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# Spatio-temporal impacts of fire on soil nutrient availability in *Larrea tridentata* shrublands of the Mojave Desert, USA

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ABSTRACT

Soil nutrients and herbaceous plant growth are patchily distributed in desert ecosystems, often restricted to "fertility islands" created by perennial shrubs. Although fire has been historically uncommon in southwestern American hot deserts (e.g., the Mojave), these regions have experienced more severe fires due to recent invasions of exotic species that increased proneness to fire. Nevertheless, the effects of fire on soil nutrients in SW deserts, including via the removal of shrubs by fire, remain unclear. We assessed the spatio-temporal impacts of fire on soil nutrient availability in burned and unburned areas of the Mojave Desert. The study was conducted in shrublands dominated by *Larrea tridentata*. We investigated both the short (seven months after fire) and long (seven years after fire) term effects of fire on soil nutrient availability within a microhabitat gradient spanning from under the shrub canopy to open inter-shrub areas. We found that nitrogen (N) and potassium (K) were higher under the canopy of burned *L. tridentata* seven months after fire. In contrast, seven years after fire, N and K availability were lower around shrubs that were killed by fire. Over the short-term, fire had a positive effect on soil nutrients. However, over the long-term, the fertility island effect diminished after removal of shrubs by fire, and the differential availability of nutrients such as N and K became more similar under shrubs and in open inter-shrub areas. This reinforces the key role of *L. tridentata* in influencing the distribution of soil nutrients and provides support for the hypothesis that post-fire herbaceous plant growth will be less restricted to areas under shrubs.



## 1. Introduction

Fire is an important disturbance that can alter vegetation and affect soil nutrient balance via losses and inputs (Whelan, 1995; Sugihara et al., 2006). Loss of nutrients usually occurs through volatilization and post-fire soil erosion by wind and water. Nutrient inputs occur when burned plant biomass and litter are incorporated back into the soil in the form of ash (Neary et al., 1999). Due to the mechanisms of nutrient losses and inputs, fire has the potential to affect both nutrient availability and the spatial distribution of nutrients in the soil, especially in systems with patchy plant communities and litter inputs (Rodriguez et al., 2009a). The effects of fire on the availability and distribution of soil nutrients can also be influenced by the topography of the burned area and the physical and chemical properties of the soil (Wan et al., 2001; Abella and Engel, 2013).

In general, desert ecosystems are not thought of as being prone to fire, primarily because of the lack of a continuous fuel bed to carry fire (Brooks and Matchett, 2006; Allen et al., 2011). However, over the last several decades, desert regions of southwestern North America (e.g., the Mojave Desert) have been invaded by exotic grasses (e.g., *Bromus* and *Schismus* species) and forbs (e.g., *Erodium cicutarium* and *Brassica tournefortii*; D'Antonio and Vitousek, 1992; Brooks et al., 2004), which has increased the susceptibility of these deserts to fire. These exotic invasive species are closely tied to seasonal and annual variation in precipitation, which may lead to greater biomass production within the inter-shrub areas. As a consequence, fire risk is often greater after rainy seasons with above-average rainfall, because of greater plant growth and litter production, which can fuel larger fires (Brooks et al., 2004; Chambers and Wisdom, 2009; Esque et al., 2013).

Even though fire risk has increased in deserts ecosystems, the potential effects of fire on soil properties remain unclear. For example, some studies have shown that nitrogen (N) availability has increased (Abella and Engel, 2013), decreased (Allen et al., 2011), or remained unchanged after fire (Brooks, 2002). The observed differences in the effects

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of fire on soil nutrients may be related to the time after fire at which measurements are made (e.g., short vs. long term effects; Debano and Conrad, 1978; Davies et al., 2008; Augustine et al., 2010). Specifically, in a recent study conducted in shrublands of the Mojave Desert, Abella and Engel (2013) found N and potassium (K) to be higher in burned areas compared to unburned areas, but differences decreased over the first year after fire, highlighting how temporal effects may influence nutrient balance in desert soils.

A clear understanding of the impact of fire on soil nutrients in desert ecosystems is complicated by the fact that soil nutrients are generally scarce and heterogeneously distributed. Many nutrients are concentrated in "fertility islands" created by trees and perennial shrubs, such as the creosote bush, *Larrea tridentata* (DC.) Cov. (hereafter referred to by genus; Schlesinger et al., 1996; Bolling and Walker, 2002). Several studies have shown that nutrient concentrations (mainly N and K) are higher under *Larrea* canopies than in open inter-shrub areas (Samson, 1986; Titus et al., 2002; Mudrak et al., 2014). Fertility islands are crucial in desert systems because they help to maintain a diverse and productive annual plant community under the shrub canopies (Esque et al., 2010; Schafer et al., 2012). Many native annual species do not readily grow in the open inter-shrub areas, unlike the exotic species described above. Furthermore, desert fires tend to be patchy in their effects (Brooks and Matchett, 2006), leading to changes in the spatial distribution of living shrubs in the landscape. Because perennial shrubs are key components in the structure and functioning of deserts in southwestern North America (Bolling and Walker, 2002; Lopez et al., 2009; Griffith, 2010; Schafer et al., 2012; Mudrak et al., 2014; Fuentes-Ramirez et al., 2015), shrub removal by fire may have cascading effects on the whole community. However, little is known about the effect of shrub removal by fire on both the availability and spatial distribution of nutrients, and the persistence of *Larrea* fertility islands.

The purpose of this study was to examine both the temporal and spatial effects of fire on soil nutrients in *Larrea* dominated areas of the Mojave Desert. We assessed the short-term effects of fire by comparing soil nutrients under and around unburned and experimentally burned *Larrea* shrubs seven months after fire. We assessed the long-term effects of fire by measuring soil nutrient availability under living *Larrea* shrubs and on soil mounds where *Larrea* was killed by a wildfire seven years prior to our study. In both cases, the effect of fire on the spatial distribution of nutrients was assessed by comparing soil nutrients under *Larrea* canopies with soil nutrients in the open inter-shrub areas. We hypothesized that soil nutrients increase over the short-term after fire and that increases are greater under the *Larrea* canopy than in the open inter-shrub areas. We also hypothesized that soil nutrients become more evenly distributed over the long-term after removal of shrubs by fire, indicating a change in the spatial pattern of nutrients and a potential disappearance of the fertility island effect created by *Larrea*.

