

Fire and Invasive Plants Special Feature

Impacts of Fire and Invasive Species on Desert Soil Ecology

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Abstract

A review of literature shows that both fire and invasive species may cause changes in biological, chemical, and physical properties of desert soils. Although soil may recover from the impacts of fire during succession, these changes are permanent under persistent invasive species. The most severe effects of fire occur under high temperatures with high fuel buildup and soil moisture that conducts heat downward. Deserts typically have low fuel mass and low soil moisture, both conditions that would contribute to lower impacts of fire than in mesic soils. Soil is a good insulator, so soil microorganisms will survive a few centimeters deep even in hot surface fires. Immediately postfire there is often an increase in mineral nitrogen (N) and a decrease in soil carbon (C) and organic N, but these changes are often minimal in desert soils, except under fertile shrub islands that have higher fuel loads and fire temperature. Both hot and cold deserts have experienced slow recovery of native shrubs and increased growth of invasive grasses following fire. Invasive species may either increase or decrease soil N and C depending on fire temperature and site and species characteristics. Mineralization and fixation of N are often high enough after fire that subsequent productivity balances N losses. The elimination of islands of fertility coupled with postfire erosion may be a major impact after fire in grass-invaded shrub lands. In the long term, the interaction of fire and invasive species may result in more frequent fires that eliminate fertile islands and reduce the productivity of deserts. Managers may use fire as a tool to control desert invasives without the concern that N will be irrevocably lost, but this must be done judiciously to avoid eliminating shrubs and further increasing invasive species.

Resumen

La revisión de literatura demuestra que tanto el fuego como las especies invasoras pueden causar cambios en las propiedades biológicas, químicas y físicas de los suelos del desierto. Mientras que el suelo puede recuperarse del impacto del fuego durante la sucesión, las especies invasoras producen cambios permanentes. Los efectos más severos del fuego ocurren bajo temperaturas altas con una alta acumulación de combustible y con una humedad del suelo que conduce el calor hacia abajo. Los desiertos tienen típicamente una humedad y masa de combustible baja, ambas condiciones podrían contribuir a un menor impacto del fuego en suelos más húmedos. El suelo es un buen aislador, así que los microorganismos del suelo pueden sobrevivir a pocos cm de profundidad incluso en fuegos superficiales calientes. A menudo, inmediatamente después del fuego hay un incremento en nitrógeno mineral (N) y una disminución en el carbón del suelo (C) y N orgánico, pero estos cambios son a menudo mínimos en los suelos del desierto, con excepción de debajo de los arbustos en las islas fértiles que tienen cargas de combustibles y temperaturas más altas. Tanto los desiertos calientes como los desiertos fríos han experimentado una recuperación muy lenta de arbustos nativos y un incremento en el crecimiento de gramíneas invasivas después de los fuegos. Las especies invasivas pueden incrementar o disminuir el N y el C del suelo dependiendo de la temperatura del fuego, así como las características de las especies y del sitio. La mineralización y la fijación del N son a menudo bastante altas después del fuego que la productividad subsiguiente estabiliza las pérdidas de N. La eliminación de las islas de fertilidad unida con la erosión después del fuego puede ser un impacto importante después del fuego en pastizales invadidos por arbustivas. A largo plazo la interacción del fuego y las especies invasivas puede dar lugar a fuegos más frecuentes que eliminen las islas fértiles y reduzcan la productividad de los desiertos. Los manejadores del recurso pueden utilizar fuego como una herramienta para controlar las especies invasivas del desierto sin la preocupación que la pérdida del N sea para siempre, pero esto puede hacerse cuidadosamente evitando la eliminación de los arbustos y fomentando un incremento en las especies invasoras.

Key Words: fertile islands, pH, soil carbon, soil microorganisms, soil nitrogen

INTRODUCTION

Wildfires have become more prevalent in American deserts and semideserts in the past several decades with increased fuel from invasive species (Brooks et al. 2004; Brooks and Matchett 2006; Chambers and Wisdom 2009). Increased fire frequency from invasive grass fuels has major ecosystem consequences, causing declines in biodiversity and conservation value (Brooks et al. 2004; Chambers and Wisdom 2009), and decreased economic value coupled with increased management costs

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(Epanchin-Niell et al. 2009). Another potential impact is the effect of fires on soil chemical, physical, and biological processes, especially in arid lands that were historically subject to infrequent fires or no fires at all. Deserts have relatively few plant species adapted to resprout after fire, and desert plants germinate and establish themselves sporadically because of unreliable precipitation, so vegetation recovery is slow compared to ecosystems adapted to fire (Abella 2009; Abella et al. 2009). Desert soils and soil organisms may be similarly slow to recover from fire. Increases in invasive species, fires, and slow recovery by native species after fire may have effects on desert biogeochemical cycles that have received little attention.

The impacts of fires on desert and semidesert soils are in general not as severe as more mesic ecosystems (Neary et al. 1999; DiTomaso et al. 2006). However, invasive grasses in both hot (Mojave, Sonoran, and Chihuahuan) and cold (Great Basin) deserts form a continuous fuel connecting shrubs that previously had sparse interspaces during the fire season, increasing the potential for larger and more frequent fires (D'Antonio and Vitousek 1992; Brooks and Matchett 2006; Chambers et al. 2009). Most invasive-species fire studies have been done in cold deserts (Chambers et al. 2009), with less information from hot deserts (Rogstad et al. 2009). Overall there is little information on impacts of fires on desert soils, so this review will focus on fire studies from arid and semiarid lands. However, studies from subhumid ecosystems such as tallgrass prairie and woodlands are included as a comparison to deserts, and also because some of the most extensive and long-term studies on ecosystem dynamics following fire have been done in subhumid systems. In addition to reviewing the literature, we present new data on impacts of fire on soils and their long-term recovery in a southern California hot desert and a semiarid Mediterranean-type grassland. Few published studies describe long-term changes to soils after fire, but the two previously unpublished studies describe soil characteristics 14–29 yr after fire.

Fire-adapted ecosystems can recover relatively rapidly from all but the most severe fires, but the invasion of exotic species, especially annual grasses, into North American deserts and semideserts has created a new dynamic whereby soil processes may be permanently altered (Ehrenfeld 2003; DiTomaso et al. 2006; Liao et al. 2008). The alterations include either soil nutrient enrichment or impoverishment, and changes in rhizosphere micro- and mesoflora and fauna, depending upon the identity of the invasive species and the ecosystem type invaded (Ehrenfeld 2003; Liao 2008). These changes will presumably last as long as the invading plant species persists, but in some cases, such as nitrogen (N) enrichment by N-fixing host plants or rapid nitrifiers in the rhizosphere, the soil enrichment or impoverishment may persist even after the invasive species is removed or controlled (Ehrenfeld 2003; Asner and Vitousek 2006; Kulmatiski et al. 2008).

The objective of this review is to examine the effects of fires and invasive species on soil ecology of desert ecosystems. We compare the impacts of fire and invasive species on soils, and describe how the interaction of the two may lead to impoverishment of desert ecosystems. Shrub-dominated deserts and semideserts form “fertile islands” that concentrate nutrients (Stubbs and Pyke 2005; Ravi et al. 2007), but if shrubs are destroyed by fire and cannot recover because of

invasive-species dominance, then the overall ability of the ecosystem to retain nutrients may decline. Research on the interaction of fire and invasive species on desert soil ecology has received little attention, so we describe how such a major change to a spatially organized shrub land replaced by a homogeneous exotic grassland has the potential to promote nutrient losses and to reduce the productivity of deserts and semideserts.

