Prescribed Fire, Soil, and Plants: Burn Effects and Interactions in the Central Great Basin

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Abstract

Pinyon and juniper expansion into sagebrush ecosystems results in decreased cover and biomass of perennial grasses and forbs. We examine the effectiveness of spring prescribed fire on restoration of sagebrush ecosystems by documenting burn effects on soil nutrients, herbaceous aboveground biomass, and tissue nutrient concentrations. This study was conducted in a central Nevada woodland and included control and burn treatment plots sampled before and after a prescribed fire. Six native understory plant species (*Crepis acuminata*, *Eriogonum umbellatum*, *Eriogonum elatum*, *Poa secunda secunda*, *Festuca idahoensis*, and *Lupinus argenteus*) important for native sagebrush obligate foragers were chosen to represent the understory plant community. *L. argenteus* is also important for system nutrient cycling and nitrogen fixation. Plants were collected from three microsites (under tree canopy, under shrub canopy, and interspace) common in transitional woodlands during peak growth the summer before a spring prescribed burn and each of two summers following the burn. Soils were collected from corresponding locations at two depth intervals (0–8 and 8–52 cm) to determine the relationships between soil and plant nutrients following fire. Microsite affected soil nutrients but did not influence plant tissue concentrations with the exception of *F. idahoensis*. Burning resulted in increases in soil surface NH_4^+, NO_3^-, inorganic N, Ca^{2+}, Mn^{2+}, and Zn^{2+}. Increases in NO_3^-, inorganic N, and Zn^{2+} were also observed in deeper horizons. Burning did not affect aboveground plant biomass or nutrient concentrations in the first year with the exception of *F. idahoensis*, which had increased tissue P. By the second year, all species had statistically significant responses to burning. The most common response was for increased aboveground plant weight and tissue N concentrations. Plant response to burning appeared to be related to the burn treatment and the soil variables surface K^+, NO_3^-, and inorganic N.

Resumen

La expansión de Pinyon y enebro en los ecosistemas de artemisa resultan en la disminución de cobertura y biomasa de gramíneas perennes y especies herbáceas. Hemos examinamos la efectividad del fuego prescrito en la primavera para la restauración de los ecosistemas de artemisa mediante la documentación'de los efectos de la quema sobre los nutrientes del suelo, la biomasa'herbácea aérea, y las concentraciones de nutrientes en el tejido. Este estudio fue realizado en un bosque central de Nevada. Se muestrearon parcelas tratadas y de control antes y después de los fuegos prescritos. Seis especies de plantas nativas (*Crepis acuminados*, *Eriogonum umbellatum*, *Eriogonum elatum*, *Poa secunda secunda*, *Festuca idahoensis*, y *Lupinus argenteus*), importantes para especies forrajeras obligadas, fueron escogidas para representar a la comunidad de plantas del sotobosque. *L. argenteus* es también una especie importante para el ciclo nutritivo del sistema y la fijación de nitrógeno. Las plantas se recolectaron de tres micrositios (bajo la cubierta arbórea, bajo el dosel arbustivo, y el espacio intermedio) comunes en bosques de transición durante el crecimiento máximo de verano antes de una quema prescrita de primavera y cada uno de los dos veranos después de la quema. Los suelos fueron recolectados'de los mismos sitios con'dos intervalos'de profundidad (0–8 y 8–52 cm) para determinar las relaciones entre el suelo y los nutrientes de las plantas subsiguientes a la quema. El micrositio afectó los nutrientes del suelo, pero no influyo en las concentraciones en el tejido de la planta, con excepción de *F. idahoensis*. La quema resultó en un incremento de NH_4^+, NO_3^-, N inorgánico, Ca^{2+}, Mn^{2+}, y Zn^{2+} en la superficies del suelo. Los aumentos de NO_3^-, N inorgánicos, y Zn^{2+} fueron también observados en los horizontes más profundos. La quema no afectó la biomasa de la planta sobre la superficie o las concentraciones de nutrientes en el primer año, con excepción de *F. idahoensis* que había aumentado el P en el tejido. Para el segundo año, todas las especies tenían'respuestas estadísticamente significativas a la quema. La respuesta más común fue el aumento de peso aéreo de la planta y las concentraciones de N en el tejido. La respuesta de la planta a la quema parece estar relacionada al tratamiento de la quema y a las variables de la superficie en suelo de K^+, NO_3^-, y N inorgánico.