## 2. Materials and methods

### *2.1 . Study area*

The study was conducted in two *L. tridentata* (DC.) Cov. shrubland sites in the Mojave Desert. Selected shrubs at one site were experimentally burned in June 2011. The other site was burned by a wildfire in May 2005 (Fig. 1). Both sites have similar physical characteristics and support similar shrub communities, being co-dominated by *Larrea* and the perennial shrub *Ambrosia dumosa* (A. Gray) Payne, with inter-shrub areas sparsely vegetated by both native and exotic forbs and grasses (Abella, 2010). Soils in both study sites are typic torripsamments in the Cajon series (Natural Resources Conservation Service, 1999). These soils are young and intermediate aged alluvial grus (i.e., alluvium derived from disintegrated granite; Amoroso and Miller, 2006) with a sandy loam texture. Soils are well drained with low moisture availability and occur in areas with slopes of 0–15%. In the experimentally burned site, soil N and K concentrations are higher under *Larrea* canopies than in the open inter-shrub areas, but phosphorus (P) availability does not vary with distance from *Larrea* (Mudrak et al., 2014). In addition, concentrations of N and K under *Larrea* canopies are up to 15 and 30 times higher, respectively, than P concentrations (Mudrak et al., 2014).

The experimentally burned site was located within the Fort Irwin National Training Center, 31 km north of Barstow, CA at an elevation of 865 m (35°9′21″ N, 116°53′6″ W). The mean annual temperature in this area is 18.8 °C and mean annual precipitation is 130.5 mm (Western Regional Climate Center, Barstow weather station), with the majority of precipitation falling between January and March. The Fire Department at Fort Irwin National Training Center used fusee flares (fusee backfiring torch, US Forest Service specification 5100-360) to burn 56 *Larrea* shrubs distributed throughout a one-hectare plot on 20–21 June, 2011. Fusee flares are commonly used in forestry for the ignition of controlled burns. These flares are easy to control, can burn as hot as 1600 °C, and produce minimal amounts of residue. Burned shrubs were intermixed with shrubs that were not burned. The unburned shrubs were used as controls for assessing the change in nutrients 7 months after fire. Only 25 shrubs (ca. 44%) showed some degree of resprouting (e.g., green tips, new foliage) 2 years after experimental burning (Erika L. Mudrak, unpublished data).

The site burned by a wildfire was located at an elevation of 746 m, 24 km NW of Barstow, CA (35°4′56″ N, 117°9′15″ W) and 26 km SW of our experimentally burned Fort Irwin site (Fig. 1). The wildfire occurred after above-average precipitation in the 2004/2005 wet season (328 mm, which is approximately 3 times higher than average), which likely caused an increase in the abundance of fine fuels that could have fueled the wildfire. This fire burned approximately 53 ha and killed approximately 46% of the *Larrea* shrubs within our burned plot (California Department of Forestry and Fire Protection, 2013, A. Fuentes-Ramirez, unpublished data).

### *2.2 . Sampling design*

At the Fort Irwin site, we characterized the short-term effects of fire on soil nutrient availability. On January 29, 2012, seven months after the shrubs were experimentally burned, we deployed Plant Root Simulator™-probes (Western Ag Innovations, Inc., Saskatoon, Canada; hereafter referred to as PRS-probes) to measure soil nutrient availability. PRS-probes are ion-exchange (cation and anion) resin membranes mounted in a plastic frame that provide an index of the availability of nutrients by mimicking the uptake of nutrients by plants (Qian et al., 1992) and are effective in measuring nutrients in arid ecosystems (Drohan et al., 2005; Collins et al., 2010).

Within the one-hectare plot, we selected eight shrubs that were completely burned and killed by fire (with no sign of resprouting) and eight unburned, living shrubs. Six PRS-probe anion/cation pairs were placed on the north side of each shrub at 20 cm intervals (from the center of the soil mound or shrub) along a transect extending up to 120 cm. We sampled on the north side of the shrub because nutrient availability is higher on the north than south side of *Larrea* (Brooks, 1999; Schenk and Mahall, 2002; Mudrak et al., 2014). The probes were buried so that the ion-exchange surface spanned a depth of 5–10 cm. To assess the effect of fire on the spatial distribution of soil nutrients, the probe locations were characterized by microhabitats (see Fig. 2a): under the canopy of *Larrea* (UC; at 20 and 40 cm), in the open near *Larrea* (ON; at 60 and 80 cm), and in the open far from *Larrea* (OF; at 100 and 120 cm). The PRS-probes were removed from the soil on March 30, 2012 after 60 days of burial, and were subsequently rinsed with distilled water and returned to Western Ag Innovations for analysis of N (measured as $NH_4^+$ and $NO_3^-$), phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), and sulfur (S). The soil nutrient concentrations are expressed as a flux rate, measured as μg of nutrient/10 $cm^2$/$day^{-1}$.

At the wildfire site, we assessed the long-term effects of wildfire on soil nutrient availability seven years after fire. In June 2011, we established two 0.5-hectare plots, one within the 2005 wildfire burn

