

European exotics drive a North American invasion: fire and cattle legacies on soil resource gradients and patterns of annual brome invasion

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Abstract

Human activities alter disturbance regimes and spatio-temporal distribution of soil resources that can affect plant invasion outcomes. The objective of this study was to test whether fire history and cattle activity alter soil resource gradients, thereby affecting patterns of annual brome invasion. Six paired burned and unburned transect lines (1-kilometer in length) were established in the northeast Mojave Desert along the boundaries of four independent wildfires. At 100-meter transect increment points, we measured the distance to the two nearest cowpats and then established two random points and measured the density, height, biomass, and seed production of red brome, soil moisture and inorganic N. Cattle activity was 29% greater along burned transects compared to unburned transects. Red brome height, density, and seed production were 11% to 34% greater along burned transects than unburned transects ($P < 0.05$). Red brome height, biomass, density, and seed production were 2- to 10-fold greater next to cowpats compared to random points ($P < 0.05$), likely due to increased soil moisture and inorganic N. Post-fire conditions and cowpats increased soil inorganic N, which was strongly correlated with red brome density, height, biomass and seed production ($R^2 = 0.60-0.85$). Transgenerational legacy effects were evident as seeds from red brome next to cowpats had 27% higher germination than seeds collected from random points. The results suggest that positive responses of red brome to increases in inorganic N related to fire and cattle activity could significantly reinforce fine fuel infill that drives invasive grass-fire cycles in deserts of North America.

Introduction

Humans throughout their history have transported plant and animal species beyond their natural range resulting in exotic species introductions across Earth's continents. The spread of exotic species increased during the agricultural revolution with trade and migration (Hulme 2009). However, it expanded most dramatically following the industrial revolution due to mechanized travel, immigration, and globalization (McNelly 2006, Meyerson et al. 2007). One of the most dramatic and widespread exotic species introductions was cattle (*Bos taurus*), domesticated by humans more than 8500 years ago in western Asia and later distributed globally (Kumar et al. 2016). Cattle arrived in North America with the Spaniards in the early 1500s (Bowling 1942). Today more than 106 million head of cattle, or about 12% of the global total, are distributed across North America, including desert rangelands (Commission for Environmental Cooperation 2015).

More than three centuries after the arrival of cattle in North America, red brome, an annual winter grass from southern Europe, was introduced to western North America, likely during a period of rapid expansion in immigration and commerce in California (Salo 2005). Red brome quickly spread and invaded the Mojave, Great Basin, and Sonoran deserts over subsequent decades (Salo 2005), particularly during cycles of warmer Pacific decadal oscillation regimes that produced abundant winter precipitation (Mantua 2000). Like *Bromus tectorum* L. (cheatgrass), its early establishment during the fall period fuels rapid growth the following spring resulting in soil resource depletion that can negatively impact native plants (Bishop et al., 2020). In addition, following seed drop in late spring, red brome's tissues become

dry, producing landscape fuel conditions that increase the frequency and size of wildfires in deserts of western North America (Brooks and Matchett 2006, Horn and St. Clair 2017).

Animals play a central role in facilitating the spread and establishment of plant invaders through seed dispersal (Hogan and Phillips 2011), soil and vegetation disturbance (Chambers et al. 2016), and nutrient enrichment (Auman et al. 1998). Livestock is known to disperse seeds both through ingestion (endozoochory) (Mouissie et al. 2005) and attachment (epizoochory) (Chuong et al. 2016). In addition, dung from various large mammals contains a variety of exotic plant seeds (Mouissie et al., 2005, Dovrat et al., 2012). Microsite conditions created by dung piles can also alter plant community composition (Auman et al. 1998, Dai 2000). However, much less is known about the role that endozoochory and dung piles play in the productivity of invasive annual grasses that are driving changing fire regimes in deserts of western North America (Eichberg et al. 2007). This is a critical knowledge gap for two reasons: first, livestock grazing is widespread in deserts of North America; and the stress gradient hypothesis (Callway 2007) predicts that dung pats may provide microsite conditions that overcome water and nutrient limitations to the establishment success of invasive annual grasses in deserts (Lopez et al. 2016).