Key Words: plant nutrition, prescribed fire, soil nutrients, woodland encroachment

INTRODUCTION

Much of the Great Basin is currently dominated by sagebrush ecosystems. At intermediate elevations, sagebrush ecosystems are increasingly influenced by encroachment of pinyon and juniper trees (Miller and Tausch 2001). Although pinyon-juniper woodlands have expanded and receded several times

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over the past 5 000 yr, the current rate of expansion is unprecedented. Less than 10% of current woodlands are older than 140 yr (Miller and Tausch 2001). The recent rapid expansion of pinyon pine (*Pinus monophylla* Torr. & Frém.) and juniper (*Juniperus osteosperma* Torr.) is due to a combination of warming after the little ice age, fire suppression, and overgrazing by livestock (Miller and Wigand 1994; Gruell 1999; Miller and Rose 1999). As pinyon and juniper stands mature, competition for available resources increases, most understory vegetation is eliminated, and the landscape becomes more susceptible to catastrophic wildfire due to increases in woody fuel loads (Reiner 2004).

Prescribed fire has been suggested as a mechanism for slowing pinyon and juniper expansion, preventing catastrophic wildfire, and restoring understory vegetation quantity and quality. This benefits native animal species dependent on sagebrush ecosystems (Connelly et al. 2004). Little information currently exists about fire's effect on understory vegetation or about plant–soil interactions following fire, especially in semiarid regions. Burning in semiarid environments can result in increased available nutrients and reduce competition for resources from woody species (Sturgis 1993). Burning has been shown to increase available soil N, P, Ca, Mg, Mn, and Zn in semiarid systems (Covington and DeBano 1988; DeBano and Klopatek 1988; Blank et al. 1994a, 1996). However, the overall effects of burning on soil resources may differ as tree expansion and stand maturation progress. Soil responses to burning differ among undershrub, undertree, and interspace cover types in pinyon woodlands because of the effects of islands of fertility and differences in both fine and woody fuels among cover types.

Burning increases nutrient content of understory vegetation (Sturgis 1993; Blank et al. 1994b; Cook et al. 1994), but the mechanisms are not greatly explored. Previous studies of understory vegetation response to prescribe fire in arid regions show that results depend on burn severity and climatic conditions following fire. Cook et al. (1994) found that production of perennial herbs was two times greater on burned than control sites following both prescribed and wildfire in sagebrush communities. They also concluded that perennial herb crude protein levels were higher through late summer for 2 yr following fire (Cook et al. 1994). Blank et al. (1994b) found that native and exotic shrubs and grasses had more aboveground biomass and higher concentrations of N, P, and SiO_2 when grown on previously burned soils. All species sampled in Spanish Mediterranean shrubland were found to have higher concentrations of mineral nutrients immediately after fire but to experience steady declines over time (Carreira and Niell 1992). Following burning on a central Florida sand dune, three of four herb species exhibited increased vegetative growth and flowering and tissue concentrations of N and P (Anderson and Menges 1997). Four months after burning in Australian subtropical semiarid grassland, concentrations of N and P were higher in aboveground plant material, but total aboveground biomass did not increase because of drier-than-normal conditions (Bennett et al. 2002).

Numerous studies in agronomy have described direct plant–soil relationships to fertilizer treatments. However, few studies examine wildland soils and their quantitative relationship to plant nutrition (Hayati and Proctor 1990).

In this study, we examined the soil chemistry and aboveground biomass and nutrient concentrations of understory grasses and forbs following a spring prescribed burn in a central Great Basin pinyon-juniper woodland. Because of the importance of islands of fertility, climatic conditions, and time since fire, we examined both spatial (cover type) and temporal (before and each of 2 yr following burning) effects. We chose control and burn treatment sites containing a mixture of tree, shrub, and interspace cover types typical of expanding woodlands and sampled soils and herbaceous vegetation on both sites and all cover types before and after the prescribed burn. We hypothesized 1) that cover type influences soil nutritional characteristics and that understory vegetation chemistry should reflect these differences; 2) that burning should have an interaction with the island-of-fertility effect and understory vegetation chemistry in heterogeneous landscapes; and 3) that soil nutritional quality will have direct measurable relationships with plant chemistry.