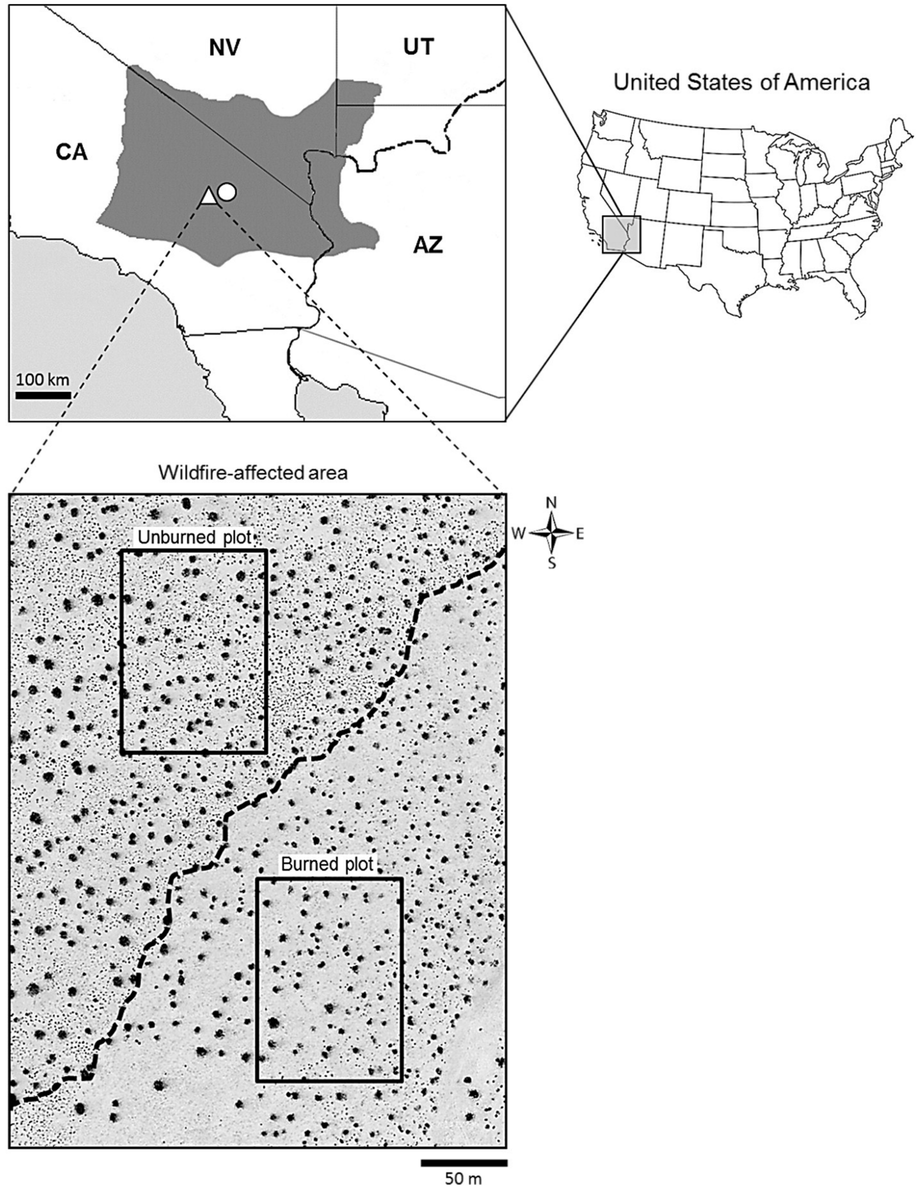


**Fig. 1.** Map of the study area in the Mojave Desert (gray-shaded area) that depicts the locations of the experimentally burned (circle) and wildfire affected (triangle) study sites. The wildfire-affected area is detailed in the aerial image with the fire boundary noted as a dashed line and the two sampling plots outlined by black rectangles. Note that the aerial image in not scaled to the shaded box in the US map.

scar and one in an adjacent unburned area (Fig. 1). There is no evidence that this unburned area has been impacted by fire in recent history, as we did not observe any burned stumps or bare soil mounds. We randomly selected 22 soil mounds that were associated with dead *Larrea* in the burned plot and 22 soil mounds associated with living *Larrea* in the unburned plot. We defined a living shrub as the collection of stems and green branches with overlapping canopies located on a single soil mound (i.e., fertility island; see methods in Mudrak et al., 2014). Similarly, a dead shrub was defined as the burned stump or the dried collection of branches and stems on a single bare soil mound. We placed one PRS-probe anion/cation pair in the center of each soil mound, which represents the under-canopy habitat (i.e., UC microhabitat) influenced by a living (unburned) or dead (burned) shrub, and one PRS-probe pair 120 cm away from the mound center (north side), outside of the area of influence of the shrub (i.e., OF microhabitat, Fig. 2b), for a total of 44 PRS-probes per plot. The PRS-probes were buried on January 11, 2013 (with the ion-exchange surface spanning a depth of 5–10 cm) and removed on March 27, 2013, after 75 days of burial. PRS-probes were processed as described above, and nutrients were measured as a flux rate (i.e., μg of nutrient/10 $cm^2$/$day^{-1}$).

## 2.3 . Data analysis

To assess the short-term effects of fire (i.e., 7 months after fire), we pooled distances into the three microhabitat categories (under canopy, UC = 20 and 40 cm, open near canopy, ON = 60 and 80 cm, and open far from canopy, OF = 100 and 120 cm). We analyzed the effects of fire on soil nutrient availability seven months after fire using a full factorial ANOVA with fire (burned and unburned) and microhabitat (UC, ON, OF) as fixed factors. In a separate analysis, the long-term effects of fire (i.e., seven years after burning) on soil nutrient availability were analyzed using a full factorial ANOVA with fire (burned and unburned) and microhabitat (UC, OF) as fixed factors. We used a posteriori Tukey's tests for pair-wise comparisons. Nutrient data were log-transformed when necessary to meet the assumption of normality.