Arid ecosystems are defined by vegetation that is both water and nitrogen limited (Yahdjian et al., 2011, Gill et al., 2018). The distribution and productivity of invasive annual brome grasses in deserts are responsive to soil resource pulses (Belnap et al. 2016, Horn and St. Clair 2017), often resulting in prolific seed production (Horn et al. 2017). Soil moisture and nutrients vary along gradients in desert landscapes, being concentrated beneath native shrubs (islands of fertility) and decreasing in inter-shrub spaces (Schlesinger 1996). This tends to produce high-density grasses beneath shrubs with sparser production between shrubs, limiting the continuity of fine plant fuels that drive desert fires (Lucero et al., 2021). Cattle which are prolific dung producers (Chastain et al. 2004), move and forage between shrubs in desert landscapes (France et al. 2008) and, as a result, leave their droppings in the more resource-limited inter-shrub spaces. Dung piles may influence three potential resources that could, in theory, fuel the spread and growth of invasive annual grasses in inter-shrub spaces, thereby increasing fire potential: seeds, nutrients, and moisture (Dai 2000). While greater resource availability around cattle dung may increase invasibility directly by priming growth and seed production, it can also influence invader fecundity by affecting seed quality in subsequent generation (Luzuriaga et al. 2006). There is some evidence for transgenerational effects in annual brome grasses (Steinger et al. 2000), but the role of plant resource availability in cross generational seed viability of invasive brome grasses is limited.

In the northeast Mojave Desert, widespread cattle grazing, and wildfires overlap with red brome invasion providing an opportunity to test how post-fire conditions and cattle dung deposition affect soil resource availability and its influence on the establishment and fecundity of red brome. We hypothesized that: 1) post-fire environments and cowpats would increase the growth and seed production of red brome via increases in soil moisture and nitrogen, and 2) soil resource enrichment in the vicinity of cowpats and along burn transects would create a transgenerational effect by improving seed quality resulting in greater germination of the F1 generation seeds.

Materials And Methods

This study was conducted in the Beaver Dam Wash in the northeast area of the Mojave Desert in May 2020. The study area is characterized by native shrubs of which *Coleogyne ramosissima* (Torr.), *Larrea tridentata* (DC. Coville), and *Ambrosia dumosa* (A. Gray Payne) are the most common. Two yucca species are common in the study area *Yucca baccata* (Torr.) and *Yucca brevifolia* (Engelm). Common native herbaceous plants included *Sphaeralcea ambigua* (A. Gray), *Baileya multiradiata* (Harv. & A. Gray), *Astragalus nuttallianus* (DC.), *Plantago* spp. (*P. patagonica* and *P. ovata*), and *Descurainia pinnata* (Walter Britton). The soil in the study area is a gravelly sandy loam (Soil Survey Staff 2015). The mean annual precipitation is 272 mm, and the mean annual temperature is 16°C (Western Regional Climate Center 2000). In recent years, plant invasions have altered fire regimes in North American Deserts by increasing fire size and frequency (Brooks et al., 2004, Horn & St Clair, 2017). Invasive annual grasses, *Schismus arabicus* Nees., and *Bromus Rubens* L. responded positively to early fall precipitation in 2004, resulting in the build-up of fine fuels that triggered multiple, large-scale fires in the study area (Beaver Dam Wash) in the summer of 2005 (Horn et al., 2017). Active cattle allotments exist in our study area in the Beaver Dam Wash, and we were able to germinate viable red brome seeds from cowpat samples from our study area indicating that cattle are grazing on red brome.

Study design

A network of six 1 km long paired transect lines were positioned along adjacent burned/unburned boundaries within four independent fires that occurred during the summer of 2005: Westside (June, 27,059 ha), Duzak (July, 7,065 ha – within Utah), Burgess 1 (July, 60 ha), and Burgess 2 (July, 712 ha) (Fig. 1). The fires were ignited by lightning and burn severity was classified as high in each of the four burns (Lybbert et al. 2017). Paired transects were placed 200m on either side of the burn boundary. Transect pairs were placed in the Burgess 1, Burgess 2 and Duzak fires. The remaining three transect pairs were spread across the Westside fire which was 4-fold larger than the Duzak fire and several orders of magnitude larger than the Burgess 1 and 2 fires making up most of the area burned during the 2005 fires. Transect pairs were selected on the above criteria using GIS mapping software to prevent any bias from choosing transects while on location.

Field Measurements

Distance to the nearest cowpat on each side of the transect lines were measured at each 100 m increment point (a total of 10 points/transect) to estimate cowpat densities using point distance methods (Diggle 1975). Red brome establishment was concentrated in distinct rings that extended several centimeters from the edge of the cowpats (Fig. 2). Since cowpats varied dramatically in size and shape using a standard size quadrat would have done a poor job of capturing red brome density concentrated around the edges of different sized cowpats. Estimating cowpat influence on red brome density was therefore estimated by counting all individuals established from the outer ring edge to the center of the cowpat. Accordingly, the area of red brome establishment relative to each cowpat used for density

calculations was estimated by measuring the longest ring edge extent and multiplying it by the ring edge distance at its perpendicular angle using a measuring tape. Based on dozens of measurements at our study site we determine that the average area inside of the red brome rings around cowpats was 0.15 m². A 0.15 m² control quadrat was constructed for measuring red brome density an adjacent location where cowpats were absent. The location of the control quadrat was randomized by throwing it over the shoulder.