MATERIALS AND METHODS

Study Area

The study is a Joint Fire Sciences Program demonstration area in the Shoshone Mountain Range on the Humboldt-Toiyabe National Forest (Austin Ranger District) in Nye and Lander counties, Nevada. Underdown Canyon (lat 39°15′11″N, long 117°35′83″W) is oriented east to west and contains infrequent springs and an ephemeral stream near the top of the drainage. Average annual precipitation ranges from 23 cm at the bottom to 50 cm at the top of the drainage and arrives mostly as winter snow and spring rains. Average annual temperature recorded in Austin, Nevada, ranges from −7.2°C in January to 29.4°C in July. Lithology of the Shoshone range consists of welded and nonwelded silica ash flow tuff. Soils developed on alluvial fans in this study are classified as coarse loamy, mixed, frigid, typic Haploxerolls (Rau et al. 2005). The soils are extremely coarse grained and have weak to moderate structure.

The vegetation is characterized by sagebrush (*Artemisia tridentata vaseyana* [Rydb.] Boivin) and single leaf pinyon (*Pinus monophylla*) with lesser cover of Utah juniper (*Juniperus osteosperma*). Herbaceous species include the grasses *Poa secunda secunda* J. Presl, *Elymus elymoides* Swezey, *Stipa comata* Trin. & Rupr., *Festuca idahoensis* Elmer, and *Pseudoroegneria spicata* (Pursh) A. Löve and the forbs *Eriogonum umbellatum* Torr., *Eriogonum ovalifolium* Nutt., *Eriogonum elatum* Dougl. ex Benth., *Eriogonum heracleoides* Nutt., *Crepis acuminata* Nutt., *Phlox longifolia* Nutt., *Agoseris glauca* (Pursh) Raf., *Lupinus argenteus* Pursh, and *Penstemon* species. *Bromus tectorum*, an invasive annual grass, is not a large component of the study area. The vegetation occurs in patches of variable tree dominance typical of intermediate-age-class woodlands in the central Great Basin. Tree dominance ranges from low (12% cover, 2 152 kg · ha^{-1}) to high (74% cover, 14 213 kg · ha^{-1}; Reiner 2004).

Yearly average precipitation measured over the 3-yr study period (2001–2003) in a standing rain gauge ranged from 27 to 34 cm during the water year. Precipitation was similar among years with most precipitation arriving between 15 October and 15 April. Little rain (1–5 cm) fell during the active growing season (15 April–16 July).

Study Design and Data Collection

The study was a split-plot design with repeated measures. Study sites (≈ 4 ha $\cdot$ site^{-1}) were located on northeast-facing alluvial fans at elevations of 2 195 and 2 225 m. The two sites were located on adjacent alluvial fans approximately 500 m apart. The control was located at 2 195 m. The burned site was located at 2 225 m and was burned by US Department of Agriculture Forest Service fire personnel on 11–14 May 2002 under favorable weather conditions (air temp $< 32^{\circ}$C, relative humidity $> 15\%$, wind speed < 9 m $\cdot$ s^{-1}, and gravimetric fuel moisture $\approx 40\%$). Because soil and fuel moisture were relatively high during the time of burning, the vegetation and duff were consumed in patches creating a landscape of burned and unburned islands. Four subplots (0.1 ha $\cdot$ plot^{-1}) were sampled on both the control and the burn study sites. Plots were characterized by intermediate tree cover (38% cover, 6 722 kg $\cdot$ ha^{-1}) and contained a mix of trees, shrubs, and interspaces. This tree cover represents the transition phase from shrub-dominated systems to tree-dominated systems and may represent a threshold for understory vegetation recovery following fire (Tausch and West 1995). Subsampled plots were further split by microsite (undertree, undershrub, and interspace).