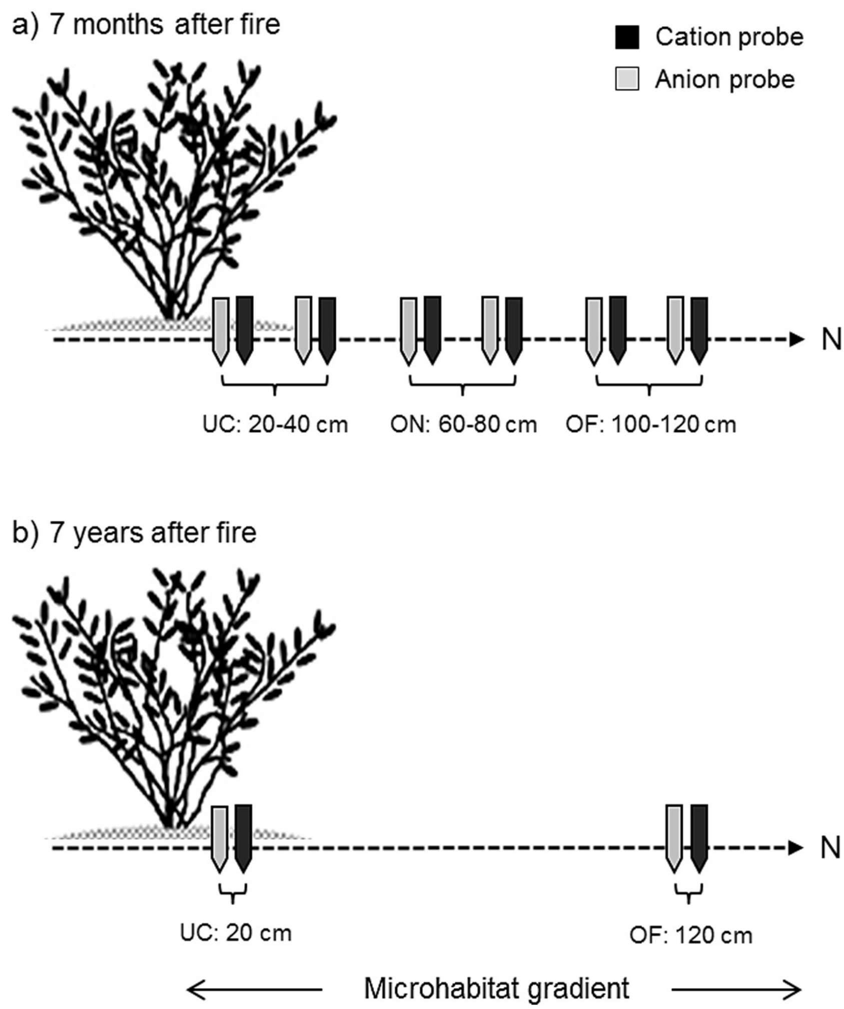


**Fig. 2.** Diagram of the soil sampling design in sites sampled (a) seven months and (b) seven years after fire. UC = under canopy microhabitat, ON = open near shrub microhabitat, and OF = open far from shrub microhabitat. Vertical black and gray bars represent the cation and anion PRS-probes used for sampling, respectively.

## 3. Results

Seven months after fire, soil N and K availability were significantly higher under the canopies (UC microhabitat) of burned *Larrea* shrubs than in the same microhabitat under unburned shrubs (Table 1). Soil N and K availability declined with distance from either the living *Larrea* canopy or soil mounds of burned *Larrea* into the open microhabitats (Table 1, Fig. 3). Neither burning nor microhabitat had a significant effect on P availability (Table 1). Fire and microhabitat had significant effects on Mg and Ca (Table 1), but only in the OF microhabitat where we observed higher availability of these nutrients associated with burned *Larrea* mounds compared to the unburned shrubs (Fig. 3). Neither burning nor microhabitat significantly affected soil S (Fig. 3).

Seven years after fire, soil N availability was significantly lower on burned than unburned *Larrea* soil mounds (the UC microhabitat), but there was no effect of fire further away from the shrub mound in the OF microhabitat (Table 1, Fig. 4). Soil K availability was significantly lower in burned sites in both the UC and OF microhabitats (Fig. 4). There was no effect of fire on P availability in either microhabitat (Table 1). Soil Mg availability was significantly higher in both the UC and OF microhabitats associated with burned, compared to unburned, *Larrea* (Table 1). We found a significant interaction between fire and microhabitat for soil Ca availability, with higher levels of Ca on burned mounds (i.e., UC microhabitat) and in the open inter-shrub areas (i.e., OF microhabitat) associated with unburned *Larrea* (Table 1, Fig. 4). Availability of S was significantly lower in both the UC and OF

**Table 1**
Summary of ANOVA analyses of the short (seven months post fire) and long (seven years post fire) term effects of fire and microhabitat (under canopy (UC), open near shrub (ON), and open far from shrub (OF) seven months after fire; UC and OF seven years after fire) and their interaction on soil N, K, P, Mg, Ca, and S. Significant effects (at $\alpha < 0.05$) are shown in bold type. D.F. = degrees of freedom.

| Time after fire | Effect | D.F. | Nitrogen (N) | | Potassium (K) | | Phosphorus (P) | | Magnesium (Mg) | | Calcium (Ca) | | Sulfur (S) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | F | P | F | P | F | P | F | P | F | P | F | P |
| 7 months | Fire | 1,42 | 8.87 | **0.005** | 11.80 | **0.001** | 0.01 | 0.935 | 5.43 | **0.025** | 4.18 | **0.047** | 0.63 | 0.432 |
| | Microhabitat | 2,42 | 7.23 | **0.002** | 26.01 | **<0.001** | 0.46 | 0.632 | 8.11 | **0.001** | 8.46 | **0.001** | 0.65 | 0.527 |
| | Fire × microhabitat | 2,42 | 1.76 | 0.184 | 0.01 | 0.994 | 0.34 | 0.712 | 1.83 | 0.173 | 2.59 | 0.086 | 0.14 | 0.865 |
| 7 years | Fire | 1,84 | 7.61 | **0.007** | 35.77 | **<0.001** | 0.11 | 0.739 | 10.64 | **0.002** | 0.01 | 0.973 | 80.88 | **<0.001** |
| | Microhabitat | 1,84 | 51.68 | **<0.001** | 64.05 | **<0.001** | 0.40 | 0.528 | 0.01 | 0.921 | 5.74 | **0.019** | 36.98 | **<0.001** |
| | Fire × microhabitat | 1,84 | 10.71 | **0.001** | 7.13 | **0.009** | 1.57 | 0.213 | 0.03 | 0.862 | 4.43 | **0.038** | 0.37 | 0.544 |