To estimate red brome height, we randomly measured 10 red brome individuals collected from each sampling location. We harvested the red brome plants established within the area where density measurement was made using clippers at soil level and placed them in a paper bag. The dried cowpats were removed from the soil surface, and several sub-samples from the top of the cowpat were collected and placed in a paper bag. A soil moisture probe (Spectrum Technologies, Aurora, Illinois) with 7.6 cm length rods were inserted into the soil where the cowpat had been removed to measure moisture content. A sampling probe was used collect two soil samples 7 cm deep, which were pooled and placed in a soil sample bag for analysis of inorganic N. Soil moisture measurements and soil sampling also occurred in the control quadrats for comparison.

Lab Measurements

Red brome plant samples were allowed to air dry at 25°C for 60 days and were weighed for vegetative and seed biomass using a balance. Allometric equations were used to estimate seed counts from seed head biomass (Bishop et al., 2020).

Soil samples were air-dried on-site and then transported to the Brigham Young University Environmental Analytical Laboratory (Provo, UT, USA), dried at 50°C for 72 h, and homogenized. Nitrate and ammonium concentrations (mg NO₃-N per kg and mg NH₄-N per kg) were extracted using two mol/L KCL following the cadmium reduction method (Keeney and Nelson 1982) and the salicylate-sodium nitroprusside method (Rowland 1983). Samples were analyzed using a rapid flow injection analyzer (Quick Chem 8500; Lachat Instruments, Loveland, CO, USA). Inorganic N concentrations were calculated as the sum of NO₃ and NH₄.

Fecundity experiments: seed germination and seedling growth

Red brome seeds were collected from the plants measured and harvested next to cowpat margins or non-cowpat controls. Seeds were homogenized and pooled by treatment group from each transect line. Three set of 25 seeds from each pooled seed sample were placed on moist germination paper discs in three separate petri-dish at 20°C for 14 days to test for the effect of fire and cowpats on germination rates in the F1 generation seed. To test for transgenerational on seedling emergence, nine red brome seeds pooled from each transect were placed in containers (10cm x 10 cm x 10 cm) and filled with soil collected from the study site that had been sieved to remove any seedbank. Containers were placed in outdoor

study plots in Provo, Utah starting March 15, 2022, and were watered to saturation every three days. Seedling emergence from soil was counted ten days after beginning the experiment.

Statistical analysis

Mixed-effects linear models were used to examine the effects of burn status (burned or unburned transect) and cowpat or control on red brome density, height, biomass, and seed production. In our mixed models, transect type (unburned, burned) and cowpat were fixed effects, and transect was specified as a random effect. Tukey's HSD was used to test mean differences across burn conditions and cowpat effects on red brome plants from the field and germination and seedling growth studies. Assumptions of normality and homoscedasticity were visually inspected using residual plots (e.g., histogram, scatterplot, and qqnorm of residuals). To meet equal variance assumptions, data were log-transformed when appropriate. Linear regression models characterized red brome productivity responses to gradients of inorganic N and soil moisture along the transect network. All calculations, models, assumption analyses, and statistical significance determinations were performed using JMP Pro statistical software (version 16).

Results

Fire and cowpat effects

Cowpat density was 29% greater along burned transects (138 per ha \pm 13) compared to unburned transects (98 per Ha \pm 13) ($P = 0.03$). Red brome height, density, and seed production were 11%, 28%, and 34% greater along burned transects than unburned transects, respectively ($P < 0.05$) (Fig. 3). Red brome biomass was not statistically different between burned and unburned transects ($P = 0.71$).

Red brome height (2-fold), biomass (3.2-fold), density (3-fold), and seed production (10-fold) were significantly greater when growing around the margins of cowpats compared to random points lacking cowpats ($P < 0.05$) (Fig. 3). The burn by cowpat interaction term was not statistically significant for red brome height, biomass, or density (Fig. 3). However, red brome seed production showed a significant burn by cowpat interaction term in which the positive effects of cowpat were amplified along burned transects compared to unburned transects ($P = 0.004$) (Fig. 3).

Soil resource gradients

Seed germination trials of dried cowpat samples indicated that, on average, only three red brome seedlings germinated per dried cowpat, suggesting that microsite conditions drove dramatic increases in red brome density around cowpats not endozoochary (Fig. 4). Soil moisture, nitrate, ammonium, and inorganic N concentrations were 1.4-fold, 10.3-fold, 3.5-fold, and 6-fold greater in the soil beneath cowpats compared to random soil points ($P < 0.05$) (Fig. 4). Nitrate, ammonium, and inorganic N concentrations were 2-fold, 1.3-fold, and 1.7-fold greater along burned transects than along unburned transects ($P < 0.05$) with no significant difference for soil moisture (Fig. 4). Inorganic N showed a strong burn by cowpat interaction term in which the positive effects of cowpats were amplified along burned

transects compared to unburned transects ($P = 0.01$) (Fig. 4). The burn by cowpat interaction terms was not significant for soil moisture.