Soil samples were collected from all sites, plots and microsites at four depths (0–8, 8–23, 23–38, and 38–52 cm) using a 10-cm bucket auger and represent the A_1 horizon and subsequent 15-cm increments. Samples were collected during early November 2001, 2002, and 2003. All soil was brought back to the lab, air-dried, and sieved to 2 mm. Subsamples were analyzed for DTPA (0.005 M) extractable metals, KCl (2.0 M) extractable NH_4^+ and NO_3^-, $NaHCO_3$ (0.5 M) ortho-P, and NH_4OAc (1 N) extractable metals (Lindsay and Norwell 1978; Keeney and Nelson 1982; Olsen and Sommers 1982; Thomas 1982). Extractable metals were determined using atomic absorption and atomic emission spectrophotometry. Extractable NH_4^+ and NO_3^- were determined using flow injection, the sum of NH_4^+ and NO_3^- nitrogen is considered inorganic N, and ortho-P was determined using molybedenate-blue chemistry. Data were then transformed into kg $\cdot$ ha^{-1} by using the formula:

$$\text{kg} \cdot \text{ha}^{-1} = (\text{d})(\text{Db})[1 - (>2\text{mm}\%)](\text{Conc})(F)$$

where d = depth (cm) of the soil horizon, Db = bulk density (g $\cdot$ cm^{-3}) of that horizon, >2 mm% is the volume percentage coarse fragment of that horizon, Conc = nutrient concentration (μg $\cdot$ g^{-1}), and F = conversion factor (0.1 cm^2 $\cdot$ μg^{-1}).

Five understory plant species were chosen for sampling because of their value as forage to native animals: *Eriogonum umbellatum*, *Eriogonum elatum*, *C. acuminata*, *F. idahoensis*, and *Poa secunda secunda* (Barnett and Crawford 1994; Drut et al. 1994; Fischer et al. 1996). A sixth species was chosen for its importance to ecosystem nutrient cycling and N fixation, *L. argenteus* (Hainds et al. 1999; Hendricks and Boring 1999). Plant sampling was conducted at similar phenology (peak biomass with flowers or seed heads) in June 2001, 2002, and 2003 to determine temporal, spatial, and burn treatment differences in understory plant biomass and nutrient concentration. Two adult plants of each species were collected adjacent to soil sampling locations at each of the three microsites. Although the six plant species considered in this study are common in the area, they are not abundant; therefore, the plants collected were those closest to soil sample locations or were the only available individuals within the subplots. Shears were used to remove all aboveground biomass. *Eriogonum umbellatum* and *Eriogonum elatum* did not occur under trees and were sampled only in interspace and undershrub microsites.

Plants were returned to the lab and dried at 60°C for 48 h and then weighed. Dried plant samples were ground in an Udi^{TM} mill. All samples were placed in a desiccator for 72 h prior to analyses. Approximately 0.5 g of dry plant material was placed into a crucible, ashed in a muffle furnace for 4 h at 500°C, solubilized with 20 mL of 1.0 N HCl solution, and diluted with deionized water in a 100-ml volumetric flask (Miller 1998). Extractable metals were determined using atomic absorption and atomic emission spectrophotometry (Miller 1998). Solution P was determined using vanomolybdenate-blue chemistry (Miller 1998). Plant total N was determined using a standard Kjeldahl digest and flow injection chemistry (Horneck and Miller 1998).

Statistical Analyses

The Kolmogorov–Smirnov test was used to test for data normality. All data were natural log transformed to meet the assumption that the data were normally distributed.

Data were evaluated using SAS^{TM} mixed-effects models with repeated measures. Overall differences in available soil nutrients between control and treatment sites, microsites, depths, and years were evaluated with treatment as a main effect, microsite as a split plot within treatment, depth as a split-split plot within treatment and microsite, and year as a split-split-split plot within treatment, microsite, and depth (Appendix A). Because most treatment effects occurred within the top 8 cm of soil and "depth" was a significant factor in the overall analysis of variance (ANOVA) for each soil nutrient evaluated, we split the soil profile into two depth increments for further analyses (0–8 and 8–52 cm). For the soil profile, kg $\cdot$ ha^{-1} was calculated as the sum of the three depths 8–23, 23–38, and 38–52 cm. Treatment effects were evaluated at each depth by considering year and treatment as main effects. Means comparisons were made with Duncan's test ($P < 0.05$) after confirming significant main effects and interactions with the mixed models ($P < 0.05$).