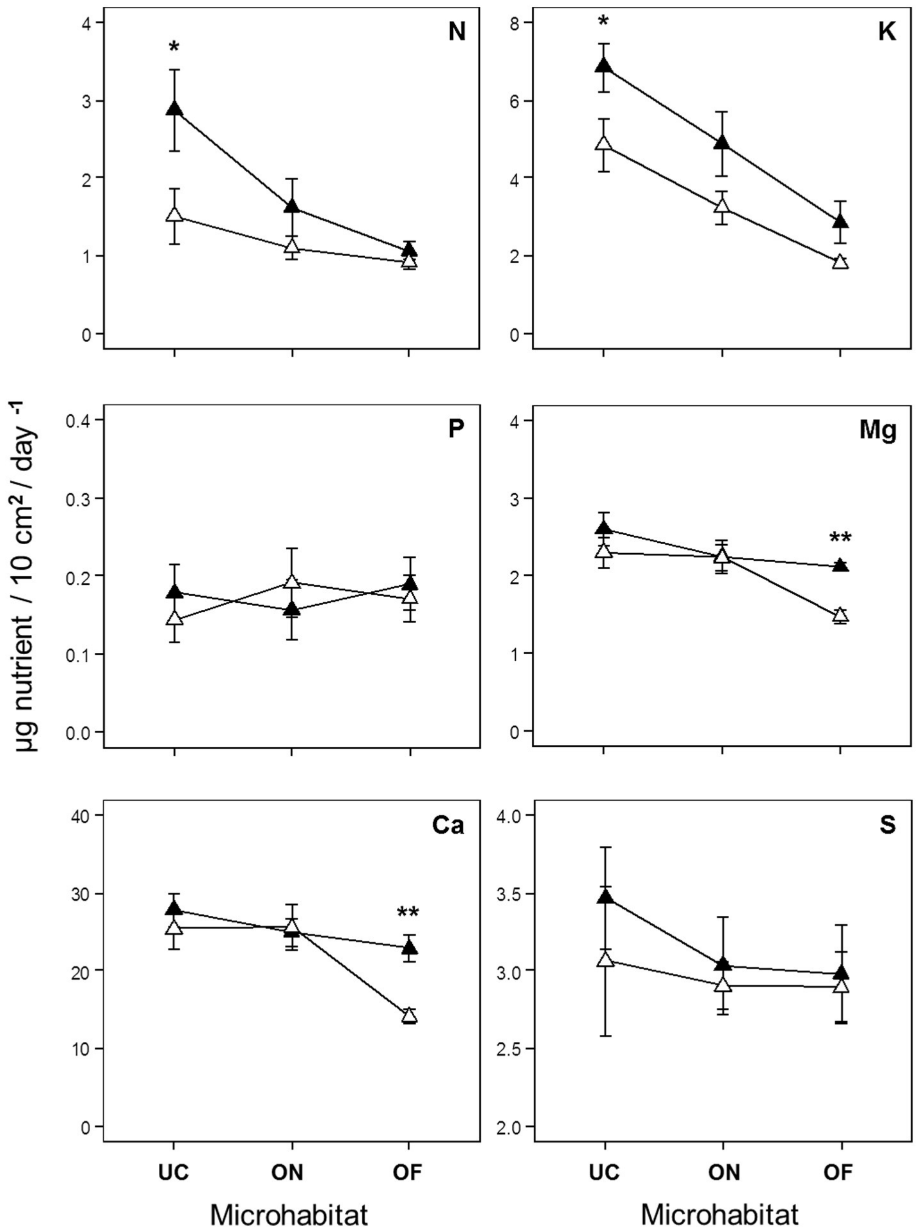


**Fig. 3.** Mean (±SE) nitrogen (N), potassium (K), phosphorus (P), magnesium (Mg), calcium (Ca), and sulfur (S) availability (expressed as µg nutrient/10 $cm^2$/$day^{-1}$) in the under canopy (UC), open near shrub (ON), and open far from shrub (OF) microhabitats around burned (black triangles) and unburned (white triangles) *Larrea* shrubs seven months after fire. Significant effects of fire on nutrient availability within microhabitat are indicated by * for $P < 0.05$ and ** for $P < 0.01$.

microhabitats associated with burned, dead *Larrea* compared to unburned *Larrea* (Table 1).

## 4. Discussion

Fire affected the availability of soil nutrients at the temporal and spatial scales examined in this study. Overall, seven months after fire, availability of N, K, Mg and Ca was higher in the vicinity of burned *Larrea* than under comparable unburned shrubs. Seven years after fire, availability of N, K and S was lower on soil mounds associated with *Larrea* killed by a wildfire, compared to shrubs in the adjacent unburned area. Similar to other studies (Titus et al., 2002; Mudrak et al., 2014), we found a consistent spatial pattern of nutrient availability, regardless of whether *Larrea* were alive or had been killed by fire, with higher concentrations of N and K in the under-canopy microhabitat than in the open areas among shrubs. However, over time (seven years post-fire) the degree of difference in nutrient concentrations under shrubs, as compared to open areas away from shrubs, diminished in the burned area.

Our hypothesis that soil nutrients increase over the short-term after fire was partially supported, as higher concentrations of N, K, Mg, and Ca were found around burned *Larrea* shrubs. The increase in soil N (measured as $NH_4^+$ and $NO_3^-$) availability seven months after fire was likely due to both increased N mineralization and oxidation of organic soil N exposed to elevated temperatures during fire (Mroz et al., 1980; Knoepp and Swank, 1993). Although usually overlooked (Choromanska and DeLuca, 2002), N originating from burned plants may also contribute to a higher amount of N after fire, especially in the first year after fire (Diaz-Ravina et al., 1996). Higher K availability after fire is more likely due to a high concentration of K in ash from the burned vegetation and litter (Debano and Conrad, 1978; Carreira and Niell, 1995). The post-fire increase in N and K also varied in its spatial distribution, as hypothesized and similar to other studies (Esque et al., 2010), with larger increases under *Larrea* canopies (UC microhabitat) than in the open inter-shrub