Soil inorganic N showed strong positive linear correlations with red brome density ($R^2 = 0.60$, $P < 0.001$), height ($R^2 = 0.72$, $P < 0.001$), biomass ($R^2 = 0.83$, $P < 0.001$) and seed production ($R^2 = 0.85$, $P < 0.001$) along the transect network (Fig. 5). Soil moisture showed weaker but significant positive correlations with biomass ($R^2 = 0.31$, $P = 0.02$) and seed production ($R^2 = 0.28$, $P = 0.03$) (Fig. 6). Red brome height and density were not significantly correlated with soil moisture.

Transgenerational effects on seed germination

There were no statistically significant differences in the germination, emergence, or seed production of red brome seeds collected from burned or unburned transects. However, seeds collected from red brome growing on the margins of cowpats had 27% greater germination rates than seeds collected from red brome growing at random points ($P = 0.02$) (Fig. 7). A similar trend was seen for seedling emergence, but statistical support was weaker ($P = 0.14$) (Fig. 7). The fire by cowpat interaction terms in the model was not statistically significant for seed germination or seedling emergence.

Discussion

Our results showed that cowpats and burned desert communities contributed to gradients of soil resources that influenced red brome's growth and reproduction patterns (Fig. 3). Livestock dung deposition can disperse seeds (Poschlod and Bonn 1998, Kowarik and Lippe 2008) and creates soil resource microsites that can affect plant community composition (Dai 2000). However, more research is needed to understand better how dung deposition may affect plant invasions. Red brome's growth and seed production are responsive to soil moisture and inorganic N (He et al., 2011, Horn and St. Clair, 2017) that, were significantly elevated under cowpats (Fig. 4). The data supported our first hypothesis that post-fire conditions and cowpats contributed to gradients of inorganic N that were positively correlated with red brome growth and fecundity (Fig. 5). There was also evidence that cowpats (but not post-fire conditions) increased soil moisture (Fig. 4), which also showed positive but weaker correlations with patterns of red brome establishment and growth (Fig. 6). Consistent with our second hypothesis, we observed transgenerational effects in which increased germination occurred in seed collected from red brome growing next to cowpats (Fig. 7).

Fire effects on soils resource gradients and red brome productivity

This study documents two significant fire-related effects. First, the higher density of cowpats along burned transects suggests greater cattle use in burned areas, consistent with another study documenting the increased movement and foraging activity of cattle in post-fire desert environments (Clark et al. 2017). We hypothesize this may be related to greater ease of movement due to reduced shrub cover or

shifts toward more palatable forage species (Lybbert et al. 2017). Second, increased red brome growth and seed production along burned transects (Fig. 3), which was correlated with greater soil N (Fig. 5). Red brome establishment and growth have been shown to increase in post-fire environments (Horn et al. 2017, Bishop et al. 2020), which could be related to various factors. For example, a reduction in native shrub cover following a fire can lead to declines in rodent populations (Horn et al. 2012) that suppress invasive brome grass establishment through granivory and folivory (St. Clair et al. 2016, Bishop et al. 2020). A surprising finding in this study was the long-term persistence of elevated inorganic N along burned transects (Fig. 4). Esque et al. (2010) documented short-term inorganic N pulses immediately following desert wildfires, but our data shows 1.7-fold greater inorganic N concentrations along burned transects fifteen years after the fire (Fig. 4). This may be partially due to N inputs from the fire itself or competition release of soil resources related to fire-related losses of native shrubs or a combination of the two (Horn et al., 2015, Molinari et al., 2019). These results suggest that red brome is perpetuated through post-fire enrichment of inorganic N, which may have important implications for increasing fine fuel continuity that drives invasive grass fire cycles in desert ecosystems.

Cowpat effects on soil resource gradients and red brome productivity

Previous research has shown the dispersal of exotic species through cattle dung (Mouissie et al. 2005) and the response of a few plant species to cowpats (Auman et al. 1998). This is the first study we are aware of documenting cowpat impacts on a dominant invasive brome grass that is changing the ecology and fire regimes in deserts of North America where cattle grazing is common. The prolific growth and seed production of red brome growing around cowpats in this study (Figs. 2 and 3) appear to be driven by increases in soil moisture and particularly inorganic N enrichment (Figs. 5 and 6). Pulses of soil moisture stimulate red brome production in the Mojave Desert sometimes dramatically (Gill et al., 2018, Horn et al., 2017). However, red brome productivity was most strongly correlated with inorganic N gradients (Fig. 5). Elevated soil moisture and inorganic N (as found under the cowpats) can produce synergistic increases in red brome growth (Rao and Allen 2010) consistent with our results (Fig. 4).

