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Effects of fire on belowground biomass in Chihuahuan desert grassland

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Citation: Burnett, S. A., J. A. Hattey, J. E. Johnson, A. L. Swann, D. I. Moore, and S. L. Collins. 2012. Effects of fire on belowground biomass in Chihuahuan desert grassland. Ecosphere 3(11):107. http://dx.doi.org/10.1890/ES12-00248.1

Abstract. Grasslands occupy large areas in the northern Chihuahaun Desert. These grasslands, dominated by *Bouteloua eriopoda*, are subjected to periodic drought, infrequent fire and grazing by herbivores. Previous work shows that *B. eriopoda* is sensitive to disturbance but much work has been based on aboveground responses. We evaluated seasonal and annual recovery of belowground production and biomass following fire at two sites in ungrazed *B. eriopoda*-dominated grassland in Central New Mexico, USA. At one site, we quantified belowground standing crop and net primary production in burned and unburned areas during the first full growing season following wildfire the previous summer. At a second site, we measured annual below- and aboveground net primary production in burned and unburned grassland from 2005 through 2010 following a fire in 2003. At the first site, belowground standing crop did not change seasonally nor differ between burned/unburned areas. Patch types were different in that belowground standing crop was higher in soils under clumps of *B. eriopoda* than patches of unvegetated soil. Patterns of belowground biomass and daily production differed between patch types and over time in burned/unburned areas. Biomass was higher in soils below clumps of *B. eriopoda* than beneath unvegetated soil patches throughout the monsoon season. Patterns of belowground biomass and daily production differed in burned and unburned areas. Earlier in the growing season, biomass in the burned area was greater than in the unburned area. By early August, biomass increased rapidly in the unburned area and was higher than in the burned area. Daily rates of belowground production generally declined throughout the growing season with a large increase in rate of production in the unburned site in early August. At the second site's measured inter-annual responses, annual belowground production did not differ consistently between burned/unburned grasslands nor over time, nor was belowground production correlated with aboveground production. Our results demonstrate that despite the years required for aboveground production to recover following fire in *B. eriopoda*-dominated grassland, belowground standing crop and production was unchanged the year following fire. These results emphasize that aboveground production is not a reliable proxy for belowground production in this grassland.

Key words: belowground biomass; belowground production; *Bouteloua eriopoda;* desert grassland; fire.

Received 20 August 2012; revised 7 September 2012; accepted 9 October 2012; **published** 16 November 2012. Corresponding Editor: D. P. C. Peters.

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Introduction

Net primary production (NPP) is a key integrating variable in terrestrial ecosystems (McNaughton et al. 1989). In grasslands, NPP is often positively related to mean annual precipitation across regional rainfall gradients (Sala et al. 1988) as well as within a site over time (Huxman et al. 2004). Grasslands exist within a complex disturbance regime that includes fire, grazing and periodic drought (Hobbs and Huenneke 1992, Milchunas et al. 1998, Collins and Smith 2006). Although the impacts of disturbances on aboveground NPP have been studied extensively in mesic grasslands (Briggs and Knapp 1995, Knapp et al. 2006, Buis et al. 2009), much less is known about the response of belowground NPP to disturbance, especially in more arid grasslands where disturbances, such as fire, occur less frequently but have lasting impacts on aboveground production.

Arid and semiarid ecosystems occupy approximately 40% of terrestrial lands (Reynolds et al. 2007, Schimel 2010). These ecosystems are undergoing rapid transformations in response to climate change and land use management, especially desert grasslands that are experiencing changes in both fire frequency and grazing regimes. The C_4 perennial grass *Bouteloua eriopoda* (black grama) is a dominant species in North American Chihuahuan Desert grasslands especially on sandy soils (Campbell and Bomberger 1934, Brown and Smith 2000, Smith et al. 2004, Peters et al. 2006). Grasslands dominated by *B. eriopoda* occupy large areas throughout the northern Chihuahuan Desert where they intergrade with shrub-dominated vegetation and may co-dominate with *Bouteloua gracilis* (Jameson 1962, Dick-Peddie 1993, Brown and Smith 2000, Kroël-Dulay et al. 2004). Aboveground production of *B. eriopoda* grasslands is strongly driven by seasonal (monsoon) precipitation and temperature (Gosz and Gosz 1996, Muldavin et al. 2008, Collins et al. 2010), but unlike aboveground responses the relationship between belowground production, climate and disturbance remains poorly understood (Ladwig et al. 2012).

Previous work has shown that *B. eriopoda* is particularly sensitive to disturbances, such as fire and grazing (Campbell and Bomberger 1934, Humphrey 1949, Reynolds and Bohning 1956, Buffington and Herbel 1965, Holechek 1991, Gosz and Gosz 1996, Ryerson and Parmenter 2001, Parmenter 2008), but much of this work is based on aboveground measurements. For example, Vargas et al. (2012) found that total production of *B. eriopoda* grassland one full growing season following fire was 70% lower than pre-fire conditions. In addition, Parmenter (2008) found that aboveground cover of *B. eriopoda* required 7–10 years to return to pre-fire abundance following a management burn. However, if large amounts of precipitation follow a burn, *B. eriopoda* canopy height can be equivalent in both burned and unburned areas after as little as one year of regrowth (Drewa et al. 2006), but such conditions are rare. Just as favorable conditions can decrease recovery time, drought or grazing likely delay regeneration of *B. eriopoda* and other perennial grasses following disturbance (Reynolds and Bohning 1956, Cable 1967, Drewa et al. 2006).