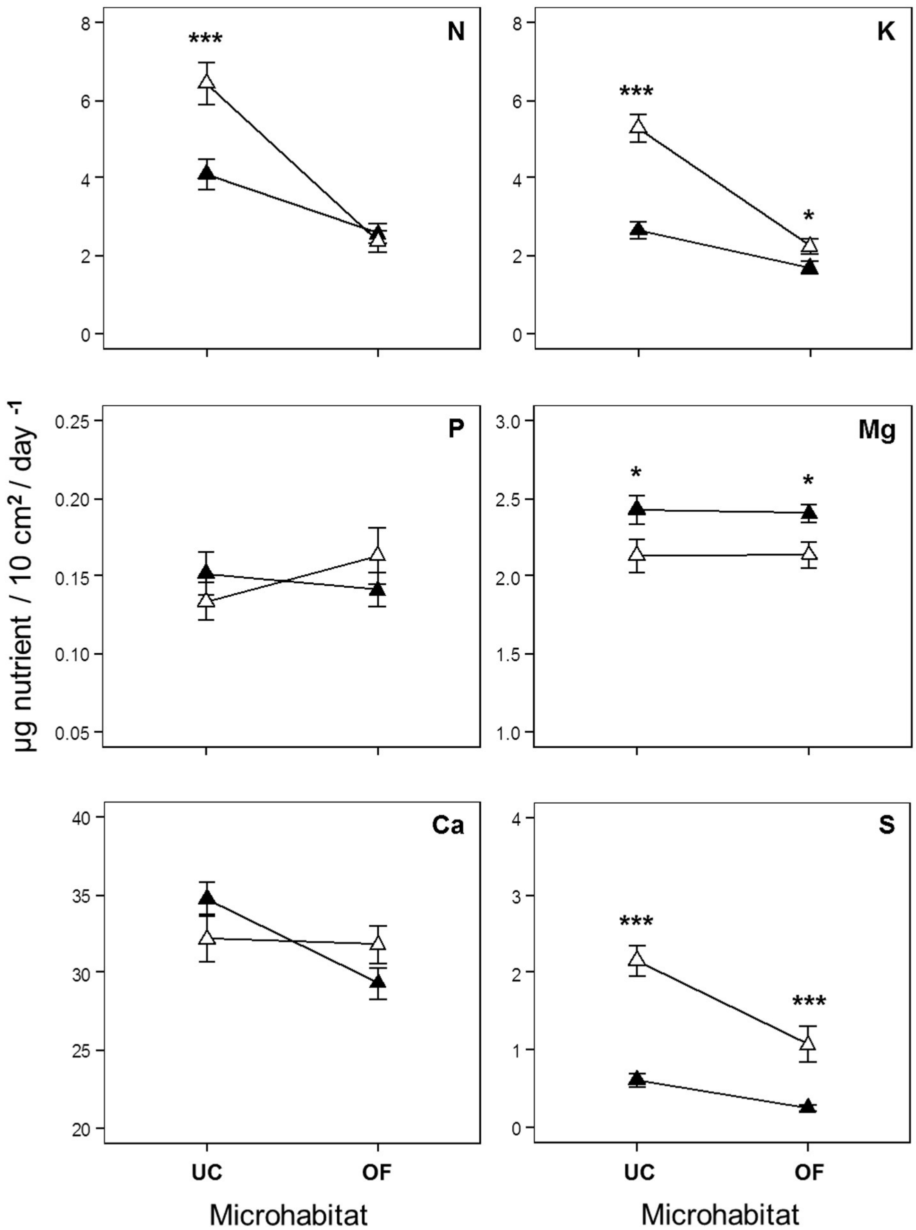


**Fig. 4.** Mean (±SE) nitrogen (N), potassium (K), phosphorus (P), magnesium (Mg), calcium (Ca), and sulfur (S) availability (expressed as µg nutrient/10 $cm^2$/$day^{-1}$) in the under canopy (UC) and open far from shrub (OF) microhabitats around burned (black triangles) and unburned (white triangles) *Larrea* shrubs seven years after fire. Significant effects of fire on nutrient availability within microhabitat are indicated by * for $P < 0.05$ and *** for $P < 0.001$.

areas. Although availability of Mg and Ca was greater under the *Larrea* canopy than in the open inter-shrub areas (overall), fire significantly increased these nutrients only in the OF microhabitat. The pattern for this change is not clear, but it may be due to the movement of ash by water and wind toward open areas after the *Larrea* shrubs were removed by fire (Raison, 1979; Carreira and Niell, 1995).

While these results may suggest a temporal enhancement of the fertility island effect (especially for N and K) over the first seven months after fire, the patterns of these changes may vary with time after fire (DeBano et al., 1998). Generally, the increase in soil nutrients persists over several months and then declines to the pre-fire level one or two years after fire (Adams et al., 1994; Wan et al., 2001; Schafer and Mack, 2010). In fact, the short-term increases in N and K availability after fire within our study area did not persist over the long term.

Our hypothesis that soil nutrients become more evenly distributed over the long-term after shrub removal by fire was partially supported, as the availabilities in N and K were lower in the microhabitats associated with burned *Larrea* than in the microhabitats associated with living *Larrea* shrubs. After shrubs are killed by fire, wind and water are likely to erode soil from the remaining mounds with lower densities of annual plants, resulting in a decrease in nutrient availability over time. Furthermore, microbial activity may decline after shrub removal due to decreased inputs of plant-derived organic matter (Ewing et al., 2007). Soil microbial activity can be further diminished due to loss of canopy shading, which can lead to reduced soil water availability (Holzapfel and Mahall, 1999). Although, surprisingly, the fertility island effect associated with *Larrea* was still present seven years after wildfire, the effect was much smaller, which emphasizes the key role of *Larrea* in maintaining crucial ecological processes in arid environments. This phenomenon has also been observed in mesquite-dominated desert grasslands (in SW Arizona), where differences in soil N content between under-canopy and open microhabitats become smaller within burned areas (Wilson and Thompson, 2005). Magnesium was the only nutrient that had higher concentrations around burned shrubs seven years after fire in both microhabitats; the reason for this pattern is again not clear, however, because persistence of ash should also contribute to higher concentrations of K and Ca.

Although we conducted our study in only one area and limited our investigation to two temporal scales (i.e., seven months and seven years after fire), both of our study areas are representative of the *L. tridentata*-dominated region of the Mojave Desert, with similar physical characteristics, soils, and plant communities in the burned and unburned areas (A. Fuentes-Ramirez, unpublished data). Thus, differences in nutrient availability between burned (dead) and unburned (living) *Larrea*, and the effects on fertility islands, are most likely due to the effects of fire rather any differences between our study sites. The biomass of herbaceous species (in both sites) is low relative to the biomass of woody shrubs, so the higher inter-shrub cover of non-native species that likely fueled the wildfire should not be large enough to cause the observed differences in changes in nutrient dynamics (i.e., the breakdown of fertility islands) from 7 months to 7 years after fire. Also, our sampling of the long-term effects of fire on soil characteristics was necessarily opportunistic, and direct comparison with the short-term effects from the Fort Irwin site is impossible as we were unable to balance factors such as location, time-since-burn, and type of fire (wild vs. experimental).

Differences in fire intensity between wildfires and experimental burns (e.g., soil surface temperature; Gimeno-Garcia et al., 2007) could affect the magnitude of post-fire increases in nutrient availability because nutrient volatilization is related to fire temperature (Raison et al., 1985). However, 54% and 44% of *Larrea* in our study sites survived wildfire and the experimental burns, respectively. This suggests that fire intensities in the wildfire and experimental burns were not different enough to cause large differences in *Larrea* resprouting rates, and thus, did not cause large differences in the proportion of nutrients that were volatilized during fire. Furthermore, in both sites, we measured nutrients where fire was severe enough to kill *Larrea*.