TEMPERATURE AS THE MAJOR CONTROL OF FIRE IMPACTS ON SOILS

The negative effects of fire on soil are caused primarily by high temperatures that affect surface as well as deeper soils (Neary et al. 1999; Korb et al. 2003, 2004), whereas low- and moderate-temperature fires can have long-term positive benefits for fire-adapted ecosystems (DeBano et al. 1998). High-temperature fires may occur where historic fire suppression has caused an increase in the fuel load, or in stand-replacing and slow-burning fires in forests and high-productivity shrub lands that may burn at temperatures $>700^{\circ}\text{C}$ (DeBano et al. 1998; Neary et al. 1999). Alternatively, grass fires and ground fires in forests (with low ground fuel load) burn at a range of $200\text{--}300^{\circ}\text{C}$ and temperatures at 5-cm depth may be 50°C (DeBano et al. 1998). Experimental burns in sagebrush steppe also produced soil surface temperatures in the range of 300°C , with 80°C at 2-cm depth (Korfmacher et al. 2003). By comparison, summer fire temperatures in Mojave Desert creosote bush scrub invaded by annual grasses were 100°C at 2 cm beneath the soil surface under shrubs, and $150\text{--}200^{\circ}\text{C}$ at ground level in interspace and undershrub herbaceous vegetation (Brooks 2002). A recent report of invasive buffel grass (*Pennisetum ciliare*) fires in Arizona measured 900°C above ground (McDonald 2009). This is surprisingly similar to the $>700^{\circ}\text{C}$ fire temperatures in woody vegetation (Neary et al. 1999), but buffel grass productivity may be high in invaded Sonoran Desert (McDonald 2009). Soil temperatures were not measured in this study (McDonald 2009). Although hot fires have the potential to impact soils, rate of burn and soil moisture are also important contributors to fire effects on soils (Neary et al. 1999). Heat damage from fire is greater in a hot smoldering fire that travels slowly across the landscape than a rapidly moving fire. Desert fires are often wind-driven and fast moving (e.g., McDonald 2009), and unlikely to cause major soil heating. A moist soil will conduct more heat downward than a dry soil in a slow-moving fire. Because deserts most often burn during the dry season, heat from the fire will only affect the surface soils, as observed by Brooks (2002). Soil chemical characteristics are little affected by temperatures less than 100°C (DeBano et al. 1998; Neary et al. 1999), although many soil organisms will succumb at this temperature.

EFFECTS OF FIRE ON SOIL CHEMICAL AND PHYSICAL PROPERTIES

Changes in Soil Carbon (C) and Nitrogen (N) After Fire

Fire temperature is the main determinant for volatilization of soil nitrogen and carbon (Neary et al. 1999; DeBano et al.

1998). Carbon volatilization begins at 180°C, and all of the organic matter is consumed at 450°C (DeBano et al. 1998). Surface litter and dry plant material are lost in the lowest-temperature fires, and moist, living plant material may also be consumed when flames or adjacent smoldering material first dries it out. Soil organic matter (SOM) is also lost when the soil temperature becomes hotter than 180°C. In a literature review on impacts of fire in arid to subhumid ecosystems, of those studies reporting SOM or soil C, seven gained SOM, eight lost SOM, and 18 did not change (Table 1). A gain in SOM occurs after an incomplete burn that adds aboveground C to the soil surface. Soil samples were collected from varying depths in the different studies; shallow samples (2–15 cm depth) more often showed significant changes in soil C than deeper samples (20–25 cm). In one semiarid grassland, SOM decreased in the top 5 cm the first year and recovered to preburn levels the second year (Snyman 2003). In contrast, SOM increased in the top 3 cm within days of a fire in pinyon–juniper woodland, and returned to preburn levels within 1 yr (Rau et al. 2009). Multiple annual burns caused no decrease in SOM in the top 25 cm in a subhumid Kansas grassland (Seastedt and Ramundo 1990), but there was a mean SOM decrease in the top 10 cm in 19 semiarid to subhumid South African grasslands (Mills and Fey 2004). No change in SOM was reported in the top 3 cm of semiarid shrub–grassland after two burns that were 3 yr apart (Castelli and Lazzari 2002). Those studies that reported only decreased SOM after a single burn were short-term field or lab studies, indicating the importance of long-term studies to assess the ability of SOM to recover.

Nitrogen is the nutrient of most concern to land managers because it begins to volatilize above 200°C. Over half of N can be volatilized when soil temperature increases to 500°C (DeBano et al. 1998). In a lab experiment with Mediterranean shrub-land soil, organic N was lost at 500°C but not 250°C (Badia and Marti 2003b, Table 1). In ecosystems where decomposition is slow because of limited precipitation, cold temperatures, or a short growing season, fire is an important agent of N mineralization. Most arid and semiarid ecosystems have relatively small amounts of total ecosystem N in litter ranging from 1% to 10% (Neary et al. 1999), with 85–95% of ecosystem N stored in soil (Johnson et al. 2009; Rau et al. 2010). Even if 100% of aboveground plant plus litter N is volatilized during a very hot fire, ecosystem N loss may only be 5–15%. Mineralization of N immobilized in plant tissue, litter, and SOM may temporarily increase productivity above prefire rates (Esque et al. 2010), offsetting potential negative effects of N losses. This requires that vegetation be adapted to fire and resprout or reseed rapidly to take up the mineralized N. However, vegetation recovery may be slow in deserts because of low and variable precipitation (Abella 2009), potentially allowing nutrient loss. In the literature survey (Table 1), five sites or studies had increased total N after fire, six decreased, and 21 had no change after fire. The mechanisms for these changes are that total N increases when aboveground biomass is partially burned and deposited on the soil surface, whereas N decreases occur when it is volatilized in a hot fire. In contrast to organic C, organic N did not recover to preburn levels after year two in South African semiarid grassland (Snyman 2003). However, in pinyon–juniper woodland, initially elevated surface N returned to preburn values within 1 yr (Rau et al. 2009).

Multiple burns were also detrimental to total soil N in 19 semiarid to subhumid South African grasslands (Mills and Fey 2004), but not in Kansas tallgrass prairie (Seastedt and Ramundo 1990). The large number of studies reporting no change in total N indicates that a single burn is not detrimental to this property. Spatial heterogeneity of the vegetation may affect postfire N, as total N increased at one site in semiarid Australian tussock grass underneath the tussock, but not in the sparsely vegetated inter-spaces between tussocks (Bennett et al. 2002).

A relatively high proportion of studies reported increases in extractable N after fire (13 of 27; Table 1). Increased mineral N on the soil surface can be expected if the fire temperature is not too hot, and if the measurements are taken before surface-deposited ions are absorbed by growing plants or are leached or eroded (DeBano et al. 1998; Neary et al. 1999). Three studies showed an initial increase in extractable N in the first few months or first year after fire, followed by no change after 1–2 yr (Fenn et al. 1993; Stubbs and Pyke 2005; Rau et al. 2007). Sites with reduced extractable N after fire may have experienced leaching, high fire temperature, or multiple fires (Castelli and Lazzari 2002; Mills and Fey 2004).

Overall losses in total N may be balanced by short-term increases in mineral N that promote increased plant productivity, and enable N pools to recover over time (DeBano et al. 1998; Neary et al. 1999). Alternatively, an opposite response was reported in semiarid South African grasslands that had reduced productivity following fire (Snyman 2004). High soil temperatures and increased drying of sandy soil was blamed for decreased productivity after fire, and an inability for total N and C to recover. This is in contrast to increased soil moisture that can occur after forest fires (Johnson and Curtis (2001). Rainfall regime and low soil moisture after fire may interact to reduce productivity in arid and semiarid lands, again emphasizing the importance of long-term postfire studies. The results of two previously unpublished long-term fire studies are reported here. These reports illustrate the ability of arid and semiarid soils to recover from fire.

The rate of recovery of C and N was studied in a fire chronosequence in Mediterranean-climate bunchgrass in southern California dominated by purple needlegrass (*Nassella pulchra*). This site, the Santa Rosa Plateau Ecological Reserve, has been invaded by exotic annual grasses (particularly brome grasses, wild oats, and fescue). Although the site was grazed by cattle historically, it is now managed as a conservation reserve by burning in spring to kill the seeds of exotic grasses before they can contribute to the next season's seed bank (Gillespie and Allen 2004). Soil cores were collected in burned sites ranging from 2 yr to 14 yr plus an unburned control (Dickens and Allen, unpublished). There were nine replicate soil cores, 10 cm deep. Soil total C and N, and KCl-extractable N were measured, and data were statistically analyzed with ANOVA. The unburned site had greater soil C and total N than 2-, 11-, and 14-yr-old burns, but not greater than the 8-yr-old burn (Figs. 1A and 1B). Higher levels of C and N at the 5-yr and 8-yr sites may be a result of elevated gopher activity rather than fire (Dickens, personal observations). Increased rates of N cycling on gopher mounds coupled with reduced live plant cover can lead to increased soil nitrogen (Eviner and Chapin 2005). There were fewer significant differences in extractable N (NH_4^+ -N plus NO_3^- -N) along the chronosequence, with the 11-yr-old

Table 1. Responses of soil chemical and physical properties to fire in arid to subhumid ecosystems, showing separate responses for multiple sites and multiple sample times as reported. + indicates an increase; – indicates a decrease; NC indicates no change in a property after fire. Blanks indicate that property was not reported. Asterisks indicate subhumid climates; others are arid or semiarid. Inorganic ions are various combinations of Ca, Mg, K, Na, and S.

Source	Location	Vegetation	Depth (cm)	Time after fire	SOM, organic C	Total N, organic N	Extractable N	Extractable Inorganic P	Inorganic ions	pH	Bulk density
Abella et al. (2009)	Nevada	Creosote/blackbrush interspace	5	2 yr	+	NC		NC	NC	NC	
Abella et al. (2009)	Nevada	Under creosote	5	2 yr	+	NC		NC	+	NC	
Abella et al. (2009)	Nevada	Under yucca	5	2 yr	+	NC		+	+	+	
Allred and Snyder (2008)	New Mexico	Desert grassland	?	1 yr			+				
Ansley et al. (2006)	Texas	Mesquite savanna*	20	2–3 yr, summer fires	+	+					
Ansley et al. (2006)	Texas	Mesquite savanna*	20	2–3 yr, winter fires	NC	NC					
Badia and Marti (2003b)	Spain	Mediterranean shrub, calcareous soil	15	lab, 500°C	–	–		+	+	+	
Badia and Marti (2003b)	Spain	Mediterranean shrub, gypsiferous soil	15	lab, 500°C	–	–		+	+	+	
Badia and Marti (2003b)	Spain	Mediterranean shrub, calcareous soil	15	lab, 250°C	–	NC		+	+	NC	
Badia and Marti (2003b)	Spain	Mediterranean shrub, gypsiferous soil	15	lab, 250°C	–	NC		+	NC	NC	
Bennett et al. (2002)	Australia	Grassland, under tussock, site 1	2	1 wk	+	+	NC	+		+	
Bennett et al. (2002)	Australia	Grassland, under tussock, site 2	2	1 wk	NC	NC	–	–		+	
Bennett et al. (2002)	Australia	Tussock grass, interspace site 1	2	1 wk	NC	NC	+	NC		NC	
Bennett et al. (2002)	Australia	Tussock grass, interspace site 2	2	1 wk	NC	NC	NC	NC		NC	
Blank et al. (2007)	Nevada	Sagebrush	15	2 yr			+	+	+		
Brooks (2002)	California	Creosote bush interspace	5	1 yr		NC		NC			
Brooks (2002)	California	Creosote bush dripline	5	1 yr		+		NC			
Castelli and Lazzari (2002)	Argentina	Shrub–grass, under shrub	3	3 yr after first burn	NC	NC	+	NC	+	+	
Castelli and Lazzari (2002)	Argentina	Shrub–grass, under grass	3	3 yr after first burn	NC	NC	NC	NC	+	NC	
Castelli and Lazzari (2002)	Argentina	Shrub–grass, under shrub	3	1 mo after second burn	NC	NC	–	NC	–	NC	
Castelli and Lazzari (2002)	Argentina	Shrub–grass, under grass	3	1 mo after second burn	NC	NC	NC	NC	–	NC	
Davies et al. (2009)	Oregon	Sagebrush interspace	15	2 yr	NC	NC	NC			NC	
Davies et al. (2009)	Oregon	Sagebrush subcanopy	15	2 yr	NC	NC	+			+	
Esque et al. (2010)	Arizona	Creosote under shrub	5	< 1 yr			+				
Esque et al. (2010)	Arizona	Creosote interspace	5	< 1 yr			+				
Ford et al. (2007)	Australia	Hummock grass, site 1	2	3 yr	NC	NC	NC			+	–
Ford et al. (2007)	Australia	Hummock grass, site 2	2	3 yr	+	+	NC			+	–
Fenn et al. (2003)	California	Chaparral	5	1 yr	NC		+				

Table 1. Continued.

Source	Location	Vegetation	Depth (cm)	Time after fire	SOM, organic C	Total N, organic N	Extractable N	Extractable Inorganic P	Inorganic ions	pH	Bulk density
Fenn et al. (2003)	California	Chaparral	5	2–80 yr	NC		NC				
Franco Vizcaino and Sosa Ramirez (1997)	Baja, CA	Mediterranean shrub	?	1 yr	NC	NC	+	NC			NC
Gimeno et al. (2000)	Spain	Mediterranean shrub	?	< 1 yr	–		–		–		
Haubensak et al. (2010)	Nevada	Salt desert scrub	12	5 yr	NC	NC			NC		+
Mills and Fey (2004)	S. Africa	Grassland/savanna*	10	Annual fire, – 28 yr	–	–	–		–		+
Picone et al. (2003)	Argentina	Grassland*	12	1 yr	–	–	+	+	+		
Rau et al. (2007)	Nevada	Pinyon–juniper/sagebrush	8	1 d			+	+			
Rau et al. (2007)	Nevada	Pinyon–juniper/sagebrush	8	5 yr			NC	NC			
Rau et al. (2009)	Nevada	Pinyon–juniper/sagebrush	8	1 d	+	+					
Rau et al. (2009)	Nevada	Pinyon–juniper/sagebrush	8	6 yr	NC	NC					
Seastedt and Ramundo (1990)	Kansas	Tallgrass prairie*	25	Annual fire, 10 yr	NC	NC				NC	NC
Snyman (2003)	S. Africa	Semiarid grassland	5	1 yr	–	–		–	+	+	+
Snyman (2003)	S. Africa	Semiarid grassland	5	2 yr	NC	–		NC	NC	NC	+
Stubbs and Pyke (2005)	Oregon	Pinyon–juniper woodland	10	4 mo			+				
Stubbs and Pyke (2005)	Oregon	Pinyon–juniper woodland	10	1 yr			NC				
Vourlitis and Pasquini (2008)	California	Chaparral	10	1 yr			+				
Sum of responses		SOM, organic C	Total N, organic N	Extractable N	Extractable P	Inorganic ions	pH				Bulk density
Total increases (+)		7 ²	5 ²	13 ¹	9	10	12				2
Total decreases (–)		8 ³	6	4	2 ³	4	0				2
Total no change (NC)		18 ^{2,3}	21 ²	10 ¹	13 ³	4	13				1

¹In three multisample or multiyear studies, initial increase followed by no change in property.

²In one multiyear study, initial increase followed by no change.

³In one multiyear study, initial decrease followed by no change.

site having significantly lower extractable N, which may be due to site characteristics (Fig. 1C). To examine the potential for a postfire nutrient pulse, extractable N was measured at another site immediately postfire. Extractable N was slightly lower immediately postfire at this site, with a mean of 3.8 (SE = 0.3) after fire and 6.0 (1.4) in the adjacent unburned site. These values are lower than extractable N in Figure 1C because they were collected at a different site and a different year, but show that fire does not always result in higher soil-extractable N in a semiarid grassland, as has been observed in other arid and semiarid lands (Table 1).

A fire chronosequence was also observed in paired burned and unburned sites in Sonoran Desert creosote bush scrub (*Larrea tridentata*), with burns from 3 yr to 29 yr (Steers and Allen 2011). Methods for the study are, briefly, six replicate soil cores, 5 cm deep, were collected in paired burned and adjacent unburned sites with burns ranging from 3 yr to 29 yr since fire. Soil total C and N, extractable N (KCl extract), and pH (water extract) were measured, and data were statistically analyzed with a *t* test for each site. Only the 13-yr-old site had

higher total N and C in the top 5 cm in unburned than burned plots, with values not significantly different in all other age burns (Figs. 2A and 2B). Extractable N was also similar in burned and unburned sites, with the exception of the 25-yr-old burn that had lower extractable N than the paired unburned site (Fig. 2C). This one significant value may be due to increased soil erosion, because the site was slightly more sloped than others in the chronosequence, although there were no differences in total N and C. Two other studies that reported total soil N immediately after fire also showed no change in N in interspaces between creosote bush fertile islands in the Mojave Desert (Table 1; Brooks 2002; Abella et al. 2009). Abella et al. (2009) also did not observe any difference in total N between understories of burned and paired unburned sites. However, postfire total N was higher at the drip line of shrub fertile islands where higher levels of SOM coupled with relatively low fire temperatures led to an accumulation of total N (Brooks 2002). The data for Figure 2 were collected randomly, irrespective of interspace and understory locations. Data from these studies (Fig. 2, Brooks 2002, Abella et al.

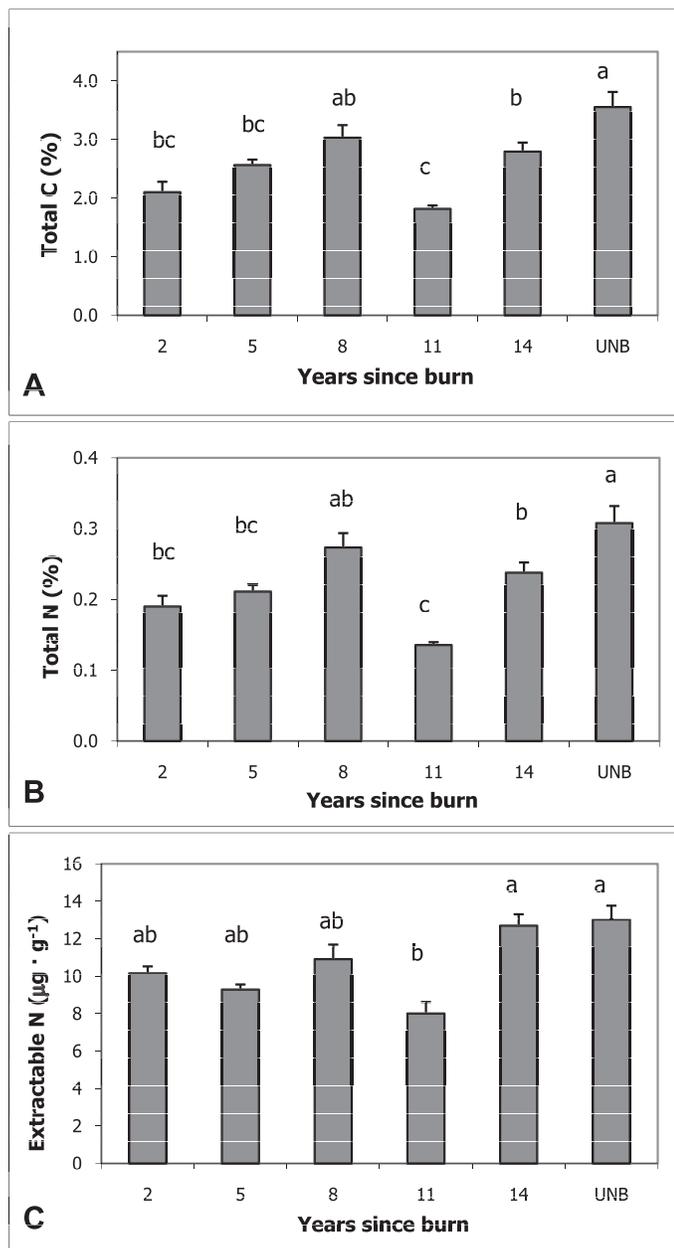


Figure 1. A, Soil carbon. **B,** Soil total nitrogen. **C,** Extractable N as NH_4^- -N plus NO_3^+ -N in a semiarid perennial grassland fire chronosequence from 2 yr to 14 yr since burn, and unburned (UNB) control in southern California (Dickens and Allen, unpublished). Different letters indicate significantly different means at $P < 0.05$.

2009) show that N either changes little or can recover quickly after fires based on measurements in sparse fuels between shrubs. Shrub islands of fertility occur in cold desert sagebrush as well, with short-term increases in N and C under shrubs and in interspaces after fire (Stubbs and Pyke 2005; Rau et al. 2009). However, the loss of shrub islands of fertility after frequent fires or when vegetation is poorly adapted to fire and recovers slowly may cause a reduction in total ecosystem nutrients, as discussed below.

The impacts of frequent fire on soil and total ecosystem C and N are also of concern, as frequent fires have become a feature of invaded deserts. The Sonoran Desert burns included

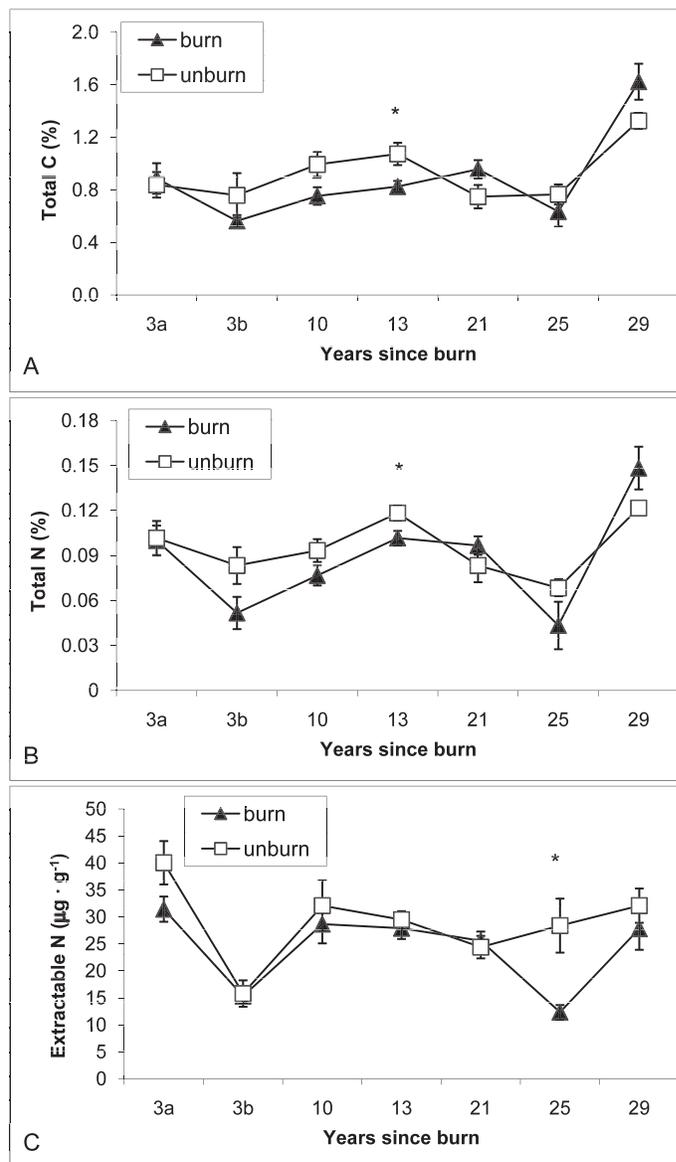


Figure 2. A, Soil carbon, **B,** soil total nitrogen, and **C,** extractable N as NH_4^- -N plus NO_3^+ -N in a Sonoran Desert creosote bush scrub fire chronosequence in paired burned and unburned sites of varying ages (two sites were 3 yr old; from Steers and Allen 2011). Asterisk indicates significantly different between burned and unburned samples within a site at $P < 0.05$.

several sites with multiple burns. Sites that burned two times within 19 yr and 21 yr and three times within 35 yr were observed in the Sonoran Desert chronosequence, but there was no significant reduction in extractable N after multiple burns (Steers and Allen 2011). Even multiple fires have not affected total C and N negatively in the intershrub spaces in these desert areas (Steers and Allen 2011). Because sampling of the unburned sites was done in interspaces and not within fertile islands, no assessment can be made of nutrient losses if soil islands of fertility were lost postfire with the loss of shrubs.

Some remarkable long-term studies were done in South African semiarid grassland to subhumid savanna. Annual burns over 28 yr showed decreases in SOM, total N, and extractable N (Mills and Fey 2004). There was also an increase in soil crusting

with reduced soil moisture due to clay dispersion, a consequence of reduced SOM in these burned subhumid grasslands. By contrast, annual burning of Kansas tallgrass prairie for 10 yr caused no losses of SOM or total N (Seastedt and Ramundo 1990). Ecosystems with a high proportion of biomass and nutrient storage below ground may be more buffered from the severe impacts of fire than those with a smaller proportion below ground (Neary et al. 1999). However, if fire causes other changes in soils such as clay dispersion (Mills and Fey 2004), then frequent fire should be reconsidered as a management strategy. In arid and semiarid lands with lower organic matter, the main concern may be loss of SOM under shrub islands following frequent burns, as discussed below.

Changes in Other Nutrients After Fire

In contrast to N, both K and P require $>700^{\circ}\text{C}$ for volatilization and their loss is usually minimal unless the fire is followed by erosion (Neary et al. 1999). Other nutrients such as Ca, Mg, and Na require much higher temperatures for volatilization. Extractable P did not change in 13 cases (Table 1). Fire temperature was not reported in most of these fires, but was most likely below 700°C , as fires seldom burn hotter than this at ground level under natural levels of fuel buildup. The mineralization of organic forms of P by fire would increase extractable P (nine studies, Table 1), whereas postfire erosion or immobilization by mineral complexes would reduce it (two studies, Table 1). Increases in pH would also affect P availability (Badia and Marti 2003b). The other inorganic ions important to plant growth measured in these studies were primarily extractable K, Ca, and Mg, which increased in 10 cases because of fire-caused mineralization, decreased in four cases because of erosion or unknown reasons, and did not change in four studies.

Changes in pH After Fire

Of the 25 studies or sites that reported effects of fire on pH, 12 had increased pH and 13 showed no change after fire (Table 1). Notably, pH did not decrease in any study. Elevated pH may be expected following fire, at least in the few surface centimeters of soil (Neary et al. 1999). The ash left behind after fire consists primarily of cations (e.g., Ca, Mg, Mn, K, Na) that were constituents of living plant tissue and SOM. Following a fire the base cation oxides are hydrolyzed with the next moisture input, creating a basic solution. The resultant basic soil pH depends upon the quantity and constituent ions of the ash, the buffering capacity of the soil, and leaching. The pH will drop again as plants grow, taking up cations whose charges will be balanced by negatively charged plant organic acids. However, the rate at which pH recovers in desert soils has been little studied.

The pH was still elevated 3–5 yr after fire in arid and semiarid soils (Castelli and Lazzari 2002, Table 1; Haubensack et al. 2010). A Sonoran Desert creosote bush scrub fire chronosequence (Steers and Allen 2011) had higher pH following fire that persisted up to 21 yr (Fig. 3). The amount of pH increase was small, typically 0.2 to 0.3 units of pH higher in burned than unburned, but surprisingly persistent. The implications for plant growth are not clear at this point, especially as these are changes in the top 5 cm surface pH. The burned sites were dominated by exotic Mediterranean split grass (*Schismus* spp.) and filaree (*Erodium*

cicutarium) with an overstory dominated by brittlebush (*Encelia farinosa*) in all but the 10-yr-old and the 3-yr-old burns. The unburned sites also had abundant exotic annuals, but the dominant shrub was always creosote bush (Steers and Allen 2011).

Fire Impacts on Soil Physical Properties

Fire also affects soil bulk density, erosion, hydrophobicity, and moisture. Bulk density may increase, decrease, or remain unchanged after fire (Table 1). An increase in bulk density is caused by combustion and decomposition of roots when shoots are fire-killed, and a decrease occurs if partially combusted aboveground material is deposited (Neary et al. 1999). With the change in soil structure due to loss of soil macropores, infiltration is reduced, and the subsequent drier soil may slow vegetation recovery, especially in semiarid areas (Snyman 2002, 2003). Lower soil moisture may also be related to higher soil temperature in burned areas that have no litter or vegetation cover to ameliorate direct radiation, and to loss of litter that slows surface movement of water and allows greater infiltration. Furthermore, soil crusting may occur after fire in soils high in clay, that also impedes water infiltration (Mills and Fey 2004).

Hydrophobicity is caused when fire-bared soil surfaces seal under the impact of raindrops, resulting in increased surface runoff (Doerr et al. 1998; Neary et al. 1999). This occurs after hot fires or certain litter types that leave hydrophobic organic compounds in the soil surface, although the hydrophobic compounds are destroyed in extremely hot fires where soil temperatures are greater than 290°C (DeBano et al. 1976; Neary et al. 1999). Hydrophobicity may contribute to wind and water erosion and loss of nutrient-rich ash and topsoils, and can initiate long-term depletion of soil nutrients. A recent study of desert fires in New Mexico reported hydrophobicity under creosote bush, but not in interspaces dominated by native perennial grasses (Ravi et al. 2007). Erosion of nutrients from islands to interspaces created a redistribution of nutrients to maintain desert grassland that had been subject to shrub invasion. Hydrophobic soils have also been reported from both unburned and burned understories of creosote, honey mesquite (*Prosopis glandulosa*), and blue paloverde (*Parkinsonia florida*) in southeastern California (Adams et al. 1970). Low annual plant abundance in shrub understories, especially after fire, was attributed to these hydrophobic soils, but other factors, like seed mortality due to high understory temperatures at the time of fire, could also be a factor (Brooks 2002).

EFFECTS OF FIRE ON SOIL MICROBIOLOGICAL PROPERTIES

Nutrient availability to plants is regulated by soil microorganisms, so their survival through fire and their ability to recover after fire are essential to succession and restoration after fire. Survival is dependent upon soil temperature, with surface temperatures $>100^{\circ}\text{C}$ killing most microorganisms. The microorganisms that are most subject to the impacts of fire are the biotic crust organisms that lie on the soil surface. Bryophytes and lichens had not recovered 5 yr after fire in Utah desert scrub, although algae recovered after only 2 yr (Johansen et al. 1984). Biotic crusts also recovered within 2–5 yr in burned sagebrush steppe if there was a low level of cheatgrass

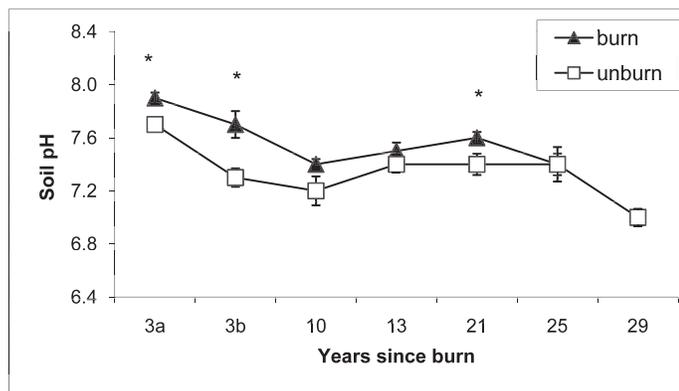


Figure 3. The pH of soil from Sonoran Desert creosote bush scrub in paired burned and unburned sites from 3 yr to 29 yr after fire (from Steers and Allen 2011). Asterisk indicates significantly different between burned and unburned samples within a site at $P < 0.05$.

invasion (Ponzetti et al. 2007); invaded sites did not recover. Bryophytes and lichens recovered from fire within a few months in Tasmanian tussock grassland (Ferguson et al., 2009), a moister site than the two desert studies.

For those microorganisms beneath the surface, soil is a good insulator, especially when it is dry, and the temperature at 2.5-cm depth may be a benign 50°C when the surface is 100°C (Neary et al. 1999). Hot-desert near-surface soils may be 50°C even under ambient summer conditions, so the survival of subsurface organisms is assured even in a moderately hot fire. When the soil surface temperature reaches 700°C , as under slash or very high fuel accumulations, the soil temperature may be as hot as 100°C down to 22 cm in a moist soil (Neary et al. 1999). Studies (summarized below) have been done on saprotrophic bacteria and fungi and mycorrhizal fungi following fire, with the use of a variety of measurements to detect abundance or activity. The measurements include soil respiration, microbial biomass, microbial C and N, nitrification, mineralization, and direct microscopy. Some studies are based on short-term laboratory incubation studies, but others included multiyear field observations. Studies in semideserts and woodlands that assessed microbial biomass after fire by measuring microbial C or respiration observed an increase in microbial activity as often as a decrease (Bauhus et al. 1993; Fonturbel et al. 1995; Acea and Carballas 1996; Badia and Marti 2003a; Andersson et al. 2004). Saprotrophic microbial activity after a fire depends upon how much of the soil organic matter was consumed by the fire. The fire may leave a large amount of dead but not completely combusted organic material, thus providing a carbon source for saprotrophs.

Processes of N mineralization and nitrification may initially increase after fire and promote increased plant production, but will eventually return to prefire levels some months to years after fire. Nitrification increases after a fire if there is an accumulation of NH_4^+ mineralized by the fire that is then converted to NO_3^- (Bauhus et al. 1993; Andersson et al. 2004; Esque et al. 2010). Effects of fire on mineralization and nitrification were short-lived in a burned Australian hummock grassland; in fact, the major differences in N turnover rates were between soils under and between hummocks, rather than between burned and unburned soils, indicating the importance

of organic matter in driving mineralization and nitrification (Ford et al. 2007). Microbial activity was reduced more by drought than by fire in hummock grassland, suggesting these low-C soils are resilient to fire (Ford et al. 2007). High mineralization rate and recovery of microbial function may promote elevated mineral N for one or multiple years after a fire. Subsequently, plant growth response is often high after a fire, as was observed for invasive annual grasses in experimentally burned Sonoran Desert soil with elevated extractable N and mineralization rates (Esque et al. 2010). Increased productivity after fire has also been observed in semiarid to subhumid ecosystems such as tallgrass prairie and Mediterranean shrub lands (Seastedt and Ramundo 1990; Carreira and Niell 1992). In contrast, fires in sandy, nutrient-poor semiarid grassland in South Africa did not promote increased plant growth, and in fact plants had reduced biomass because of soil moisture loss (Snyman 2004).

Mycorrhizal fungi are also of concern because they are important in procuring nutrients and water for plants, as well as performing other functions such as drought stress tolerance and pathogen protection. Most plants of arid and semiarid ecosystems form arbuscular mycorrhizal fungi (Allen et al. 1995), a major exception being ectomycorrhizal pinyon pine or scrub oak woodlands. However, no studies have specifically focused on recovery of arbuscular mycorrhizal fungi after fire in these vegetation types. Two studies on ectomycorrhizal fungi of subhumid ecosystems showed a limitation of mycorrhizal inoculum for plant establishment following fire. One of these was a Ponderosa pine slash-pile fire that burned for several days, where soil biota were charred to 10 cm depth (Korb et al. 2004). Attempts to restore pines failed unless they were inoculated with ectomycorrhizal fungi. The Yellowstone fire of 1988 burned patchily across the landscape in mature lodgepole pine forest. In some locations the fires were so hot that they burned large roots to 0.3 m deep and killed soil microorganisms. Recolonizing pine seedlings had 50% mortality in the first growing season, likely because of lack of mycorrhizal fungi (Miller et al. 1998). Ectomycorrhizal plants are typically obligately mycorrhizal in a field setting, meaning they will die eventually without inoculum. However, those that did survive became mycorrhizal by the end of the first growing season. It was not clear whether the inoculum came from deep buried living inoculum, or colonized as spores from a distant source. Spores of ectomycorrhizal fungi are easily dispersed by wind (Allen 1991), so either mode of inoculation is plausible.

Fires of the heat and intensity reported for pine forests (Miller et al. 1998; Korb et al. 2004) would not occur in drier ecosystems with lower fuel loads, so fire temperatures would likely not get hot enough to kill soil inoculum below 1–2-cm depth. The effects of differential soil temperature effects on mycorrhizal fungi was observed in pinyon–juniper woodland (Klopatek et al. 1994). Fires burn hotter under trees because of accumulated litter, and the percentage of arbuscular mycorrhizal inoculum under junipers was reduced more under trees than in interspaces. With the exception of the two severe fires described above (Miller et al. 1998; Korb et al. 2004) studies report little or temporary reduction in root mycorrhizal infection of plants resprouting following fire in subhumid to seasonally dry mesic systems (Anderson and Menges 1997; Allen et al. 2003; Korb et al. 2003). Fires in Australian

eucalyptus woodland caused reduced infection in some sites but not in others, possibly related to soil type (Launonen et al. 1999). Even though there is considerable inoculum in the soil after fire, the fungal species composition is changed by fire (Baar et al. 1999; Stendell et al. 1999; Allen et al. 2003). Recovery of some fungal species may take years after a fire (Allen et al. 2003), and in fact fungi and other microorganisms undergo fire-induced succession just as do plants. Studies documenting the effects of fires on mycorrhizal inoculum are not available for deserts, but the impacts are likely to be even smaller than those reported for regions with higher productivity and hotter fire temperatures.

IMPACTS OF INVASIVE SPECIES ON SOILS

A growing body of literature shows that invasive species impact soil and ecosystem properties even in the absence of fire; before considering the effects of fire on invaded desert ecosystem properties, researchers and managers must first understand how invasive species have affected ecosystem properties prior to fire. A review of 79 studies on ecosystem impacts of invasive species showed varying impacts on ecosystem C and N (Ehrenfeld 2003). Most invaded sites had greater biomass than native vegetation, with 16 of 20 sites reporting greater biomass and four with decreased biomass following invasion (Table 2). The remaining studies did not report plant biomass. Invasions with increased biomass are caused by productive plants such as woody species or fast-growing grasses that replace native grasslands, whereas those that cause a decrease in stand biomass include annual grasses that replace native shrub lands. Net primary productivity and growth rate similarly tended to increase in invaded stands. However, increased or decreased litter mass and soil C were reported in an equal number of studies following invasion, in spite of increased biomass of invaders. The elevated plant biomass was likely offset by an increased decomposition rate, as 10 of 12 studies reporting decomposition had higher rates following invasion. A majority of sites also reported increased mineralization and increased microbial C. A more recent meta-analysis of 94 studies showed a mean increased shoot productivity of 133% following invasion (Liao et al. 2008).

Changes in N following invasion were also dramatic, with a majority of studies reporting increased total soil N, extractable N, rates of N mineralization, N fixation, and biomass N (Table 2, Ehrenfeld 2003; Liao et al. 2008). Many invasive species are leguminous or actinorhizal with N-fixing nodules, and these are especially problematic in causing permanent alterations in nutrient cycling. Both of these reviews (Ehrenfeld 2003; Liao et al. 2008) included a range of ecosystem types from semiarid to mesic; some specific impacts of invasive species in deserts are described next.

Mesic ecosystems most often have increased productivity following an invasion (Ehrenfeld 2003; Liao et al. 2008), whereas desert ecosystems invaded by cheatgrass (*Bromus tectorum*) appear to have variable responses. In one study extractable soil N and N mineralization rates were lower in 1–2-yr-old invaded sites, and cheatgrass invasions were predicted to have reduced soil N over time with frequent fires and erosion (Evans et al. 2001). However, cheatgrass productivity was

Table 2. Number of studies showing changes in ecosystem properties following invasions by exotic species (from Ehrenfeld 2003).

Property	Increase	Decrease	No change
Plant biomass	16	4	0
Net primary productivity	10	0	2
Growth rate	10	0	0
Litter mass	7	5	2
Root/Shoot	1	5	1
Soil C	6	6	1
C mineralization	4	2	2
Decomposition	10	2	0
Microbial C	3	1	2
Total soil N	9	6	6
Extractable soil N	9	4	4
N mineralization	13	3	2
N fixation	8	2	0
Biomass N	11	1	2
Soil C/N	2	1	1

higher after 10 yr than 3 yr following invasion in another study, a result of increased N availability (Blank 2008). Similarly, cheatgrass stands had higher extractable nutrients than native perennial grass stands (Belnap et al. 2005). The reasons for different conclusions in these studies are not clear at this point, but may be related to length of time of observations or initial site conditions. In another study, soils invaded by cheatgrass had either higher or lower extractable and total N depending on the identity of the native species invaded (Belnap and Phillips 2001). Invasive species may preferentially select nutrient rich soils for colonization (Bashkin et al. 2003), and nitrophilous species such as cheatgrass respond to N fertilization with high growth rates (Monaco et al. 2003; Blank et al. 2007; Chambers et al. 2007).

Changes in soil physical as well as chemical properties have been observed in invaded soils. Perennial grassland soils invaded by cheatgrass had higher silt content on the Colorado Plateau (Belnap and Phillips 2001), whereas invaded Great Basin sagebrush (*Artemisia tridentata*) steppe had higher sand and lower surface roughness (Boxell and Drohan 2009). It is not clear at this time whether the differences were caused by postinvasion changes in geomorphic processes, or whether the invasive species selected certain soils to invade. Invaded soils also had lower infiltration rates, suggesting the possibility of increased runoff and long-term reduction in productivity. Coastal sage scrub invaded by red brome (*Bromus rubens*) in southern California had reduced water infiltration that was attributed to the loss of deep shrub roots that channel water downward (Wood et al. 2006). The long-term impacts of changes in hydrology vs. changes in N availability on productivity of ecosystems invaded by annual grasses still need to be assessed.

Finally, invasive plants may cause changes in the species composition of soil microorganisms. Red brome formed an association with a species of arbuscular mycorrhizal fungus termed the “fine endophyte,” whereas native shrubs formed associations with the normal “coarse endophyte” (Sigüenza et al. 2006). This had a functional response, in that the fine endophyte promoted a relatively greater growth response of the exotic grass than the coarse endophyte did for the native shrub,

compared to nonmycorrhizal controls. In another study, the shift in arbuscular mycorrhizal species composition caused by another exotic grass, slender wild oats (*Avena barbata*), was reversed after native grasses were planted again (Nelson and Allen 1993). Other species of soil organisms may also change following invasions. Soils recently invaded by *B. tectorum* had higher litter cover and experienced a decrease in richness and abundance of fungi and invertebrates coupled with higher bacteria density (Belnap and Phillips 2001). Furthermore, invaded soils tend to inhibit the postfire reestablishment of biotic crusts (Ponzetti et al. 2007). These microorganisms control the rate of nutrient mineralization, and understanding their changes will help to explain soil fertility and plant productivity changes of invaded ecosystems.

THE INTERACTIONS OF INVASIVE SPECIES AND FIRES ON SOIL ECOLOGY: LOSS OF FERTILE ISLANDS

The most immediately noticeable effect of invasive grasses in hot and cold deserts may be to homogenize vegetation with a near-monoculture of one grass species (Chambers et al. 2009; Rogstad et al. 2009). In cold desert the main culprit is cheatgrass. In the Mojave Desert with predominant winter precipitation, annual red brome dominates at high elevation and annual Mediterranean split grass (*Schismus barbatus* and *Schismus arabicus*) at lower elevation (Brooks 2000). In the Sonoran Desert the warm-season perennial buffel grass (*P. ciliare*) colonizes during summer rainfall events (Rogstad et al. 2009), although split grass occurs in some Sonoran Desert areas that have winter/spring precipitation (Walters 2003). Invasive grasses have the potential to eliminate fertile islands if shrub reestablishment is hindered. Fertile islands are formed around desert shrubs because they “mine” the interspaces and deep soil for nutrients and water, and accumulate nutrients and organic matter under the shrub (Charley and West 1975). The contributions of fertile islands to nutrient dynamics have been studied in sagebrush steppe (Charley and West 1975; Allen and MacMahon 1985; Ryel et al. 1996), pinyon-juniper woodlands (Stubbs and Pyke 2005), and creosote bush scrub (Kieft et al. 1998). Desert shrubs also act as nurse plants for establishment of other species (e.g., Drezner 2006), so their elimination by invasive species and frequent fire has the potential to cause major changes in plant community as well as nutrient dynamics.

The dynamics of fertile islands have been studied during the transition from shrub land to native perennial grassland, although none have considered the case of invasive annual species. In central New Mexico creosote bush is invading perennial warm-season desert grasslands, creating islands of fertility (Ravi et al. 2007; Ravi and D’Odorico 2009). However, when fires occur, creosote bush is frequently killed and does not resprout, providing an opportunity to study the breakdown of fertile islands. Creosote bush leaves behind hydrophobic secondary chemicals on burned soil surfaces that decrease infiltration and increase wind erosion of fertile islands. The nutrients are redistributed into the adjacent perennial grasses, which respond postfire with increased growth rates. Ground cover of grasses is much higher than shrub cover at this ecotone, so the grassland actually has higher nutrient content at

Table 3. Hypothetical calculations of amounts of total N and extractable NO_3^- -N and extractable P in unburned creosote bush scrub with 14% shrub cover compared to burned desert with no shrub cover and loss of nutrients in fertile islands. Soil nutrient concentrations are from 5-cm-deep soil cores in creosote bush scrub at Joshua Tree National Park (Allen, unpublished).

	Soil nutrient concentrations		
	Total N (%)	NO_3^- ($\mu\text{g}\cdot\text{g}^{-1}$)	P ($\mu\text{g}\cdot\text{g}^{-1}$)
Interspace	0.04	1.4	1.8
Under shrub	0.064	11.7	12.3
	Soil nutrients per m^2		
	$\text{g}\cdot\text{m}^{-2}$	$\text{mg}\cdot\text{m}^{-2}$	$\text{mg}\cdot\text{m}^{-2}$
Unburned with 14% shrub cover	2.6	17.1	19.6
Burned, no shrub cover	2.4	8.4	10.8

the stand level. The loss of shrub islands in perennial grassland may actually increase ecosystem fertility (Kieft et al. 1998).

While soil redistribution was local after fire in perennial grassland invaded by creosote bush (Ravi et al. 2007, 2009), nutrient redistribution of burned shrub- and woodlands invaded by annual grasses may be more extensive and have more extreme ecosystem impacts (Sankey et al. 2009). The invasion of cheatgrass was called a factor that causes ecosystem impoverishment because long-term dominance causes frequent fire that does not allow sagebrush to reestablish (Billings 1991). Nutrients of juniper fertile islands maintained higher extractable N than interspace soils up to 1 yr after fire (Stubbs and Pyke 2005), but the researchers concluded that long-term persistence of nutrient islands is not assured after tree removal, and cheatgrass may invade and dominate in the nutrient-rich patches. The long-term fertility of soil after sagebrush is fire killed and invaded is not clear, especially as studies differ about the impacts of cheatgrass on productivity (Evans et al. 2001; Blank 2008). Recent measurements showed that the rate of erosion from burned sagebrush steppe increased up to 67 times compared to unburned controls (Sankey et al. 2009), indicating that nutrient-rich topsoil may be deposited off site and impoverish soils after fire.

Fires in the Sonoran and Mojave Deserts have resulted in exotic annual grasslands that burn frequently and have poor recovery of shrubs (Brooks et al. 2004; Brooks and Matchett 2006; Steers and Allen 2011). The long-term nutrient impacts have not been assessed for these altered systems, but a hypothetical calculation suggests a considerable loss of total nutrients if shrub islands cannot recover and soil is eroded off site (Table 3). Total and extractable N and extractable P were all lower in interspaces than under creosote bush at Joshua Tree National Park. Shrub cover averaged 14% at this site. Calculating these values on an areal basis with and without shrub cover results in a reduction of extractable N and P by about 50%, and a 10% reduction for total N. This suggests that extractable nutrients could be as much as 50% lower in a burned site that does not have shrub recovery. This assumes that, in the absence of shrubs, the invasive annual grasses continue to maintain the lower fertility of interspaces, unlike the studies (Kieft et al. 1998; Ravi et al. 2007; Ravi and D’Odorico 2009) that showed a shift of nutrients from burned

shrubs to adjacent perennial grasses. The soil-nutrient data (Table 3) were collected in interspaces invaded by exotic split grass, as native cover had been eliminated by fire. The calculation also assumes that the burned mineral nutrients are moved out of the system, either by volatilization in a hot fire or erosion off-site after fire (Sankey et al. 2009). If there is no persistent litter or perennial plants to capture the nutrients, erosion may be severe enough to move minerals off site rather than to interspaces. Under frequent fire and dominance by invasive annual grasses, as has occurred in both hot and cold deserts, shrubs will not be able to reestablish and remnant fertile islands will eventually erode away. Because the fate of these nutrients is unknown because measurements are not available, the calculations in Table 3 are presented as a hypothetical example of the worst-case scenario for a nutrient balance following destruction of shrub islands by fire, if their nutrients move out of the system.

Fires are still a relatively recent phenomenon in invaded deserts, so knowledge of their impacts on soil ecology is lacking. Because soils are dry and fire severity is relatively low in the sparse fuels of deserts, the impacts on soil are less than for hot fires of more productive ecosystems. Furthermore, the burned soils were already dominated by invasive species, so their dynamics were likely changed by invasive species prior to burning. We have observed that desert fires have little impact on soil N and C in sites that have already become invaded or recovered rapidly once invasive species recolonize (Fig. 2), but we have not observed burned soils in uninvaded deserts. Fires are less frequent in uninvaded deserts, as are the opportunities for studying impacts on soil ecology. The loss of woody vegetation and fertile islands is the main concern in understanding nutrient dynamics, and should be a focus of future research for understanding altered ecosystem dynamics following fire and invasions.

IMPLICATIONS

Desert fires remove relatively little total ecosystem N, both because they burn at low temperatures that minimize N volatilization, and because much of the ecosystem N content is belowground. Available studies suggest that N either generally recovers or is little affected by fire (Figs. 1 and 2, and Table 1). However, invasive species may have a greater impact on soil N and C than single or in some cases even multiple fires. Both N and C often increase following invasions. The implications for managers is that prescribed fires may be used to control exotic species without the worry of excessive N losses in most cases (DiTomaso et al. 2006). Where invasive species increase N cycling and mineral N is higher, managers may also consider using fire to decrease soil N, but this will likely require multiple, carefully timed burns over several years before total ecosystem N is reduced to preinvasion levels (Johnson et al. 2009). Although this approach shows promise in more mesic and fire-adapted vegetation types, using fire as a tool in invaded desert communities is counterproductive, as invasive plants will eventually regain dominance and repeated burning will eliminate woody perennials. Erosion of soil nutrients is a concern in deep-rooted shrub lands replaced by shallow-rooted annual grasslands. Recent and ongoing studies

in sagebrush steppe have documented high rates of soil loss that may obliterate fertile islands (Sankey et al. 2009), but the particular case of fertile island persistence after long-term invasion still needs to be studied in sagebrush steppe and creosote bush scrub. Control of invasive species and restoration of desert fertile islands are obvious management needs, but must be coupled with a greater understanding of how invasive species affect desert soil ecology in different ecosystem types.

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