In general, little is known about the effects of fire on belowground production in *B. eriopoda*-dominated grassland. In many grassland ecosystems, more biomass typically exists below than above ground (Coupland 1979, Sims and Coupland 1979, Jackson et al. 1996, Fitter et al. 1999, Gill et al. 2002). The majority of *B. eriopoda* roots reside in the first 20–30 cm of the soil surface (Campbell and Bomberger 1934, Brown and Smith 2000, Bhark and Small 2003), but roots and meristems growing near the soil surface may be vulnerable to damage from fire. As a consequence, it is possible that disturbances, such as fire, that occur during the growing season could reduce belowground biomass and root production following fire resulting in a long recovery time similar to that for aboveground production.

Our objectives were to determine both the within-season (short-term) and interannual (long-term) effects of fire on belowground standing crop biomass and root production in *B. eriopoda*-dominated grassland in central New Mexico, USA. We hypothesized that (1) belowground production and standing crop would be lower in burned compared to unburned grassland the year following fire, (2) that production and standing crop would be greater beneath patches of grass relative to patches of unvegetated soil in both burned and unburned areas, and (3) that production would recover slowly following fire similar to patterns observed for aboveground production.

METHODS

Study site

Our measurements of belowground standing crop and net primary production were conducted at the Sevilleta National Wildlife Refuge (SNWR) located approximately 80 km south of Albuquerque, New Mexico, USA. Several major biotic zones converge in this area including Chihuahuan Desert grassland and shrubland, Great Plains grassland, Piñon-Juniper woodland, Colorado Plateau shrub-steppe, and riparian vegetation along the middle Rio Grande. Average annual temperature is 13.2°C with the highest average temperatures in June (33.4°C) and the lowest average in January (1.6°C) (Muldavin et al. 2008). Annual precipitation is highly variable and averages 250 mm with the majority falling as large summer monsoon events from June through September (Gosz et al. 1995, Pennington and Collins 2007); sporadic precipitation occurs throughout the winter and spring as a consequence of frontal systems from the west and northwest. This precipitation pattern creates two distinct growing seasons, spring and late summer, with virtually all herbaceous plants dying or going dormant between the two seasons (Notaro et al. 2010). Soils are sandy loams with >65% sand and a silt content ranging from 18 to 22%. In addition, a petrocalcic layer occurs between 15–50 cm below the soil surface (Kieft et al. 1998, Buxbaum and Vanderbilt 2007). No livestock grazing has occurred on the SNWR since 1973.

Seasonal belowground standing crop, production, and turnover in B. eriopoda grassland

Our research was conducted in a previously unburned area of desert grassland where vegetation covers approximately 60% of the soil surface with intervening unvegetated patches dominated by light soil crusts (Bhark and Small 2003). In August 2009, a lightning-caused fire burned approximately 3400 ha of desert grassland in the SNWR. To determine the within-season effect of fire on belowground standing crop, net primary production, and turnover, we established two sites in May 2010 in an area dominated by *B. eriopoda*: one located in the area burned by the wildfire and another in adjacent unburned *B. eriopoda* grassland immediately across a dirt road which served as a firebreak. Between 1 and 3 June 2010, a total of 360 root ingrowth bags were inserted 15 cm into the soil at each of the sites. The bags were 5 cm in diameter by 15 cm long and made of 2 mm mesh screen. Each bag was filled with sieved, root-free soil from an adjacent area corresponding to the respective treatments.

At each site, a third of the bags were buried in areas of unvegetated soil. The remaining bags were buried beneath vegetative clumps of *B. eriopoda*, and all were marked with stake-wire flags. Half of the ingrowth bags placed under vegetative clumps were watered to simulate a large monsoon season and watering continued until actual monsoon rains occurred on 28 June. Watering began on 9 June with an applied precipitation event of 20 mm followed by simulated rain events of 10 mm on 14 June, 15 mm on 22 June, and 13 mm on 27 June. All simulated rain events were applied using a backpack sprayer to an area measuring 625 cm^2 centered on each root ingrowth bag. Thus, the six patch-type treatments were burned unvegetated soil, unburned unvegetated soil, burned vegetation, unburned vegetation, burned and watered vegetation, and unburned and watered vegetation. Each treatment consisted of 60 root ingrowth bags.

Bags were harvested on 15 June (14 days following burial), 29 June (28 days), 13 July (42 days), 6 August (66 days), 1 September (92 days), and 16 September (107 days) 2010 to determine root biomass at each harvest date and daily belowground production. At each sampling period, 10 ingrowth bags were harvested from each treatment. In addition to root ingrowth bags, 10 replicate soil cores (7.62 cm diameter by 15 cm deep) were collected with a bucket auger on 2 June, 13 July, and 16 September 2010 to measure belowground standing crop in both the burned and unburned areas. Samples were collected in the rooting zone beneath clumps of *B. eriopoda* and in unvegetated soil patches.