Overall differences in plant nutrients and weights between control and treatment sites, microsites, species, and years were evaluated by considering treatment as a main effect, microsite as a split plot within treatment, species as a split-split plot within treatment and microsite, and year as a split-split-split plot within treatment, microsite, and species (Appendix B). Because "species" was a significant factor in the overall ANOVA for all measured plant variables, treatment effects were assessed at the species level by considering year and treatment as main effects. Means comparisons were made with Duncan's test ($P < 0.05$) after confirming significant main effects and interactions with the mixed models ($P < 0.05$).

Relationships between soil and plant nutrients among all species were explored using SAS^{TM} canonical correspondence procedures (Ter Braak 1986). Soil surface and soil profile

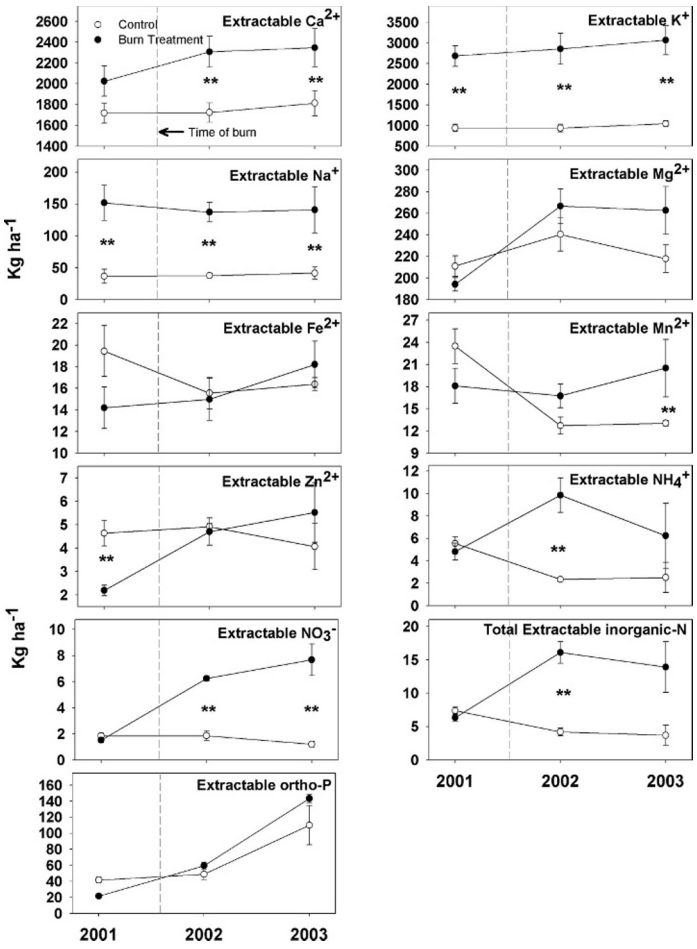

Figure 1. Mean extractable soil nutrient contents ($kg \cdot ha^{-1}$) and standard errors in 2001, 2002, and 2003 for the soil surface (0–8 cm) at the control (2 195 m) and burned (2 225 m) sites. Asterisks indicate differences between sites.

