https://doi.org/10.2307/1942260)
- Olsen SR, Watanabe FS (1957) A method to determine a phosphorus adsorption maximum of soils as measured by the langmuir isotherm. *Soil Sci Soc Am J* 21:144. doi:[10.2136/sssaj1957.03615995002100020004x](https://doi.org/10.2136/sssaj1957.03615995002100020004x)
- R Core Team R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ravi S, D'Odorico P (2009) Post-fire resource redistribution and fertility island dynamics in shrub encroached desert grasslands: a modeling approach. *Landsc Ecol* 24:325–335. doi:[10.1007/s10980-008-9307-7](https://doi.org/10.1007/s10980-008-9307-7)
- Runyon EH (1934) The organization of the creosote bush with respect to drought. *Ecology* 15:128–138. doi:[10.2307/1932782](https://doi.org/10.2307/1932782)
- Schlesinger WH, Fonteyn PJ, Reiners WA (1989) Effects of overland flow on plant water relations, erosion, and soil water percolation on a Mojave Desert landscape. *Soil Sci Soc Am J* 53:1567–1572. doi:[10.2136/sssaj1989.03615995005300050045x](https://doi.org/10.2136/sssaj1989.03615995005300050045x)
- Schwinning S, Ehleringer JR (2001) Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *J Ecol* 89:464–480
- Schwinning S, Hooten MM (2009) Mojave desert root systems. In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, Miller DM (eds) *The Mojave Desert: ecosystem processes and sustainability*. University of Nevada Press, Reno, pp 278–311
- Smith SD, Hartsock TL, Nobel PS (1983) Ecophysiology of *Yucca brevifolia*, an arborescent monocot of the Mojave Desert. *Oecologia* 60:10–17
- St. Clair SB, Monson SD, Smith EA, Cahill DG, Calder WJ (2009) Altered leaf morphology, leaf resource dilution and defense chemistry induction in frost-defoliated aspen (*Populus tremuloides*). *Tree Physiol* 29:1259–1268. doi:[10.1093/treephys/tpp058](https://doi.org/10.1093/treephys/tpp058)
- Steers RJ, Allen EB (2011a) Native annual plant response to fire: an examination of invaded, 3 to 29 year old burned creosote bush scrub from the western Colorado Desert. *Nat Resour Environ Issues* 17:20
- Steers RJ, Allen EB (2011b) Fire effects on perennial vegetation in the western Colorado Desert, USA. *Fire Ecol* 7:59–74. doi:[10.4996/fireecology.0703059](https://doi.org/10.4996/fireecology.0703059)
- Stevenson BA, McDonald EV, Caldwell TG (2009) Root Patterns of *Larrea tridentata* in relation to soil morphology in Mojave Desert Sols of different Ages. In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, Miller DM (eds) *The Mojave Desert: ecosystem processes and sustainability*. University of Nevada Press, Reno, pp 278–311
- Strain BR (1969) Seasonal adaptations in photosynthesis and respiration in four desert shrubs growing in situ. *Ecology* 50:511–513. doi:[10.2307/1933911](https://doi.org/10.2307/1933911)
- Vamstad MS, Rotenberry JT (2010) Effects of fire on vegetation and small mammal communities in a Mojave Desert Joshua tree woodland. *J Arid Environ* 74:1309–1318. doi:[10.1016/j.jaridenv.2010.04.002](https://doi.org/10.1016/j.jaridenv.2010.04.002)
- Vander Wall SB, Kuhn KM, Beck MJ (2005) Seed removal, seed predation, and secondary dispersal. *Ecology* 86:801–806.
- Walker LR, Thompson DB, Landau FH (2001) Experimental manipulations of fertile islands and nurse plant effects in the Mojave Desert, USA. *Western North American Naturalist* 61:25–35
- Webb RH, Belnap J, Thomas KA (2009) Natural recovery from severe disturbance in the Mojave Desert. In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, Miller DM (eds) *The Mojave Desert: ecosystem processes and sustainability*. University of Nevada Press, Reno, pp 343–377
- Weigand J, Rogers J (2009) Active restoration for the Mojave Desert. In: Webb RH, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, Miller DM (eds) *The Mojave Desert: ecosystem processes and sustainability*. University of Nevada Press, Reno, pp 378–409
- Zouhar K, Smith JK, Sutherland S, Brooks ML (2008) Wildland fire in ecosystems: fire and nonnative invasive plants. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden