

Post-Fire Resource Redistribution in Desert Grasslands: A Possible Negative Feedback on Land Degradation

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ABSTRACT

Desert grasslands, which are very sensitive to external drivers like climate change, are areas affected by rapid land degradation processes. In many regions of the world the common form of land degradation involves the rapid encroachment of woody plants into desert grasslands. This process, thought to be irreversible and sustained by biophysical feedbacks of global desertification, results in the heterogeneous distribution of vegetation and soil resources. Most of these shrub-grass transition systems at the desert margins are prone to disturbances such as fires, which affect the interactions between ecological, hydrological, and land surface processes. Here we investigate the effect of prescribed fires on the landscape heterogeneity associated with shrub encroachment. Replicated field manipulation experiments were conducted at a shrub-grass transition zone in the northern Chihuahuan desert (New Mexico, USA) using a combination of erosion monitoring techniques, microtopography measure-

ments, infiltration experiments, and isotopic studies. The results indicate that soil erosion is more intense in burned shrub patches compared to burned grass patches and bare interspaces. This enhancement of erosion processes, mainly aeolian, is attributed to the soil–water repellency induced by the burning shrubs, which alters the physical and chemical properties of the soil surface. Further, we show that by enhancing soil erodibility fires allow erosion processes to redistribute resources accumulated by the shrub clumps, thereby leading to a more homogeneous distribution of soil resources. Thus fires counteract or diminish the heterogeneity-forming dynamics of land degradation associated with shrub encroachment by enhancing local-scale soil erodibility.

Key words: land degradation; drylands; soil erosion; fire; water repellency; shrub encroachment.

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INTRODUCTION

Drylands, which include arid, semi arid, and hyper-arid regions, cover over 40% of the earth’s surface and support over 2 billion inhabitants (MEA 2005), mainly in the developing world. According to the

United Nations Convention to Combat Desertification, 70% of the world's drylands are affected by land degradation, due to the combined effects of regional or global climate change and anthropogenic disturbances, such as overgrazing, changes in fire pressure, and land cultivation without adequate soil conservation. Land degradation is a major contributor to the expansion of desert margins and loss of productive grasslands (Nicholson and others 1998; Reich and others 2000), with important impacts both on regional climate (Nicholson 2000; Dregne 2002; Hui and others 2008) and on the loss of ecosystem functioning and services (Daily 1995; Hibbard and others 2001). This process often occurs in conjunction with the encroachment of shrubs in regions historically dominated by grasses as observed in North America (Buffington and Herbel 1965; Archer 1989; Van Auken 2000), South America (Cabral and others 2003), Africa (Roques and others 2001), Asia (Singh and Joshi 1979) and Australia (Fensham and others 2005) (Figure 1). Even though shrub encroachment is considered as a major contributor to land degradation in several regions around the world (Schlesinger and others 1990; Van Auken 2000) with important environmental and socio-economic implications (UNCCD 1994; MEA 2005), little is known about mechanisms that could counteract this process.

In many arid and semiarid landscapes shrub encroachment is associated with an increase in bare soil (for example, Huenneke and others 2002; Gillette and Pitchford 2004; Baez and others 2006), the removal of nutrient-rich soil by wind and water from unvegetated areas (Parsons and others 1996; Schlesinger and others 1999; Wainwright and others 2000; Li and others 2007, 2008), and its partial redeposition in shrub-dominated soil patches through mechanisms of canopy trapping (Charley and West 1975; Schlesinger and others 1990; Okin and Gillette 2001). These processes

trigger a self-sustained cycle of erosion, depletion of soil resources, and vegetation loss in grass-dominated areas (Archer and others 1995), although it can be speculated that the encroachment of shrubs is favored by the deposition of nutrient-rich sediments transported by wind and water (Breshears and others 2003; Ravi and others 2007a), and the subsequent accumulation of fertile soils beneath the shrubs (Charley and West 1975; Schlesinger and others 1990). At the same time, loss in grass fuel decreases the pressure of fires on shrub vegetation thereby further enhancing woody plant encroachment (Archer and others 1995; Van Auken 2000; van Langevelde and others 2003; van Wilgen and others 2003; Goldammer and de Ronde 2004). The resulting landscape exhibits a mosaic of nutrient-depleted barren soil bordered by nutrient-enriched shrubby areas known as "islands of fertility" (Charley and West 1975; Schlesinger and others 1990) with implications on ecological, hydrological, and biogeochemical processes (Schlesinger and others 1990; Hibbard and others 2001; Huxman and others 2005).

Is this land degradation process irreversible? Here we demonstrate that at the early stages of shrub encroachment, when sufficient connectivity (grass cover) exists between shrub patches, fire can play an important role in the local-scale redistribution of soil resources within the landscape. This process generates a more homogeneous distribution of soil resources, providing some form of reversibility to the dynamics of land degradation. Using microtopography measurements, $\delta^{15}\text{N}$ isotope tracers, and quantifying post fire-erosion processes we show that in a landscape covered by a mixture of native grasses and invading shrubs, fires change the spatial patterns of soil erosion, favoring the local-scale redistribution of soil nutrients from the islands of fertility beneath the burned shrubs to the adjacent bare interspaces.

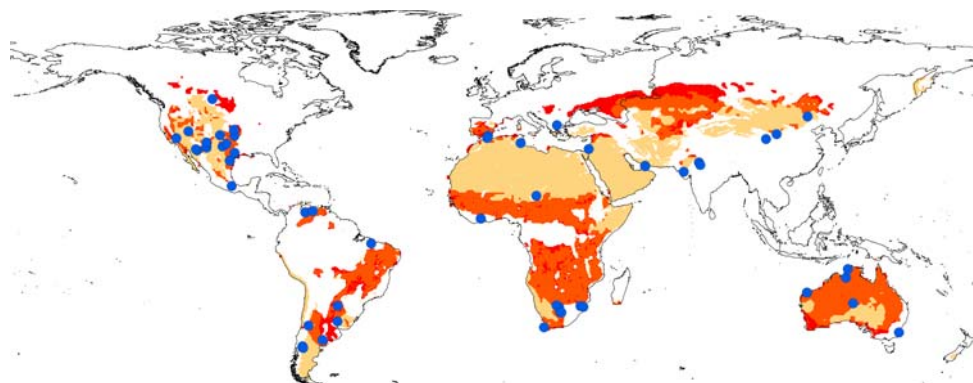


Figure 1. Global map of woody plant encroachment. Map showing locations (blue points) where encroachment of woody plants has been reported. Colors: Red indicates fire, Yellow represents desert vegetation, and orange represents areas where they overlap [refer color images in online].

MATERIALS AND METHODS

To illustrate the global relevance of woody plant encroachment and emphasize the possible relevance of our findings, we present a global woody plant encroachment map. The global map of woody plant encroachment (Figure 1) was prepared using MODIS land cover product (desert vegetation), Terra MODIS fire data (global annual burned area estimates from Giglio and others 2006) and locations where woody plant encroachment has been reported (based on over 200 published studies on woody plant encroachment around the world).

The field experiments were conducted at the Sevilleta National Wildlife Refuge (New Mexico, USA) in the northern Chihuahuan Desert, in a transition zone where creosote bush (*Larrea tridentata*) is now invading black grama (*Bouteloua eriopoda*) dominated grassland (N 34°23.961', W 106°55.710'). The field sites are chosen in an area where creosote populations are observed to be increasing episodically (Kieft and others 1998; Baez and Collins 2008; Allen and others 2008). Studies have shown that the size-abundance relationships (at the population level) within creosote stands in this area deviate strongly from patterns observed for steady-state vegetation due to episodic recruitment events, most likely in response to climate pulses (Allen and others 2008). The field sites were located in a heterogeneous landscape with a mosaic of grass (*Bouteloua eriopoda*, *Sporobolus spp.*) and shrub (*Larrea tridentata* and *Gutierrezia spp.*) cover with bare interspaces. The grass cover was minimal at the shrub base but provided enough connectivity among shrubs to allow for the spread of fires in the presence of strong winds. The soil is a sandy loam.

Three treatments (cleared, burned, and unmanipulated control plots), with three replicates each were used for this study. The plots were circular (6 meters in diameter) and laid out in such a way that each plot captured the heterogeneous nature of this landscape, with at least 2–3 shrub patches in each plot. In our field sites we eliminated the effects of small mammals by selecting undisturbed study sites where no detectable signs of small mammal activity was observed. Each set of replicated plots was more than 50 m from the others, whereas treatments within a replicated set were approximately 20 m apart. In the cleared plots, shrubs and grasses were cut close to the soil surface and removed without disturbing the soil surface using a system of platforms to walk over the plots. For the second treatment, prescribed burns were done, which were confined inside the circular plots. Scatter plots of wind speed values measured

over burned and cleared plots did not significantly deviate from a 1:1 dependence ($R^2 = 0.83$), indicating that burned and cleared plots experienced comparable wind shear. However, the relation between wind speed on the cleared and control plots deviated significantly from a 1:1 dependence ($R^2 = 0.52$), due to the different surface roughness.

In each plot wind-blown sediments were collected using Big Spring Number Eight (BSNE) isokinetic dust samplers (Custom Products, TX, USA) installed at 5 cm and 30 cm from the surface (Fryrear 1986). The saltation activity (that is, soil movement close to the surface) was measured using SENSIT wind eroding mass sensors (SENSIT Company, ND, USA) buried in the ground and with the sensitive part of the sensor at a height of 2 cm from the soil surface (Stout and Zobeck 1997). The SENSIT is a piezoelectric sensor that produces a signal upon impact of saltating soil grains and provides the number of particles impacting the sensor per second (Gillette and Stockton 1986). This SENSIT data can be used as an indicator of wind erosion activity at the soil surface (Gillette and Stockton 1986; Stout and Zobeck 1997). Wind velocity was measured with an array of cup anemometers installed at four heights (0.2 m, 0.6 m, 1.2 m, and 2 m). Both wind speed and saltation activity were monitored in each plot for a continuous 10-day period after the manipulation. Statistical tests (ANOVA) were done to show that the amount of dust samples collected from the different treatments were significantly different.

Locations were established in each plot to measure with a soil bridge, the small scale changes (microtopography) in soil elevation over time (White and Loftin 2000). The soil erosion bridges used in the study were 1.5 m long with 31 measuring points, and were oriented from the center of a shrub toward adjacent grass patches and bare interspaces. Soil microtopography measurements were conducted in all plots both 1 month and 4 months after the experimental manipulation. To estimate the elevation loss from the shrub islands, only the microtopography measurements near the shrub islands were considered. Using the point measurements of soil elevation on the islands and on the interspaces, the post-fire changes in the elevation on the shrub islands compared to the interspaces were calculated for all the experimental plots. The soil microtopography change differences between burned, cleared, and control plots were tested using one-way ANOVA and mean separations were calculated by a Tukey post hoc test at $\alpha = 0.05$ using SAS (SAS v. 9.1, SAS Institute Inc., Cary, North Carolina).

To trace the post-disturbance redistribution of soil nutrients, a ^{15}N tracing experiment was conducted (Wang and others 2006). To avoid a fertilization effect only a relatively low concentration of NH_4NO_3 fertilizer was applied. The total fertilizer addition was two grams for each shrub. This value corresponds to $33 \mu\text{g N/g soil}$ and is comparable to the higher end of natural NH_4NO_3 ($32 \mu\text{g N/g soil}$). The labeled ammonium nitrate ($\text{NH}_4^{15}\text{NO}_3$, $\sim 200\%$) mixed with 500 ml water was uniformly applied within 10 cm of the shrub base beneath two randomly selected shrubs in each plot. The application rates were slow and the wetting front was less than 5 cm, which minimized the potential nitrate leaching. In the burned plots the tracer was applied 2 days before the prescribed burn. Two weeks after the application, 2-cm deep surface soil samples were collected from shrub islands within 10 cm of the shrub base, and in bare interspaces more than 100 cm from shrub base. In each plot, soil samples were collected from under the two labeled ^{15}N shrubs and three adjacent bare interspaces (100–150 cm away from the shrubs). Samples of the new grass growth in the interspaces were collected from each plot 2 weeks after the fire. Leaf and soil samples were dried at 60°C for 72 h and then ground and homogenized using a mortar and pestle. Stable nitrogen (^{15}N) isotope analysis was performed using a Micromass Optima Isotope Ratio Mass Spectrometer (IRMS) (GV/Micromass, Manchester, UK) coupled to an NA1500 elemental analyzer (EA) (Carlo Erba, Italy). The ^{15}N compositions are reported in the conventional form (‰):

$$\delta^{15}\text{N}(\text{‰}) = \left[\left(\frac{(^{15}\text{N}/^{14}\text{N})_{\text{sample}}}{(^{15}\text{N}/^{14}\text{N})_{\text{standard}}} \right) - 1 \right] \times 1000$$

where $(^{15}\text{N}/^{14}\text{N})_{\text{sample}}$ and $(^{15}\text{N}/^{14}\text{N})_{\text{standard}}$ are the respective isotope compositions of a sample and the standard material. The standard material for stable N isotopes is atmospheric molecular N (AIR). Reproducibility of these measurements is approximately 0.2‰ (Wang and others 2007). The interspace foliar $\delta^{15}\text{N}$ differences between burned, cleared, and control plots were tested using one-way ANOVA and mean separations were calculated by a Tukey post hoc test at $\alpha = 0.05$ using SAS (SAS v. 9.1, SAS Institute Inc., Cary, North Carolina). To quantitatively assess the ^{15}N source for the grasses growing in the interspaces, a mixing ratio calculation was performed using the initial shrub mound tracer level (the $\delta^{15}\text{N}$ value just after the ^{15}N application) and the initial concentration of ^{15}N in

the interspaces as two end members. The calculation is as follows, $\delta^{15}\text{N}_{\text{grass}} = \delta^{15}\text{N}_{\text{shrub mound}} \times f_{\text{shrub mound}} + \delta^{15}\text{N}_{\text{interspace}} \times f_{\text{interspace}}$, where $\delta^{15}\text{N}_{\text{grass}}$ is the $\delta^{15}\text{N}$ value of new-growth grasses at the interspace microsites, $\delta^{15}\text{N}_{\text{shrub mound}}$ and $\delta^{15}\text{N}_{\text{interspace}}$ are the two end-member values. The $f_{\text{shrub mound}}$ and $f_{\text{interspace}}$, which must sum to one, are relative contributions of two end members to $\delta^{15}\text{N}$ in the grass. The plant nitrate uptake fractionation factors depend on species and location and ‰ were used in the calculation (Yoneyama and others 2001). The ‰ fractionation value is arbitrary based on the available literature value. It may not reflect the true fractionation for species in this particular ecosystem. But because we applied the ‰ fractionation value for all the treatments, it will be sufficient for our comparisons between control, burn and vegetation remove treatment. The differences in soil $\delta^{15}\text{N}$ difference between ^{15}N -labeled shrub mounds and interspaces for the three treatments (burned, cleared, and control) were also compared using one-way ANOVA and Tukey post hoc test at $\alpha = 0.05$.

To investigate the effects of fire on soil properties such as hydrophobicity and infiltration capacity, an additional ($\sim 25 \text{ m}^2$) area with similar vegetation cover and soil properties was burned in the surroundings of the replicated treatment plots. The properties of soils from this burned area were compared to those from an adjacent unburned area. In this burned area water repellency was quantified in terms of Water Drop Penetration Time (WDPT), which is the average time required for the drops to penetrate into the soil surface (Doerr 1998; Ravi and others 2007b). To this end, a pipette was used to place uniformly sized water drops on the soil surface. The WDPT was measured in the shrub patches (30 cm around the shrub base), grass patches, and bare interspaces in the burned, cleared, and control areas. At each patch the WDPT was reported as the mean of ten WDPT measurements. The fire temperatures were measured using a range of temperature sensitive colors (Tempilstik-Temperature Indicators, Tempil Inc., New Jersey, USA) spread on ceramic tiles left in the plot during the control burn. The Tempilstik colors indicate the fire temperature by the melting (smearing) of a specific color at its rated temperature (accuracy of $\pm 1\%$ of the rated temperature).

Infiltration rates were determined using a mini disk infiltrometer (Decagon, Pullman, WA, USA), which were used to calculate the hydraulic conductivity of the soil (Ravi and others 2007a). The mini disk infiltrometer, with an adjustable suction (0.5–7 cm), consists of a 32.7 cm long water

reservoir with a porous stainless steel disk (4.5 cm diameter and 3 mm thick) at the base. Infiltration was measured using a suction of 2 cm and the saturated hydraulic conductivity at that suction (K) was calculated using the infiltration data by the method suggested by Zhang (1997), which is ideal for soils in these arid regions. These measurements were compared to corresponding measurements in the adjacent control areas. Statistical tests (t -tests) were used to show that the K values of the burned and unburned microsites are significantly different.

RESULTS

The microtopographic measurements of small scale changes in soil elevation with time showed a post-fire decrease in soil surface height near the shrub islands and an increase in soil surface height in the bare interspaces as shown in Figure 2A (for one burned plot). This rapid microtopographic change was observed even just 2 weeks after the burn and continued in the following weeks. Further, comparing microtopography measurements from burned areas, areas cleared of the aboveground vegetation and undisturbed control areas (for all the plots), we found that the overall changes in soil surface height of the shrub islands were greater in the burned areas than in the cleared and control areas of this replicated field experiment. In fact, the mean soil loss from shrub islands in the burned areas (8.25×10^{-3} m) was 5 times higher than in the cleared areas (1.63×10^{-3} m), whereas in the control areas the microtopographic changes were negligible (Figure 2B). Moreover, changes in soil surface elevation near the shrub islands were significantly different from those in cleared and control plots ($P = 0.01$). In fact, one of the control plots showed an increase in the elevation near the shrub micro-sites over time, indicating soil accumulation by canopy trapping. Further, the ^{15}N tracer study also indicated a post-fire redistribution of soil resources. The signature of ^{15}N initially applied on shrub islands was detected in new grass growth collected 2 weeks after the fire up to 150 cm away from the pre-burn island of fertility (Figure 3A). The redistribution of ^{15}N was also observed in the cleared areas, but redistribution rates were higher in the burned areas, as indicated by the more elevated interspace grass foliar $\delta^{15}\text{N}$ values in the burned areas compared to cleared and control areas ($P < 0.05$). Mixing ratio calculations show that 45%, 19%, and 1% of the grass foliar ^{15}N came from the ^{15}N -labeled shrub mounds for the grass in burned, cleared, and control areas, respectively. The post-fire redistribution of soil resources is fur-

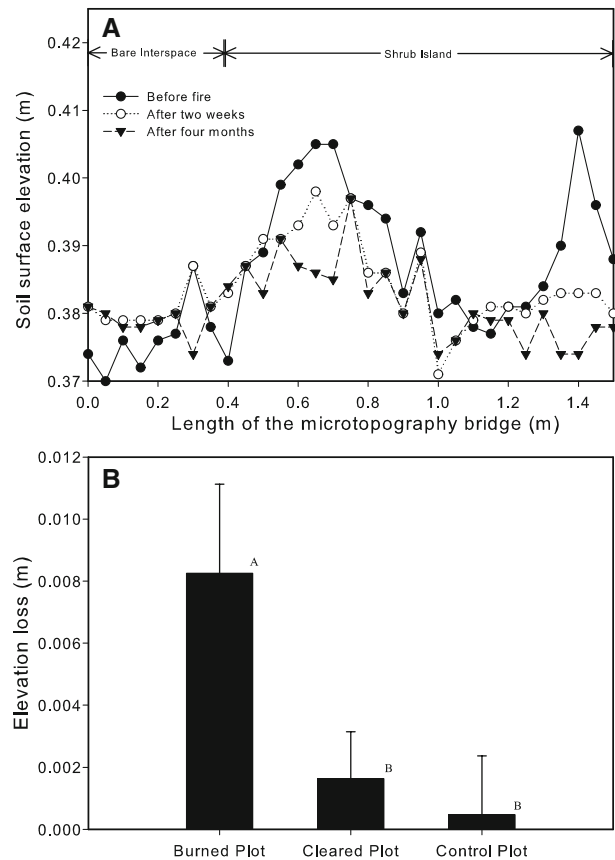


Figure 2. Changes in soil microtopography. **A** Redistribution of soil resources from around the shrub islands to bare interspaces with time following the fire as measured by repeat measurements with a soil microtopography bridge in one replicate of the burned treatment. **B** Average elevation loss around the shrub islands following fire in all treatments when only the microtopography measurements near the shrub islands were considered. Error bars represent the standard deviation of elevation loss between all the replicates of each treatment. The results are from one-way ANOVA and Tukey post hoc test at $\alpha = 0.05$. The same capital letters indicate the same mean values.

ther evidenced by the observed decrease in differences in soil $\delta^{15}\text{N}$ between ^{15}N -labeled shrub mounds and interspaces. Two weeks after the fire these differences were found to be significantly smaller ($P < 0.05$) in the burned areas, whereas in the cleared and control areas these differences were not significant (Figure 3B).

Two weeks after the burn, the sediment samplers in all the burned areas collected significantly more wind-blown sediments ($P < 0.05$) than on the other two treatments (Figure 4A). Even though the overall dust collection in all plots decreased in the following weeks, the samplers collected significantly more sediments ($P < 0.05$) in the burn

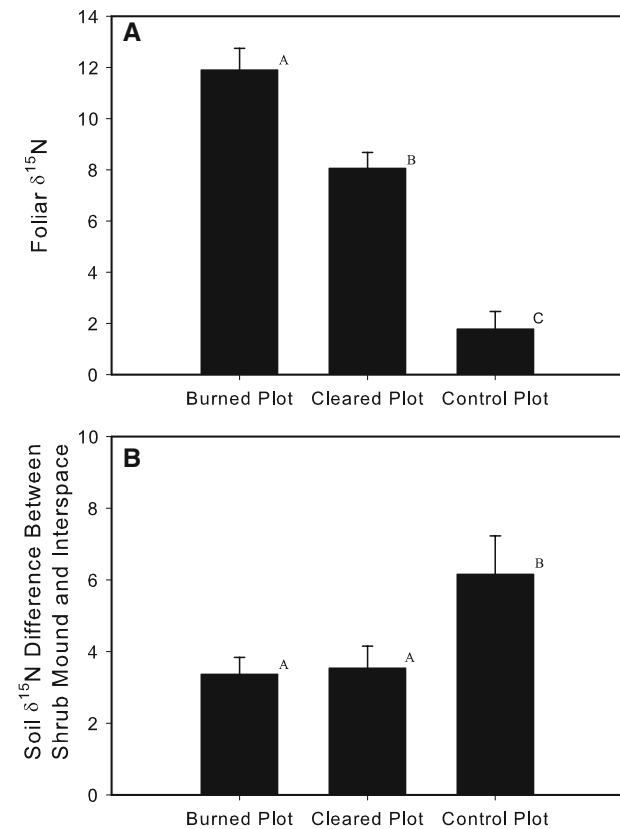


Figure 3. The ^{15}N isotope tracer experiment. **A** The interspace grass foliar $\delta^{15}\text{N}$ values from burned, cleared, and control plot and **B** the soil $\delta^{15}\text{N}$ difference between ^{15}N -labeled shrub mounds and grasses growing in shrub interspaces for the three treatments (burned, cleared, and control). The results are from one-way ANOVA and Tukey post hoc test at $\alpha = 0.05$. The same capital letters indicate the same mean values.

plots even 3 months after the fire (Figure 4B). The records from particle impact sensors indicate that the frequency and intensity of saltation (indicator of soil movement at the surface) were higher in the burned areas than in the cleared and control areas. There were three times more erosion events (that is, 5 min data collection intervals with soil particle movement at the surface) in the burned areas (234 events per month) than in the cleared plots (79 events per month). The intensity of each dust event (that is, total impact counts in 5-min intervals) was also higher for the burned plots (843 particle impacts per month) compared to cleared (331 particle impacts per month) and control plots (47 particle impacts per month). These results clearly show that in the burned areas, saltation events are more frequent and intense, indicating the occurrence of a post-fire enhancement in soil erodibility in the burned plots compared to the cleared and control areas.

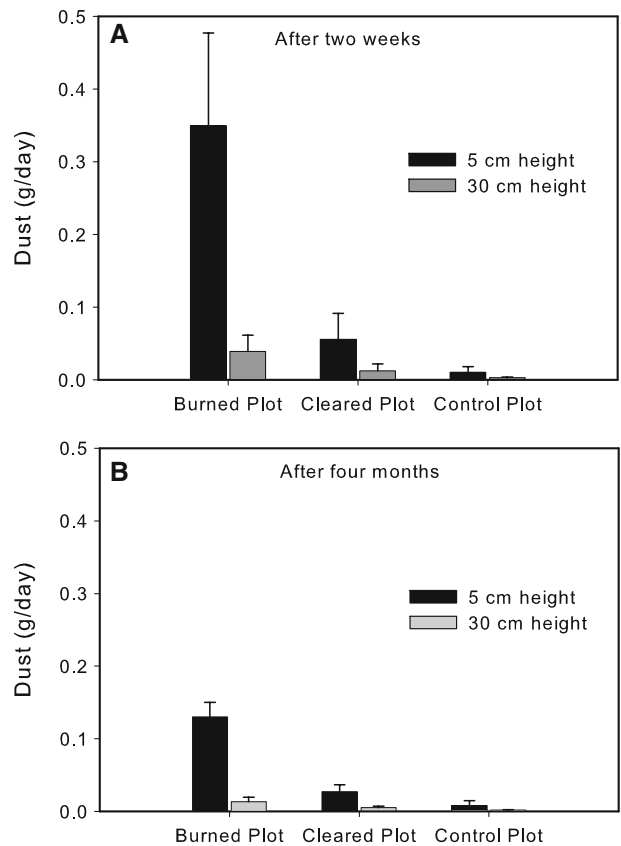


Figure 4. Enhancement of post-fire aeolian processes. Amount of dust collected by the BSNE dust samplers (at 5 cm and 30 cm height) **A** 2 weeks and **B** 4 months after the fire. Error bars represent the standard deviation of dust collected in three replicates of each treatment.

Fire-induced water repellency was observed in the burned areas, and the impact of fire on soil properties differed among shrub, grass, and bare soil microsites (Table 1). Fire temperatures were higher beneath the shrubs (average temperature 260°C) compared to grass patches (average temperature 120°C) and bare interspaces ($<90^{\circ}\text{C}$), whereas no difference in temperature was detected at 3–5 cm depth regardless of the aboveground vegetation. Measurements of WDPT along a transect from a burned area to a control (unburned) area indicated that the fire-induced soil–water repellency was higher within the burned shrub islands (WDPT average ~ 138 s and maximum ~ 300 s) compared to burned grass patches (WDPT average ~ 4 s and maximum ~ 50 s), whereas no soil–water repellency was observed in the bare interspaces (WDPT ~ 0 s) (Table 1). The decrease in infiltration rates (and corresponding K values) beneath and around burned shrubs compared to unburned shrubs indicate that fire-induced water repellency resulted in the altered

Table 1. Water Drop Penetration Time (WDPT) and Hydraulic Conductivity (K) of the Soils

	Shrub patch		Grass patch		Bare (soil) interspace	
	Burned	Unburned	Burned	Unburned	Burned	Unburned
WDPT (s)						
Mean	138	0	4	0	0	0
Minimum	0	0	0	0	0	0
Maximum	300	0	50	0	0	0
K (m/s)						
Mean	1.08×10^{-5}	2.75×10^{-5}	3.20×10^{-5}	3.60×10^{-5}	9.25×10^{-6}	8.51×10^{-6}
Minimum	7.50×10^{-6}	1.50×10^{-5}	1.97×10^{-5}	2.47×10^{-5}	6.40×10^{-6}	6.40×10^{-6}
Maximum	1.30×10^{-5}	4.75×10^{-5}	5.0×10^{-5}	5.65×10^{-5}	1.20×10^{-5}	1.08×10^{-5}

hydrological response of the surface soil (Table 1). The hydraulic conductivity values (mean K) were significantly smaller ($P < 0.0001$) under the burned shrubs (1.08×10^{-5} m/s) when compared to unburned shrubs (2.75×10^{-5} m/s). The K values in the shrub islands were higher than in the bare interspaces before the fire ($P < 0.0002$). However, following the prescribed burn, the K values around the shrub islands and the bare interspaces were not significantly different ($P = 0.18$). Differences in hydraulic conductivity values and infiltration rates were negligible (not significant) between burned and unburned grass patches ($P = 0.30$) as well as in the bare interspaces ($P = 0.57$).

DISCUSSION

Our field experiments at a shrub-grass transition zone in the Northern Chihuahuan desert margin indicate that fires result in enhanced redistribution of soil resources (for example, nitrogen) from the shrub islands ("Islands of fertility") to the interspaces, where they contribute to the post-fire establishment and growth of grasses. The enhancement of resource redistribution in the burned areas can only be attributed to an increase in the rates of post-fire soil erodibility by wind and water, as the burned and cleared plots had comparable surface roughness and experienced the same wind shear. Overall, the enhancement of soil erosion in the fertile shrub islands remobilized nutrient-rich sediments that were trapped in the sheltered area beneath the shrub canopy. This sediment was redistributed by wind and water; the ^{15}N tracer indicated that the interspaces receive a significant amount of nutrients, including nitrogen, from the nearby fertile islands, and that some of these nutrients are taken up by grasses (Figure 3A), which recovered rapidly after a burn. These results are consistent with recent observational evidence

of post-fire loss of heterogeneity in the distribution of soil resources (organic matter and nitrogen) in arid grasslands (White and others 2006).

In our study, fire-induced soil hydrophobicity was observed in the soils beneath burned shrubs. Fire temperatures were highly heterogeneous, with higher surface soil temperature beneath the shrubs (average temperature 260°C) than in grass patches (average temperature 120°C) and bare interspaces ($<90^\circ\text{C}$), whereas no difference in temperature was detected at 3–5 cm depth regardless of the aboveground vegetation. Recent studies have shown that post-fire enhancement of soil erosion results from soil hydrophobicity induced by the burning vegetation (Doerr and others 2000; Ravi and others 2006). Soil erodibility was found to significantly increase in the microsites affected by the burning of shrub biomass. These microsites were also the areas that developed higher soil-water repellency (Table 1), presumably due to the higher fire temperatures and the more hydrophobic compounds released by the burning of shrub vegetation. The interpretation of the fire temperature measurements calls for a clarification: despite the differences observed in the temperature measurements, the temperature of combustion for plant material at these two microsites might have been about the same. What is measured by the colored plates is actually the amount of radiated energy they absorb and, consequently, how hot they become. Thus, the "higher temperatures" beneath shrubs actually reflect the fact that there was a greater mass of fuel and that the fuel was coarse and took longer to burn out rather than the existence of major differences in the temperature of the flames. Regardless, these differences in "fire temperatures" (read "radiated energy") and the consequently different levels of soil heating have been observed to be associated with the development of different levels of soil hydrophobicity (for example, Doerr and others 2000).

The hydraulic conductivity (K) values of the unburned shrub islands were much higher than the interspaces. However, the post-fire K values were comparable to the burned interspaces. The heterogeneity in K values in the burned areas is attributed to the heterogeneity in the fire-induced water repellency (Table 1). The fire-induced water repellency decreases soil hydraulic conductivity and increases surface runoff from the burned shrub islands, which results in enhanced sediment transport from these burned areas. The post-fire decrease in infiltration rates combined with the higher soil elevation of the fertility islands resulted in increased runoff from these soil mounds to the interspaces, and in the enhancement of sediment redistribution by water erosion.

Even though the role of water repellency in enhancing water erosion is well-documented, very few studies have addressed its effect on aeolian processes, the dominant transport process in these arid landscapes (Ravi and others 2007b). Wind erosion occurs when the wind speed exceeds a critical threshold value that depends on soil erodibility. The dust flux measured using BSNE sediment collectors has been shown to depend on the threshold velocity for wind erosion (Lu and Shao 1999). The threshold velocity depends both on factors affecting the impact of wind on the soil surface (for example, surface roughness, vegetation cover) and on factors determining the interparticle bonding forces acting between soil grains (McKenna Neuman 2003; Cornelis and others 2004). It has been found that the effect of fires on soil properties results in the enhancement of soil erodibility. Thus, weaker interparticle forces are associated with lower values of threshold velocity, hence with more frequent and intense aeolian transport. Ravi and others (2006) demonstrated that the interparticle bonding forces (nonlinearly) decrease with increasing degrees of fire-induced water repellency. Thus, the enhancement of aeolian transport in soil plots affected by the fire treatment can be likely explained as an effect of hydrophobic compounds (released by the burning biomass) on interparticle bonding. These results are consistent with other field (Whicker and others 2002) and wind tunnel (Ravi and others 2007b) studies on the effect of fires on aeolian transport processes in soils from arid and semi arid regions.

Our experimental findings indicate that the post-fire resource homogenization in these degraded landscapes is a rapid process occurring in the time frame of weeks. Further, field measurements 1 month after the prescribed fire showed no traces of water repellency in the burned plots, which

indicate that the fire-induced water repellency in these systems is short-lived. Thus, by altering soil surface physical and chemical properties for a short period, fires can counteract the heterogeneity-forming dynamics of land degradation associated with shrub encroachment. Due to this effect of fires, "islands of fertility" can be dynamic rather than static features of these landscapes.

In this study we compared processes occurring in burned and vegetation denuded areas (that is, areas with similar roughness and experiencing same wind shear) to show that the post-fire enhancement of soil erodibility in the fertility islands is not a mere result of the higher topography of the shrub mound. We acknowledge the existence of some confounding factors such as the effect of fires on microbial crusts, which could affect the stability of the surface soil in these landscapes. However, we note that this effect of fires on microbial crusts cannot have enhanced soil erodibility beneath the shrubs, as the microbial crusts were observed only in the bare interspaces and not directly under the shrub patches, consistently with the findings from other arid systems (Schlesinger and Pilmanis 1998). The soils in these landscapes are characterized by less developed microbial crusts and other studies have shown that in these areas the wind speed typically exceeds the stability threshold of surface crusts (Belnap and Gillette 1998).

We acknowledge the fact that there are multiple pathways for ^{15}N transportation in the system such as fungi transfer, diffusion and uneven volatilization. This is why we used highly enriched ^{15}N tracer (200‰, the background $\delta^{15}\text{N}$ is only $\sim 6\text{‰}$), and collected both plant and soil samples. We do not think fungi transfer is the major transport pathway for two reasons: 1) if fungi transfer was the major transport pathway, we would have observed higher foliar $\delta^{15}\text{N}$ in the control, rather than in the treatments (burned and vegetation removed plots). This is because, we would expect a more intact belowground fungi network to exist in the control plots; 2) fungi-mediated mechanisms of N transfer have been reported mostly for woody species (for example, He and others 2006). In this study we used $\delta^{15}\text{N}$ to investigate the uptake of N by grasses and collected grass samples from the interspace areas. We do not expect our results to be affected by the fungi network. Diffusion is not a possible pathway for two reasons: (1) we took soil samples from the surface, which is unlikely affected by the subsurface diffusion; (2) in this water limited system, diffusion is a very slow process and we observed changes in the foliar and soil $\delta^{15}\text{N}$ signature a couple of meters away from the ^{15}N

treatment area in only 2 weeks. Indeed diffusion is a very ineffective mechanism of hydrologic transport in unsaturated soils. In fact, the typical literature values for diffusivity in a moist soil are around 10^{-3} m²/y, whereas in dry soils the diffusivity can range between 10^{-6} and 10^{-7} m²/y (for values of soil moisture typical of the root zone). It could be possible that the results are affected by volatilization, although in this study we took multiple soil samples around the burned shrub to average out the effect of an uneven volatilization, if any.

We stress that, the response of shrub encroached grasslands to fires depends on several other factors like shrub species, fire intensity and duration, post-fire soil moisture condition and grazing management. For example, if burning is followed by a period of low precipitation or drought, the grass regrowth is inhibited, leading to irreversible loss of resources from the system. In the early stages of the encroachment process, when the shrubs are relatively young, fires can result in high shrub mortality. However, in later stages when the shrubs are in a mature state, the fire mortality is significantly reduced. The mortality and post-fire re-sprouting capacity of shrubs depend on several factors like plant species, growth stage, and fire intensity (McLaughlin and Bowers 1982; Trollope 1996; Williams and others 2002). Moreover, the prescribed burns should be used in combination with grazing management, as high grazing rates can weaken the grass cover and also facilitate enhanced shrub seed dispersal (for example, Ravi and D'Odorico 2008).

CONCLUSIONS

Our findings suggest the existence of a potentially important role of fire as a management strategy to reverse the early stages of land degradation associated with the encroachment of woody plants in arid and semi arid fire-adapted grasslands (that is, grasslands that have evolved with fires, in which fires do not kill the grasses). These grasslands at desert margins are affected by fire occurrences (Figure 1), suggesting that a sufficient amount of grass biomass exists in these transitional zones to carry the fires from the points of ignition and through the surrounding vegetation. In these conditions fires short-circuit the processes that reinforce heterogeneity by activating the transport of nutrient-rich soil from islands of fertility to the adjacent interspaces. It is expected that the consequent enhancement of ecosystem functioning and services at the desert margins may contribute to counteract or limit desert expansion. Shrub encroached grasslands can be found throughout the

world (Figure 1) and our findings may have implications for the sustainable management of these systems.

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