High labile C availability in cattle dung promotes microbial decomposition that primes high N mineralization rates (Wang et al., 2018). Evidence for N limitation of red brome growth in desert soil is mechanistically supported by N fertilization studies (Brooks 2003, Rao and Allen 2010). However, this is the first study we are aware of showing strong correlations of annual brome grass distribution and productivity in response to landscape-scale gradients in inorganic N. Furthermore, the data suggest that fire legacy and cattle via dung deposition significantly contributed to spatial variability in N gradients across the study landscape that appears to influence patterns of red brome growth and reproduction. A critical question left unanswered by this study is: 1) how long does the influence of cowpats on red brome persist across time? We observed partially and fully decomposed cowpats that still appeared to be stimulating red brome growth (Fig. 2), likely through inorganic N enrichment but more research is needed to address this question.

Transgenerational effects

Two factors that influence invasion success are the quantity and quality of seeds produced (Chambers et al. 2016). Due to early germination and rapid growth rates, annual brome grasses vigorously compete for soil resources (Salo et al. 2005), which are utilized for prolific seed production (Rao and Allen, 2010). However, a potential tradeoff between the quantity and quality of seeds produced likely varies depending on the resource environment of the parent plant. Our results show that the micro-environment created by cowpats simultaneously increased seed production and seed viability (Figs. 3 and 7) likely due to increased soil moisture and N availability (Larigauderie et al. 1988). This suggests that soil resource hotspots may amplify *Bromus* fecundity by stimulating the production of high numbers of high-quality seeds. This is the first study we are aware of documenting transgenerational increases in seed viability of invasive brome grasses in response to gradients of soil resource availability.

Conclusions

Our results suggest that cattle and fire, steepen soil resource gradients that contribute to invasive grass-fire cycles in the Mojave Desert. In the case of cattle, their dung creates soil resource hotspots in resource-limited shrub interspaces that fuels prolific seed production and enhanced seed viability (Figs. 3 and 7). The building of red brome's viable seed bank in the inter-shrub space due to prolific seed production in response to cowpats likely contributes to fine fuel continuity in inter-shrub spaces, particularly in wetter years that spread large-scale wildfires in the Mojave Desert (Brooks et al. 2004, Horn and St. Clair, 2017). These wildfires facilitated by red brome (Horn and St. Clair 2017) appear to create a legacy effect of elevated inorganic N pools in post-fire environments that correlate with red brome's increased growth and reproduction success (Figs. 4 and 5). These results suggest that red brome may create a positive fire feedback loop mediated by sustained increases in inorganic N that reinforces its growth.

While this study was conducted in the Mojave Desert, similar issues also likely exist in the other deserts of western North America, where invasive annual brome grasses also overlap with cattle grazing (Esque and Schwalbe 2002, Chambers et al. 2016). Additional studies are needed to explicitly determine the spatio-temporal dynamics of post-fire environments and cowpats on annual brome invasions in deserts of western North America.

Declarations

Author contributions statement:

EAS performed the research, analyzed the data, and co-wrote the article. SBS, SIS, BES, SJL helped perform the research and edit the paper. GES and DAS performed the research and compiled the data. SBS designed the study, analyzed the data, and co-wrote the article.

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Data Availability Statement

Data will be made available at Dryad Repository upon publication.

Conflict of interest: The authors declares that they have no conflict of interest.

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Figures

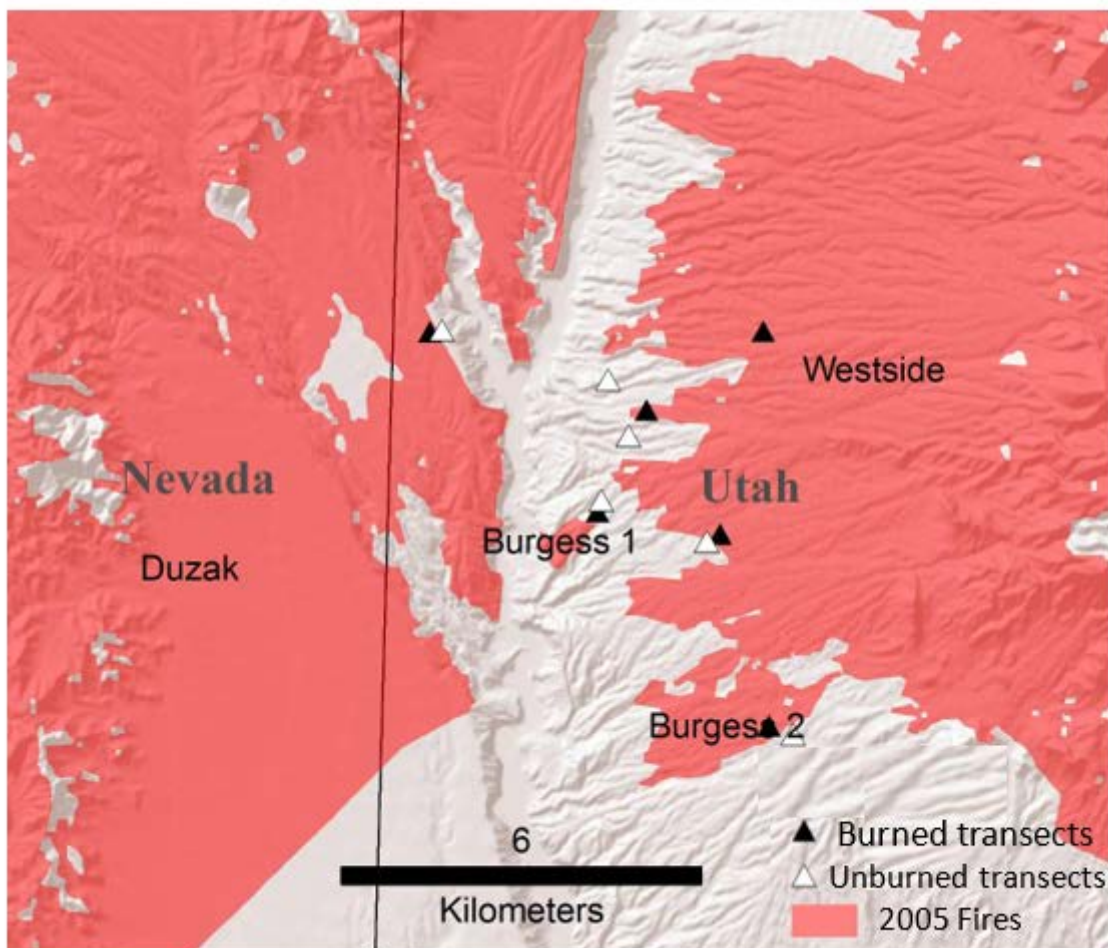


Figure 1

Map of the transect network in the study area in the Mojave Desert along the Utah-Nevada border 80-kilometers northeast of Las Vegas Nevada. The six 1-kilometer paired transect were arranged along the burn boundaries of the Duzak, Westside, Burgess 1 and Burgess 2 fires that burned in the summer of 2005.



Figure 2

Photos of prolific red brome growth and seed production around the edges of a cowpat (top) and recently decomposed cowpat (bottom) along our transect lines.

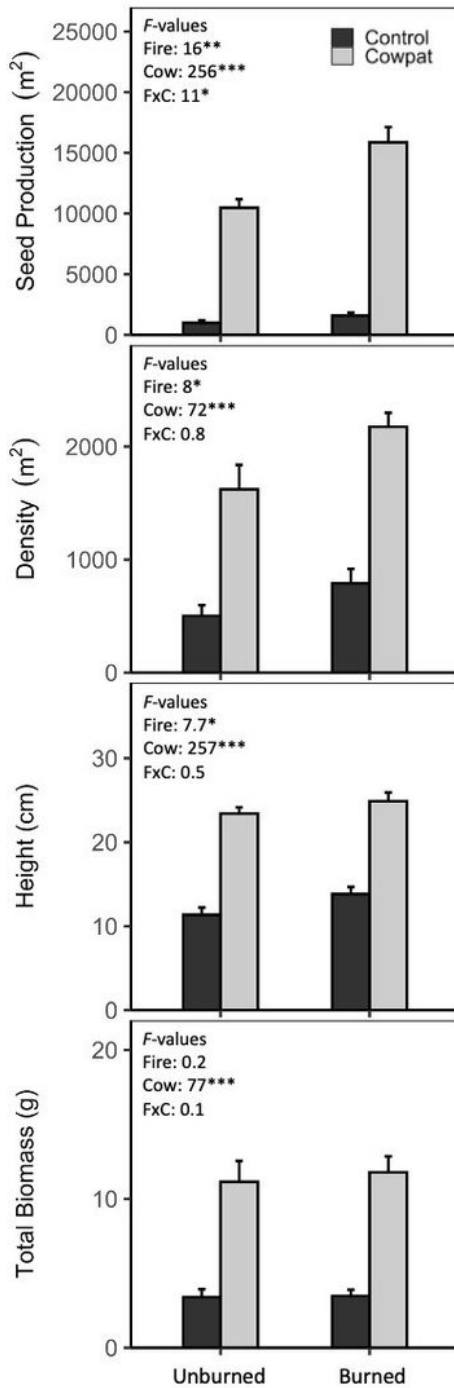


Figure 3

The influence of burned and unburned transects and cowpats on the growth, density, and seed production of red brome. F-values presented with asterisks indicating level of significance for P-values: *P ≤ 0.05, **P ≤ 0.001, ***P ≤ 0.0001. Mean values presented with ± 1 SE.

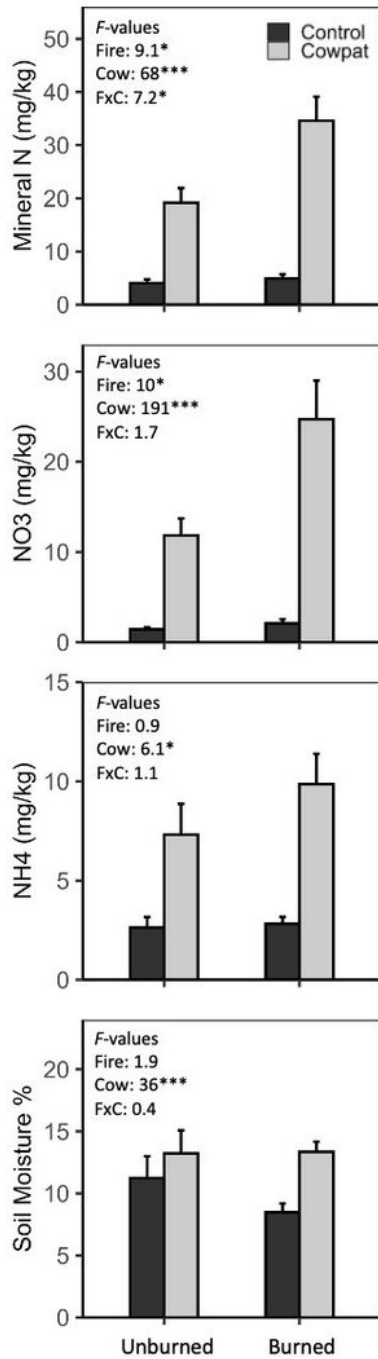


Figure 4

The influence of burned and unburned transects and cowpats on inorganic N availability and soil moisture. F-values presented with asterisks indicating level of significance for P-values: *P ≤ 0.05, **P ≤ 0.001, ***P ≤ 0.0001. Mean values presented with ± 1 SE.

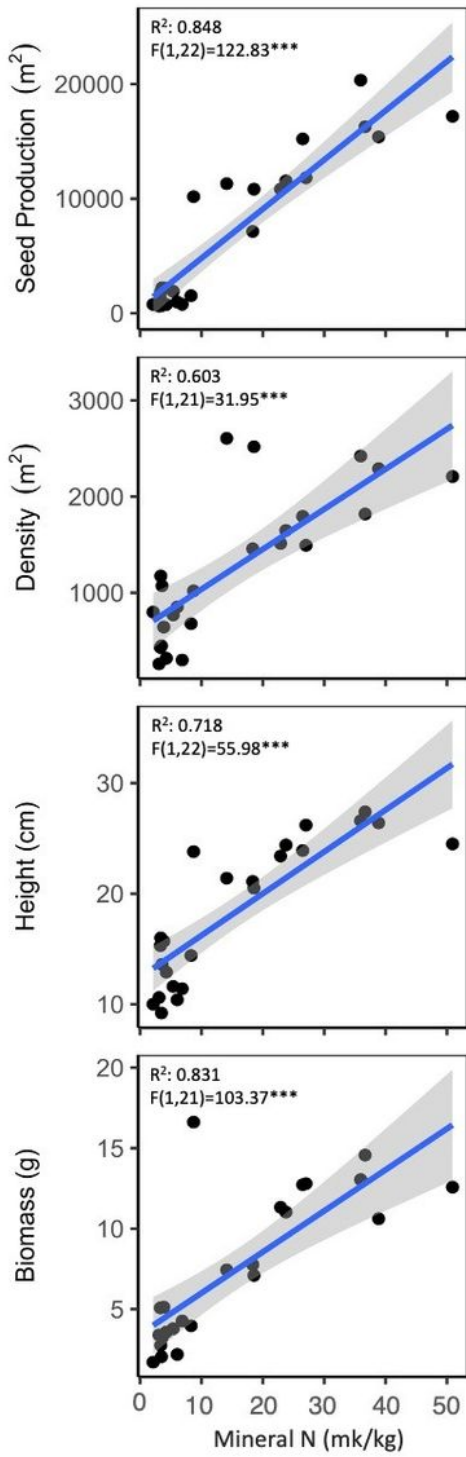


Figure 5

Regression plots quantifying the relationships of inorganic N and red brome productivity along the study transect network.