We did not find any difference in P availability between burned and unburned shrubs at either of the two temporal scales examined in this study. Loses and gains of P may occur at extremely low rates in low-fire-frequency systems (Wardle et al., 2003; Lagerstrom et al., 2009), such as deserts. This phenomenon, in combination with low P availability in the soil (see Fig. 4 in Mudrak et al., 2014) may potentially explain why we did not find any effects of fire on P availability. While ash often contains high concentrations of P (Rodriguez et al., 2009b), in our study, there was not enough P in ash to significantly affect soil P availability.

## 5. Conclusions

Although the positive effects on desert soils characteristically associated with *Larrea* (Schade and Hobbie, 2005; Ravi and D'Odorico, 2009) may persist after the shrub is killed by fire, our study indicates that these effects are weak in the long-term. Considering that *Larrea* has low post-fire resprouting (3–44%) and low reproductive success (Abella, 2009), it is unlikely that *Larrea* will recover quickly after fire. With nutrients (i.e., N and K) becoming more evenly distributed between the fertility islands associated with fire-killed shrubs and the inter-shrub areas, this may result in alterations of the annual plant community associated with fertility islands. Exotic grasses (e.g., *Bromus* spp. and *Schismus* spp.) have been shown to have enhanced competitive abilities relative to native annuals in acquiring scarce soil nutrients (Brooks, 2000). Post-fire increases in cover of exotic invasive grasses can lead to more frequent and intense fires in the future (Brooks et al., 2004; Olsson et al., 2012). By killing *Larrea* shrubs, which are key components of the Mojave Desert, fire may alter soil nutrients by facilitating the degradation of fertility islands over time. This is likely to have cascading effects on the diversity and density of the native and exotic annual plant communities, as heterogeneous landscapes with *Larrea* fertility islands may become more uniform landscapes dominated by exotic invasive grasses.

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## References

Abella, S.R., 2009. Post-fire plant recovery in the Mojave and Sonoran deserts of western North America. J. Arid Environ. 73 (8), 699–707.
Abella, S.R., 2010. Disturbance and plant succession in the Mojave and Sonoran deserts of the American southwest. Int. J. Environ. Res. Public Health 7 (4), 1248–1284.
Abella, S.R., Engel, E.C., 2013. Influences of wildfires on organic carbon, total nitrogen, and other properties of desert soils. Soil Sci. Soc. Am. J. 77, 1806–1817.
Adams, M.A., Iser, J., Keleher, A.D., Cheal, D.C., 1994. Nitrogen and phosphorus availability and the role of fire in Heathlands at Wilsons promontory. Aust. J. Bot. 42 (3), 269–281.
Allen, E.B., Steers, R.J., Dickens, S.J., 2011. Impacts of fire and invasive species on desert soil ecology. Rangel. Ecol. Manag. 64 (5), 450–462.
Amoroso, L., Miller, D.L., 2006. NTC_Soils.pp. Superficial Geologic Map of Arid Southwest USA. U.S. Geological Survey, Washington D.C.
Augustine, D.J., Derner, J.D., Milchunas, D.G., 2010. Prescribed fire, grazing, and herbaceous plant production in shortgrass steppe. Rangel. Ecol. Manag. 63, 317–323.
Bolling, J.D., Walker, L.R., 2002. Fertile island development around perennial shrubs across a Mojave Desert chronosequence. W. N. Am. Nat. 62 (1), 88–100.
Brooks, M.L., 1999. Habitat invasibility and dominance by alien annual plants in the Western Mojave Desert. Biol. Invasions 1 (4), 325–337.
Brooks, M.L., 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. Am. Midl. Nat. 144 (1), 92–108.
Brooks, M.L., 2002. Peak fire temperatures and effects on annual plants in the Mojave Desert. Ecol. Appl. 12 (4), 1088–1102.
Brooks, M.L., Matchett, J.R., 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. J. Arid Environ. 67, 148–164.
Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. Bioscience 54 (7), 677–688.
California Department of Forestry and Fire Protection, 2013. Fire perimeters, edition 13-2. Standard Digital Geospatial Metadata: Opal file (URL: http://frap.fire.ca.gov/data/frapgisdata-sw-fireperimeters_download.php).
Carreira, J.A., Niell, F.X., 1995. Mobilization of nutrients by fire in a semiarid gorse-scrubland ecosystem of southern Spain. Arid Soil Res. Rehabil. 9 (1), 73–89.
Chambers, J.C., Wisdom, M.J., 2009. Priority research and management issues for the imperiled Great Basin of the Western United States. Restor. Ecol. 17 (5), 707–714.
Choromanska, U., DeLuca, T.H., 2002. Microbial activity and nitrogen mineralization in forest mineral soils following heating: evaluation of post-fire effects. Soil Biol. Biochem. 34 (2), 263–271.
Collins, S.L., Fargione, J.E., Crenshaw, C.L., Nonaka, E., Elliott, J.R., Xia, Y., Pockman, W.T., 2010. Rapid plant community responses during the summer monsoon to nighttime warming in a northern Chihuahuan Desert grassland. J. Arid Environ. 74 (5), 611–617.
D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Syst. 23, 63–87.
Davies, K.W., Sheley, R.L., Bates, J.D., 2008. Does fall prescribed burning *Artemisia tridentata* steppe promote invasion or resistance to invasion after a recovery period? J. Arid Environ. 72 (6), 1076–1085.
Debano, L.F., Conrad, C.E., 1978. Effect of fire on nutrients in a chaparral ecosystem. Ecology 59 (3), 489–497.
DeBano, L.F., Neary, D., Folliott, P.F., 1998. Fire's Effects on Ecosystems. John Wiley & Sons, New York, USA.
Diaz-Ravina, M., Prieto, A., Baath, E., 1996. Bacterial activity in a forest soil after soil heating and organic amendments measured by the thymidine and leucine incorporation techniques. Soil Biol. Biochem. 28 (3), 419–426.
Drohan, P.J., Merkler, D.J., Buck, B.J., 2005. Suitability of the plant root simulator probe for use in the Mojave Desert. Soil Sci. Soc. Am. J. 69 (5), 1482–1491.
Esque, T.C., Kaye, J.P., Eckert, S.E., DeFalco, L.A., Tracy, C.R., 2010. Short-term soil inorganic N pulse after experimental fire alters invasive and native annual plant production in a Mojave Desert shrubland. Oecologia 164 (1), 253–263.
Esque, T.C., Webb, R.H., Wallace, C.S.A., Riper, C.I.I.I.v., McCreedy, C., Smythe, L., van Riper III, C., 2013. Desert fires fueled by native annual forbs: effects of fire on communities of plants and birds in the Lower Sonoran Desert of Arizona. Southwest. Nat. 58 (2), 223–233.
Ewing, S.A., Southard, R.J., Macalady, J.L., Hartshorn, A.S., Johnson, M.J., 2007. Soil microbial fingerprints, carbon, and nitrogen in a Mojave Desert creosote-bush ecosystem. Soil Sci. Soc. Am. J. 71 (2), 469–475.

Fuentes-Ramirez, A., Mudrak, E.L., Caragea, P.C., Holzapfel, C., Moloney, K.A., 2015. Assessing the impact of fire on the spatial distribution of *Larrea tridentata* in the Sonoran Desert, USA. Oecologia 178 (2), 473–484.
Gimeno-Garcia, E., Andreu, V., Rubio, J.L., 2007. Influence of vegetation recovery on water erosion at short and medium-term after experimental fires in a Mediterranean shrubland. Catena 69 (2), 150–160.
Griffith, A.B., 2010. Positive effects of native shrubs on *Bromus tectorum* demography. Ecology 91 (1), 141–154.
Holzapfel, C., Mahall, B.E., 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. Ecology 80 (5), 1747–1761.
Knoepp, J.D., Swank, W.T., 1993. Site preparation burning to improve southern Appalachian pine hardwood stands: nitrogen responses in soil, soil–water, and streams. Can. J. For. Res. 23, 2263–2270.
Lagerstrom, A., Esberg, C., Wardle, D.A., Giesler, R., 2009. Soil phosphorus and microbial response to a long-term wildfire chronosequence in northern Sweden. Biogeochemistry 95 (2–3), 199–213.
Lopez, R.P., Larrea-Alcazar, D.M., Teresa, O., 2009. Positive effects of shrubs on herbaceous species richness across several spatial scales: evidence from the semiarid Andean subtropics. J. Veg. Sci. 20 (4), 728–734.
Mroz, G.D., Jurgensen, M.F., Harvey, A.E., Larsen, M.J., 1980. Effects of fire on nitrogen in forest floor horizons. Soil Sci. Soc. Am. J. 44 (2), 395–400.
Mudrak, E.L., Schafer, J.L., Fuentes-Ramirez, A., Holzapfel, C., Moloney, K.A., 2014. Predictive modeling of spatial patterns of soil nutrients related to fertility islands. Landsc. Ecol. 29 (3), 491–505.
Natural Resources Conservation Service, 1999. Official Soil Series Descriptions (OSD) with series extent mapping capabilities. United States Department of Agriculture (USDA), Washington, DC (URL https://soilseries.sc.egov.usda.gov/OSD_Docs/C/CAJON.html, accessed on May 14 of 2015).
Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. For. Ecol. Manag. 122 (1–2), 51–71.
Olsson, A.D., Betancourt, J., McClaran, M.P., Marsh, S.E., 2012. Sonoran Desert ecosystem transformation by a C4 grass without the grass/fire cycle. Divers. Distrib. 18 (1), 10–21.
Qian, P., Schoenau, J.J., Huang, W.Z., 1992. Use of ion-exchange membranes in routine soil testing. Commun. Soil Sci. Plant Anal. 23 (15–16), 1791–1804.
Raison, R.J., 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant Soil 51 (1), 73–108.
Raison, R.J., Khanna, P.K., Woods, P.V., 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. Can. J. For. Res. 15, 132–140.
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 (3), 325–335.
Rodriguez, A., Duran, J., Maria Fernandez-Palacios, J., Gallardo, A., 2009a. Wildfire changes the spatial pattern of soil nutrient availability in *Pinus canariensis* forests. Ann. For. Sci. 66 (2), 1–7.
Rodriguez, A., Duran, J., Maria Fernandez-Palacios, J., Gallardo, A., 2009b. Short-term wildfire effects on the spatial pattern and scale of labile organic-N and inorganic-N and P pools. For. Ecol. Manag. 257 (2), 739–746.
Samson, D.A., 1986. Community Ecology of Mojave Desert Winter Annuals. University of Utah.
Schade, J.D., Hobbie, S.E., 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. Biogeochemistry 73 (3), 541–553.
Schafer, J.L., Mack, M.C., 2010. Short-term effects of fire on soil and plant nutrients in palmetto flatwoods. Plant Soil 334 (1–2), 433–447.
Schafer, J.L., Mudrak, E.L., Haines, C.E., Parag, H.A., Moloney, M.A., Holzapfel, C., 2012. The association of native and non-native annual plants with *Larrea tridentata* (creosote bush) in the Mojave and Sonoran deserts. J. Arid Environ. 87, 129–135.
Schenk, H.J., Mahall, B.E., 2002. Positive and negative plant interactions contribute to a north–south-patterned association between two desert shrub species. Oecologia 132, 402–410.
Schlesinger, W.H., Raikes, J.A., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77 (2), 364–374.
Sugihara, N.G., van Wagtendonk, J.W., Fites-Kaufman, J., 2006. Fire as an ecological process. In: Sugihara, N.G., Wagtendonk, J.W.V., FitesKaufman, J., Shaffer, K.E., Thode, A.E. (Eds.), Fire in California's Ecosystems. University of California Press, Berkeley, CA, USA, pp. 58–74.
Titus, J.H., Nowak, R.S., Smith, S.D., 2002. Soil resource heterogeneity in the Mojave Desert. J. Arid Environ. 52, 269–292.
Wan, S.Q., Hui, D.F., Luo, Y.Q., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol. Appl. 11 (5), 1349–1365.
Wardle, D.A., Hornberg, G., Zackrisson, O., Kalela-Brundin, M., Coomes, D.A., 2003. Long-term effects of wildfire on ecosystem properties across an island area gradient. Science 300 (5621), 972–975.
Whelan, R.J., 1995. The Ecology of Fire. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, UK.
Wilson, T.B., Thompson, T.L., 2005. Soil nutrient distributions of mesquite-dominated desert grasslands: changes in time and space. Geoderma 126 (3–4), 301–315.