Belowground biomass (in growth bags) and standing crop (bucket auger samples) were extracted by passing the soil samples through a 4 mm sieve followed by sieving through either a 1 mm or 0.5 mm sieve, and then the remaining root material was floated in water for collection. Samples were then oven dried for 24 hours at 70°C and massed. Belowground biomass and standing crop are expressed as g m^{-2}. Daily production was determined by dividing root ingrowth biomass samples by the number of days between each sample period and expressed as g m^{-2} d^{-1}. Root turnover for the growing season was calculated following Allard et al. (2005). The initial belowground standing crop, the 2 June samples, was divided by the average of root biomass (ingrowth bags) from the 6 sampling times. Due to the absence of watered standing crop samples, turnover is only calculated for roots underneath soil and vegetative patches in both the burned and unburned areas.

Annual below- and aboveground production in desert grassland

In June 2003, a prescribed fire burned approximately 1200 ha of grassland also dominated by *B. eriopoda* along with *B. gracilis*. In November 2004, 10 root ingrowth "donuts" were installed (Milchunas et al. 2005) in the area burned by the prescribed fire and another ten across a road in an adjacent unburned area to determine the effect of fire on annual belowground net primary production (BNPP) in burned and unburned grassland. Root ingrowth donuts were created by excavating a 20 cm diameter by 30 cm deep cylinder of soil with a custom-made auger. The surface wall of the hole from which the soil core was removed was lined with 2 × 2 mm mesh plastic cross-stitch fabric. A 15 cm diameter by 30 cm tall cylinder of PVC pipe was then inserted into the center of the soil core to take up space, and filled with bags of sand to hold it in place. Root-free sieved soil was then added to the space between the PVC cylinder and the cross-stitch fabric, creating a cylinder of root-free soil. Root ingrowth donuts were harvested annually at two depths, 0–15 cm and 15–30 cm. Each fall, newly collected soil from adjacent areas from 0-30 cm depth was then sifted and used to reconstruct the root ingrowth donut for the next annual harvest. Following harvest, the volume of collected soils was measured by depth, roots were sifted (2 mm) and floated out of each sample, collected, dried at 60°C for 48 hours, and weighed. BNPP is expressed as g m^{-2} yr^{-1} (see Ladwig et al. 2012).

Aboveground net primary production (ANPP) was measured in 30 permanently located 1-m^2 quadrats in burned and unburned grassland adjacent to the root donuts. ANPP measurements were recorded at the start of the spring growing season and again in fall after perennial grasses had reached peak biomass. For every quadrat, biomass was determined from cover and height size classes based on weight-to-volume regressions developed by harvesting various sizes of each species from adjacent areas following Muldavin et al. (2008). A positive change in green biomass from one season to the next averaged over all quadrats was used as a measure of annual aboveground net primary production.

Statistical analyses

The SAS GLM procedure with repeated measures ANOVA was used to determine if within-season belowground standing crop, biomass, or production varied over time and between the various treatments. In this case, time period was the within-subjects factor, and the between-subjects factors included fire (burned and unburned) and treatment (watered/not watered, vegetation/unvegetated soil). For assessing changes in BNPP, time period was the within-subjects factor, and the between-subjects factors included fire (burned and unburned) and sampling depth (shallow, deep). All data except the daily production values were log transformed to normalize prior to analyses.

RESULTS

Seasonal belowground standing crop, production and turnover in B. eriopoda grassland

Belowground standing crop in *B. eriopoda*-dominated grassland did not change significantly during the growing season in any patch type (RMANOVA: $F \leq 2.90$, $p > 0.05$ in all cases). In addition, fire had no effect on belowground standing crop at the beginning, middle, or end of the growing season (RMANOVA: $F \leq 0.13$, $p > 0.05$ in all cases; Fig. 1A). However, standing crop beneath grass patches was significantly higher than beneath unvegetated soil

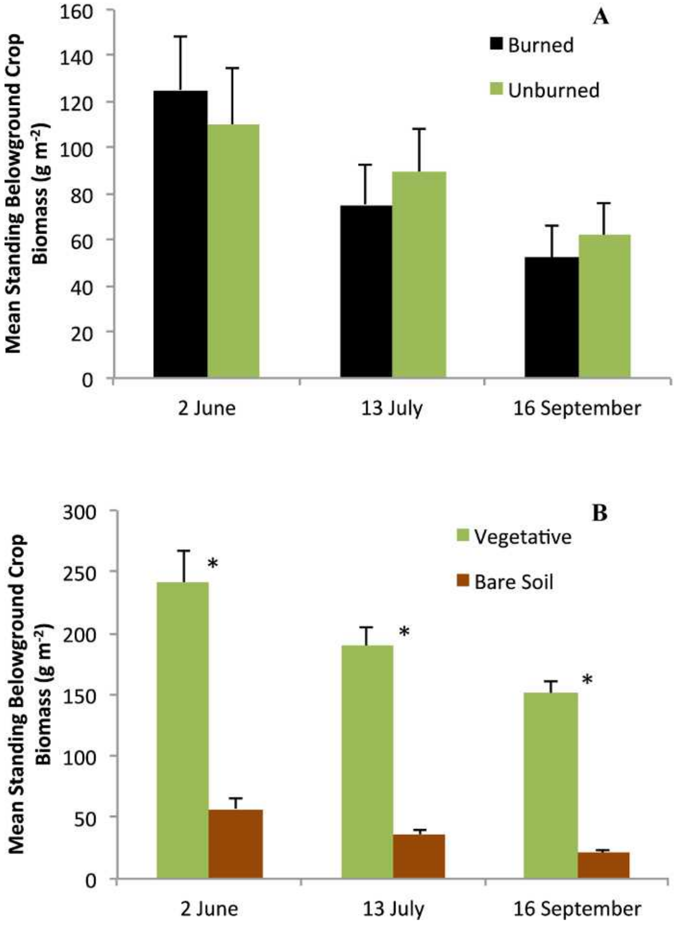

Fig. 1. Comparison of mean (±1 SE) belowground standing crop biomass (g m^{-2}) in (A) burned and unburned grassland and (B) beneath grass clumps and unvegetated soil during the first full growing season following a lightning-caused wildfire in ungrazed *Bouteloua eriopoda* grassland ($n = 10$). Asterisks indicate significant differences ($p < 0.05$) based on analysis of variance.

(RMANOVA: 2 June, $F = 69.90$, $p < 0.0001$; 13 July, $F = 139.39$, $p < 0.0001$; 1 September, $F = 207.39$, $p < 0.0001$; Fig. 1B). Standing crop under grass patches averaged 190.7 ± 10.3 g m^{-2} whereas interstitial spaces averaged only 35.2 ± 3.1 g m^{-2}. There was no fire by patch type interaction for belowground standing crop (RMANOVA: $p > 0.05$ in all cases).

Belowground biomass increased beneath watered and unwatered grass patches and unvegetated soil over most of the growing season (significant biomass × time interaction, RMANOVA: $F = 8.19$, $p < 0.0001$, Fig. 2A, C). Additionally, belowground biomass differed among these patch types over the growing season (RMANOVA: $F = 606.89$, $p < 0.0001$). Belowground biomass beneath grass patches did not differ between plots that were watered early in the monsoon season and those that were not; however, biomass in these treatments differed significantly from biomass beneath patches of unvegetated soil at all sample times (RMANOVA: 15 June, $F = 281.25$, $p < 0.0001$; 29 June, $F = 171.74$, $p < 0.0001$; 13 July, $F = 114.31$, $p < 0.0001$; 6 August, $F = 106.54$, $p < 0.0001$; 1 September, $F = 65.66$, $p < 0.0001$; 16 September, $F = 97.50$, $p < 0.0001$). Biomass beneath grass patches with and without watering was greater (overall means of 24.3 ± 1.4 and 23.5 ± 1.0 g m^{-2}, respectively) than under unvegetated soil where mean biomass overall was 2.7 ± 1.0 g m^{-2} (Fig. 2A, C).

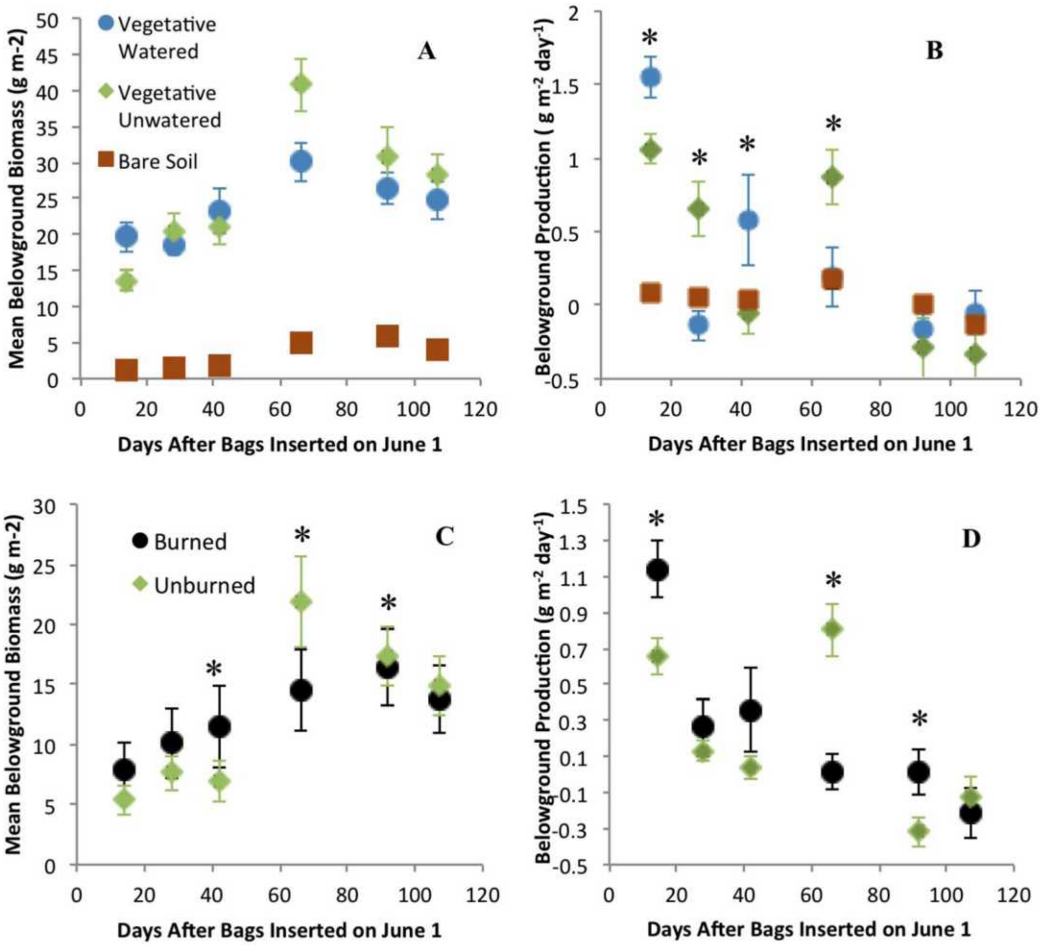

Fig. 2. Comparison of mean (±1 SE) (A) belowground biomass (g m^{-2}) and (B) daily production (g m^{-2} day^{-1}) beneath watered and unwatered grass patches and unvegetated soil, and (C) belowground biomass (g m^{-2}) and (D) daily production (g m^{-2} day^{-1}) in burned and unburned areas during the first full growing season following a lightning-caused wildfire in ungrazed *Bouteloua eriopoda* grassland. Asterisks indicate significant differences ($p < 0.05$) based on analysis of variance.

Although daily rate of belowground production generally declined over the growing season (Fig. 2B, D) daily production differed significantly between patch types during the first four sample periods (RMANOVA: 15 June, $F = 94.86$, $p < 0.0001$; 29 June, $F = 14.03$, $p < 0.0001$; 13 July, $F = 3.50$, $p = 0.04$; 6 August, $F = 9.19$, $p < 0.0004$) and between fire treatments on three dates (RMANOVA: 15 June, $F = 27.41$, $p < 0.0001$; 6 August, $F = 27.82$, $p < 0.0001$; 1 September, $F = 6.88$, $p = 0.0115$). However, these differences were not consistent between fire treatments (Fig. 2D). Daily production increased significantly under unburned vegetated patches in August but was significantly lower under burned patches in June and early September. In contrast, daily production was low and relatively constant under patches of unvegetated soil.

Fire had no significant effect on overall belowground biomass (RMANOVA: $F = 0.55$, $p = 0.19$). However, a significant fire effect occurred at the 15 June, 13 July, and 6 August sample periods (RMANOVA: 15 June, $F = 11.46$, $p = 0.0014$; 13 July, $F = 6.87$, $p = 0.0115$; 6 August, $F = 10.96$, $p = 0.0017$; Fig. 2B). Mean belowground biomass was greater at the burned site on 15 June (burned = 7.9 ± 1.3 g m^{-2}, unburned = 5.4 ± 1.3 g m^{-2}) and on 13 July (burned = 11.5 ± 3.4 g m^{-2}, unburned = 7.0 ± 1.7 g m^{-2}). On 6 August, mean belowground biomass at the burned site was significantly lower (14.5 ± 3.4 g m^{-2}) than the unburned site (21.8 ± 3.8 g m^{-2}).

A significant fire by patch type interaction occurred in five of the six belowground biomass sample dates (RMANOVA: 15 June, $F = 4.49$, $p = 0.016$; 29 June, $F = 10.74$, $p = 0.0001$; 13 July, $F = 3.56$, $p = 0.0357$; 6 August, $F = 5.75$, $p = 0.0056$; 16 September, $F = 4.04$, $p = 0.0236$). Only the 1 September sample period was not significant (RMANOVA: $F = 2.90$, $p = 0.0644$). Biomass was significantly higher beneath burned patches than unburned patches, leading to an overall significant fire by patch type interaction on belowground biomass (RMANOVA: $F = 21.01$, $p < 0.0001$).

Fire did not have an overall significant effect on belowground biomass turnover (RMANOVA: $F = 1.27$, $p = 0.27$; Fig. 3). However, during the 6 August and 16 September sampling periods biomass turnover was higher in the unburned compared to the burned sites (RMANOVA: $F = 19.83$, $p < 0.0001$ and $F = 7.45$, $p = 0.0098$, respectively). Results also differed by patch type over the growing season (RMANOVA: $F = 19.08$, $p = 0.0001$). In general, belowground biomass turnover was higher beneath grass patches than underneath unvegetated soil with the exception of the 1 September sample. At this time, biomass turnover was not significantly different between grass patches and unvegetated soil (RMANOVA: $F = 2.50$, $p = 0.12$). A fire by patch type interaction occurred over the growing season (RMANOVA: $F = 11.00$, $p = 0.0021$).

Overall, biomass turnover differed significantly over time (RMANOVA: F = Infty, $p < 0.0001$). There was a significant time by fire, time by patch type, and time by fire by patch type interaction (RMANOVA: F = Infty, $p < 0.0001$, in all cases). Biomass turnover gradually increased during the growing season (Fig. 3). At the start of the growing season, biomass turnover was highest beneath grass patches in the burned area. By mid-July, following the start of the monsoon season, biomass turnover in both the grass patches and unvegetated patches at the unburned site was comparable to rates beneath grass patches in the burned area (Table 1). Biomass turnover beneath unvegetated patches in the burned area was relatively low throughout the growing season.

Annual below- and aboveground production in desert grassland

From 2005 to 2010, fire had no effect on annual BNPP (RMANOVA: $p > 0.05$ in all cases; Fig. 4A). Annual BNPP differed by depth in some years (RMANOVA: $F = 38.67$, $p < 0.0001$; Fig. 4B). No differences in BNPP by depth occurred in 2005, 2009, and 2010 (RMANOVA: 2005, $F = 3.38$, $p = 0.0763$; 2009, $F = 2.41$, $p = 0.1312$; 2010, $F = 3.50$, $p = 0.0715$) whereas from 2006 to 2008 BNPP was significantly higher at 0–15 cm compared to 16–30 cm depth (RMANOVA: 2006, $F = 21.56$, $p < 0.0001$; 2007, $F = 10.82$, $p = 0.0026$; 2008, $F = 25.71$, $p < 0.0001$, Fig. 4B).

Overall, there were no fire by depth interactions (RMANOVA: $F = 1.59$, $p = 0.2176$) except in 2007. BNPP at 0–15 cm was significantly higher in burned compared to unburned grassland while at 15–30 cm, BNPP was significantly higher in the unburned area compared to the burned area (RMANOVA: $F = 7.54$, $p = 0.0102$). There were no significant time by fire interactions (RMANOVA: $p > 0.05$ in all cases) nor time by depth interactions (RMANOVA: $F = 3.54$, $p = 0.0073$).

From 2005 through 2008, ANPP fluctuated, but was always significantly higher in the unburned grassland compared to the vegetation recovering from the management burn that occurred in 2003 (Fig. 4C; RMANOVA: 2005, $F = 11.25$, $p = 0.0014$; 2006, $F = 1489$, $p = 0.0003$; 2007, $F = 10.42$, $p = 0.0021$; 2008, $F = 25.98$, $p < 0.0001$). ANPP in 2009 on the formerly unburned grassland was greatly reduced because of the wildfire. In 2010, ANPP on the site burned in 2009 (previously unburned grassland) was not significantly different than ANPP on the grassland burned in 2003 (RMANOVA: $F = 0.36$, $p = 0.5502$). Overall, from 2004 to 2010, ANPP was higher in the grassland not burned in 2003 (RMANOVA: $F = 24.82$, $p < 0.0001$). We found a significant year effect (RMANOVA: $F = 85.20$, $p < 0.0001$), and a significant interaction between year and fire (RMANOVA: $F = 16.98$, $p < 0.0001$). As a consequence, there is no temporal correlation between above- and belowground production ($r^2 = 0.015$, $p > 0.5$) in this desert grassland.

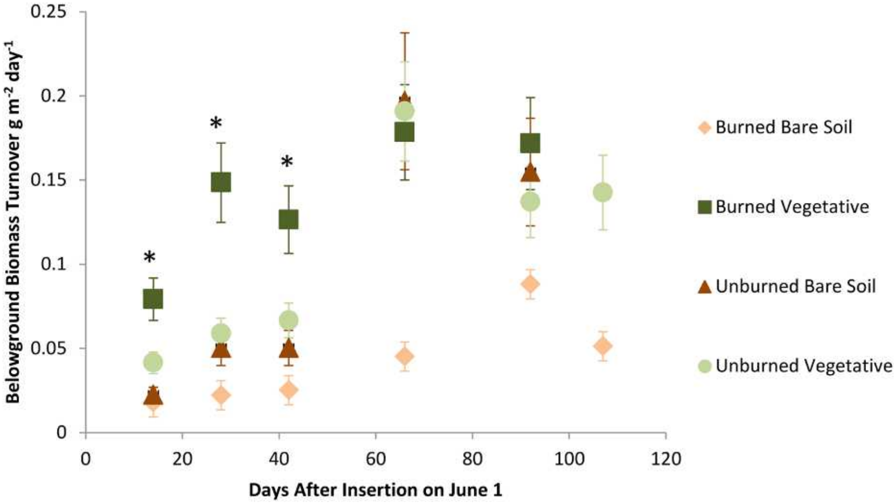

Fig. 3. Mean (±1 SE) rates of belowground biomass turnover (g m^{-2}) beneath grass patches and unvegetated soil in burned and unburned *Bouteloua eriopoda* grassland.

Table 1. Belowground biomass turnover during the growing season for each treatment (g m^{-2} biomass turnover per day, ± 2 SE).

Treatment	15 Jun	29 Jun	13 Jul	6 Aug	1 Sep	16 Sep
Burned soil	0.020 ± 0.005	0.025 ± 0.006	0.028 ± 0.007	0.050 ± 0.013	0.098 ± 0.025	0.057 ± 0.014
Burned vegetation	0.089 ± 0.032	0.167 ± 0.061	0.143 ± 0.052	0.201 ± 0.073	0.194 ± 0.070	0.145 ± 0.052
Unburned soil	0.027 ± 0.009	0.060 ± 0.021	0.060 ± 0.021	0.233 ± 0.082	0.183 ± 0.065	0.140 ± 0.052
Unburned vegetation	0.046 ± 0.016	0.066 ± 0.023	0.075 ± 0.026	0.213 ± 0.073	0.153 ± 0.053	0.160 ± 0.055

DISCUSSION

Burning has generally been reported to have long-term impacts on community composition and ecosystem processes in arid grasslands. Nevertheless, we found that belowground standing crop did not differ between burned and unburned areas of *B. eriopoda* grassland during the first full monsoon season following fire, nor did it change significantly over the growing season (Fig. 1). Moreover, within-season belowground root biomass and daily production were initially higher in burned compared to unburned areas (Fig. 2). Both high production and lack of difference in belowground standing crop between burned and unburned sites are in sharp contrast to post-fire patterns of aboveground production in *B. eriopoda* grassland (Valone and Kelt 1999, Drewa et al. 2006, Parmenter 2008). Indeed, several studies have shown that both aboveground cover and abundance of *B. eriopoda* are highly sensitive to fire. Depending on rainfall, recovery of aboveground cover to pre-fire levels can take up to 10 years or more in some cases (Reynolds and Bohning 1956, Gosz and Gosz 1996, Parmenter 2008). Thus, the lack of difference in standing crop and production between burned and unburned areas indicates that belowground processes in *B. eriopoda*-dominated grassland are highly resistant to growing season fire.

We used root cores and ingrowth methods to assess belowground standing crop and production over time. Although all such methods have their biases (Neill 1992, Tierney and Fahey 2007), these standard approaches are considered to provide reasonable estimates of production and standing crop biomass in grasslands although they likely underestimate production because of root turnover (Zhou et al. 2012). In our study, standing crop beneath vegetated patches ranged from about 150–250 g m^{-2}, a range that is comparable to amounts reported from other desert grasslands. For example, Sims and Coup-

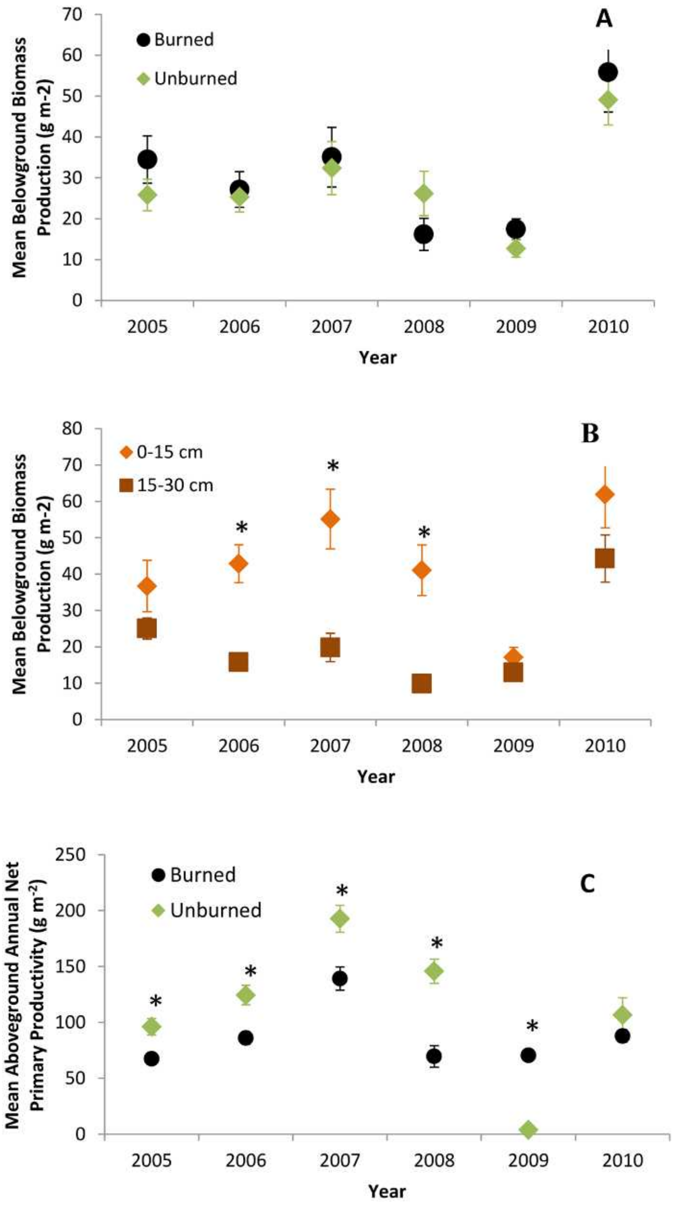

Fig. 4. Mean (±1 SE) annual belowground net primary production (g m^{-2} yr^{-1}) from 0-30 cm soil depth during 2005 through 2010 in (A) burned and unburned desert grassland, and (B) at 0–15 and 16–30 cm depths (burned and unburned combined). (C) Mean (±1 SE) annual aboveground net primary production (g m^{-2} yr^{-1}) in burned and unburned *B. eriopoda* grassland. Asterisks indicate significant differences ($p < 0.05$) based on analysis of variance.

land (1979) reported belowground standing crop to be 169 g m^{-2} in desert grassland at the Jornada Experimental Range (JER) in southern New Mexico. Thus, we believe our methods provided reasonable estimates of belowground standing crop and production within and among years.

We did find large differences in belowground standing crop and within-season production beneath vegetated patches compared to unvegetated areas (Figs. 1 and 2), indicating that *B. eriopoda* roots forage primarily beneath its canopy where infiltration is greatest and nutrients are concentrated (Kieft et al. 1998, Bhark and Small 2003, Pockman and Small 2010). We also found that biomass accumulation beneath clumps of *B. eriopoda* peaked between 32-44 g m^{-2} by late August after which rate of production declined (Fig. 2) likely as a function of increased root mortality and turnover (Stewart and Frank 2008). This range of root production is much lower than that found in mesic grasslands (Frank 2007, Fiala et al. 2012, Zhou et al. 2012). In contrast, biomass beneath unvegetated soils was consistently below 10 g m^{-2} throughout the growing season. *B. eriopoda* possesses a finely divided and well developed root system (Campbell and Bomberger 1934, Brown and Smith 2000) and the majority of these roots are concentrated beneath the plant with limited lateral spread. Overall, vegetation covers on average about 60% of the soil surface in this system (Bhark and Small 2003), therefore, integrating these peak biomass values on a per area basis results in a net peak accumulation of biomass of approximately 23 g m^{-2} in the top 15 cm of soil. In contrast, aboveground net primary production during 2010 was 85 g m^{-2} and 61 g m^{-2} in unburned and burned grassland, respectively (Vargas et al. 2012), although most of the post-fire production in the burned grassland was from forbs and grasses other than *B. eriopoda* (Herrera et al. 2011).

Two key factors may lead to the different responses between aboveground and belowground production following fire in *B. eriopoda* grassland: meristem limitation and plant-microbe interactions. Knapp and Smith (2001) proposed that production in more arid grassland ecosystems was constrained by the "bud bank," the pool of meristems near the soil surface available to generate new tillers each year or following disturbance. Fire in *B. eriopoda* grassland significantly increases temperature in the upper few centimeters of soil (Neary et al. 2005), and fire damage and mortality can occur at temperatures as low as 48 to 54°C depending on soil moisture content (Hare 1961, Kaspar and Bland 1992, Neary et al. 1999, 2005). Given that *B. eriopoda* is shallowly rooted and rhizomatous, most of its meristems are near the soil surface where they can be damaged by heat from fire. Dalgleish and Hartnett (2006) reported that grasslands in the SNWR were "meristem limited" and thus they are constrained in their ability to respond to environmental variability. This constraint may be exacerbated by fire-caused meristem mortality, which could limit the post-fire aboveground production response. Based on our belowground production data, we surmise that the 2009 fire did not cause significant root damage but it may have caused significant mortality to shallow-rooted tiller meristems. The lack of damage to roots is significant because they are important contributors to plant recovery following fire (Ravi et al. 2010).

A second factor related to recovery is altered plant-microbial interactions, particularly regarding root associated fungal endophytes. Dominant grasses at the SNWR exhibit high fungal diversity in their roots and rhizophere (Porras-Alfaro et al. 2011, Herrera et al. 2011). This diversity is reflected in a tight coupling between grasses and their associated fungi via the exchange of carbon and other nutrients, especially nitrogen (Collins et al. 2008, Green et al. 2008). Non-mycorrhizal fungi have been shown to rapidly transfer nitrogen from soil crusts to adjacent grasses in exchange for carbon (Green et al. 2008, Whiteside et al. 2009). Indeed, grasses rapidly provide carbon to rhizosphere fungi and other microbes via root exudates following a rainfall pulse (Vargas et al. 2012). The ability of grasses to provide this labile carbon source is likely limited by reduced leaf area and lower aboveground production following fire. As a consequence, plant-microbe interactions are likely altered, which could ultimately limit the post-fire recovery of aboveground biomass in these grasslands.

Our finding that within-season production was unaffected by fire was also borne out by our inter-annual study of belowground production in burned and adjacent unburned grassland. As we found for belowground production during the 2010 growing season, there was no difference in annual root production between burned and unburned areas several years following a management fire that occurred prior to the monsoon season in June 2003. Instead, belowground production, which ranged from 20–73 g m^{-2} yr^{-1} fluctuated over time in response to interannual climate variability. This rate of production is within the low end of the range reported for other arid ecosystems (Pavon 2005). The largest monsoon on record occurred in 2006. Root production peaked in 2007 and then gradually declined thereafter (Fig. 4), a pattern similar to that reported by Ladwig et al. (2012) in fertilized and unfertilized desert grassland. The majority of production occurred in the top 15 cm of soil (Bhark and Small 2003). Thus, this long-term data set provides further evidence that belowground production generally is unaffected by growing season fire.

Overall, our results demonstrate that belowground processes are highly resistant to growing season fire in this desert grassland. This production response is in stark contrast to aboveground patterns in which fire dramatically alters species composition and abundance, and greatly reduces aboveground production, which may take nearly a decade to recover to pre-fire levels. Together these patterns also demonstrate that rates of above- and belowground production are decoupled in this ecosystem (Ladwig et al. 2012). That is, aboveground and belowground production fluctuate over multi-year cycles that are weakly linked with growing season precipitation (Muldavin et al. 2008). Within a growing season, however, high aboveground production does not necessarily reflect high belowground production, and vice versa. Instead, it appears that belowground resistance to disturbances, such as fire, serves as the stabilizing mechanism by which aboveground production in these grasslands gradually recovers from disturbance.

ACKNOWLEDGMENTS

We thank the 2010 SNWR REUs for field assistance, and the US Fish and Wildlife Service for permission to work in the Sevilleta National Wildlife Refuge. This research was supported by NSF REU Sites award DBI-1062564 and NSF LTER award DEB-0620482 to the University of New Mexico.

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