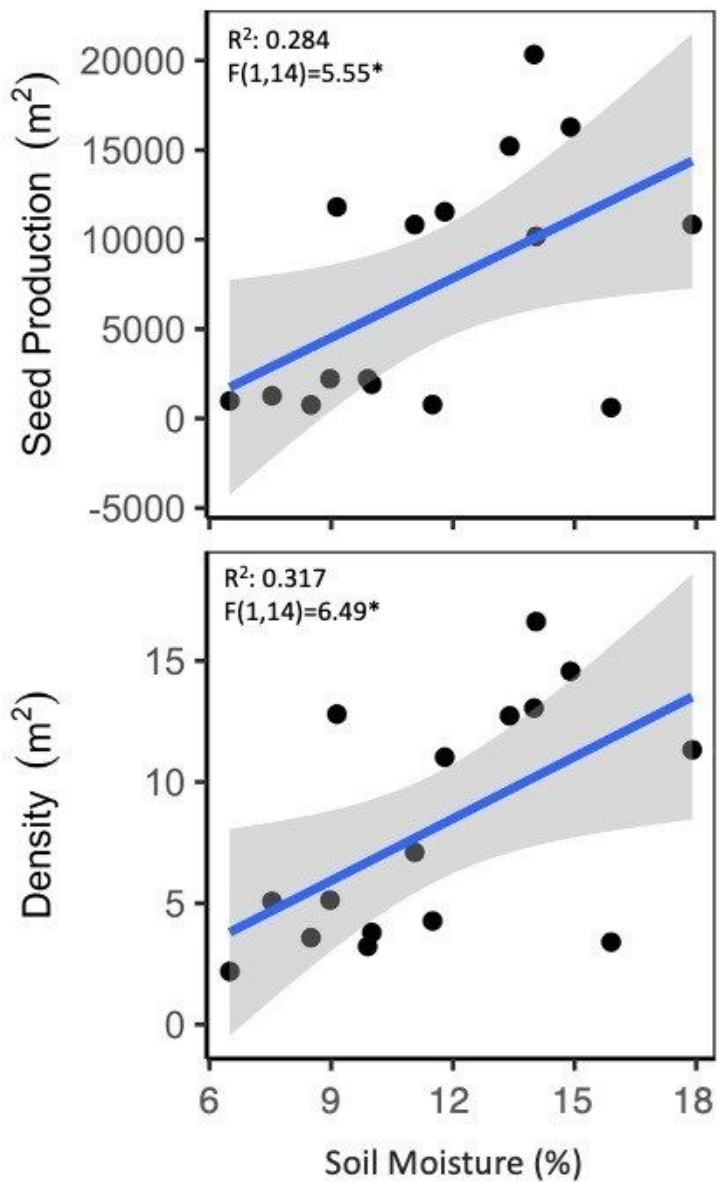


Figure 6

Regression plots quantifying the relationships of soil moisture and red brome productivity along the study transect network.

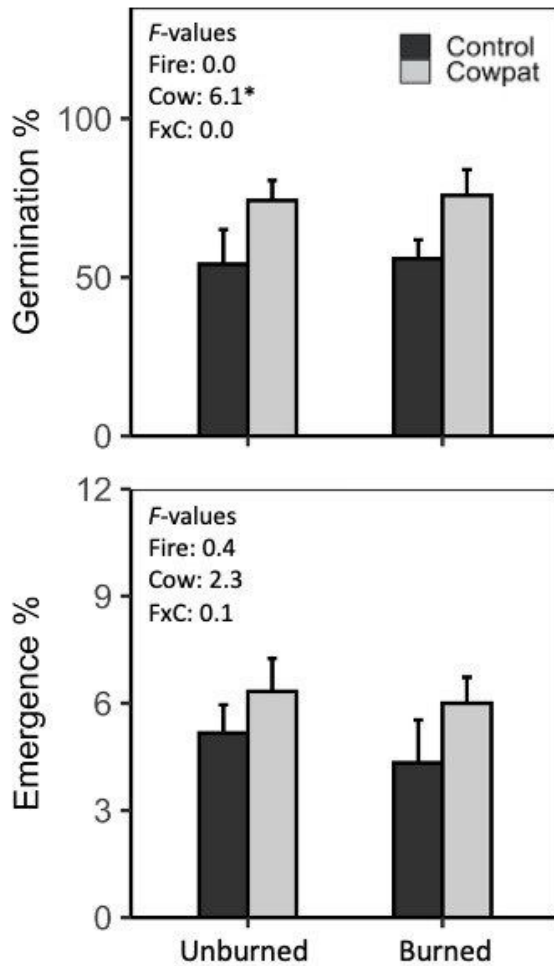


Figure 7

The influence of burned and unburned transects and cowpats on the germination and seedling emergence from red brome seed collected along the study transect network. F-values presented with asterisks indicating level of significance for P-values: * $P \leq 0.05$, ** $P \leq 0.001$, *** $P \leq 0.0001$. Mean values presented with ± 1 SE.