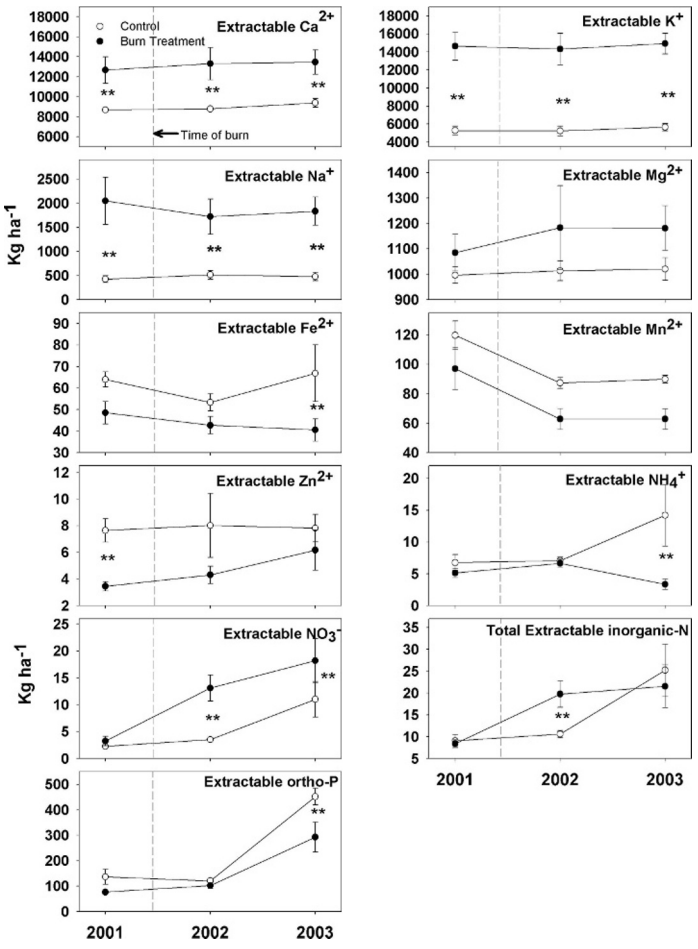

Figure 2. Mean extractable soil nutrient contents ($kg \cdot ha^{-1}$) and standard errors in 2001, 2002, and 2003 for the soil profile (8–52 cm) at the control (2 195 m) and burned (2 225 m) sites. Asterisks indicate differences between sites.

variables were used as predictors for the plant variables. All vegetation collected from the control site as well as vegetation collected from the burn site before the burn occurred was designated "unburned." Vegetation collected from the burn site after the prescribed burn was designated "burned." Because it is difficult to separate the effect of woody vegetation removal and fire-induced soil changes on understory plant characteristics, we created a binary variable named "treatment." This binary variable was used as a predictor to take into account all attributes related to burning not measured in this study. Unmeasured variables that may fall into this category include soil water content, competition for mineral nutrients, shading from overstory vegetation, soil temperature, and removal or production of organic compounds that inhibit or promote vegetation or microbial communities (Sturges 1993; Neary et al. 1999; Certini 2005).

RESULTS

Spatial, Temporal, and Burning Effects on Soils

Near-soil-surface K^+ and Na^+ contents were higher on the burn site before and after burning ($P < 0.05$; Fig. 1). Surface Zn^{2+} was higher on the control site but only before the burn ($P < 0.05$; Fig. 1). All other nutrients were similar on both sites before the burn (Fig. 1). Burning increased near-surface NH_4^+, NO_3^-, total inorganic N, and Ca^{2+} ($P < 0.05$; Fig. 1). Burning also appears to have influenced levels of extractable surface soil Mn^{2+} and Zn^{2+}. Prior to the burn, extractable Zn^{2+} was greater on the control site when compared to the burn site. However, following the burn (2002 and 2003), extractable Zn^{2+} on the burn site was similar to the control site, possibly indicating that burning increased extractable Zn^{2+} ($P < 0.05$; Fig. 1). A similar trend is evident for extractable Mn^{2+}. Extractable Mn^{2+} was similar on control and burn plots before burning and in the first year postburn (2002). However, by 2003, extractable Mn^{2+} was higher on the burned site compared to the control ($P < 0.05$; Fig. 1). The nutrients Mn^{2+}, Zn^{2+}, Mg^{2+}, Na^+, and ortho-P differed by microsite, and contents were typically greater under trees and shrubs than in interspace microsites ($P < 0.05$; Rau et al. 2007).

Trends for soil profile nutrients were almost identical to near-surface nutrients before treatment, and Ca^{2+}, K^+, and Na^+ contents were higher on the burn site before and after burning (Fig. 2). Before the burn, Zn^{2+} was higher on the control site ($P < 0.05$). All other nutrients were similar on both sites before

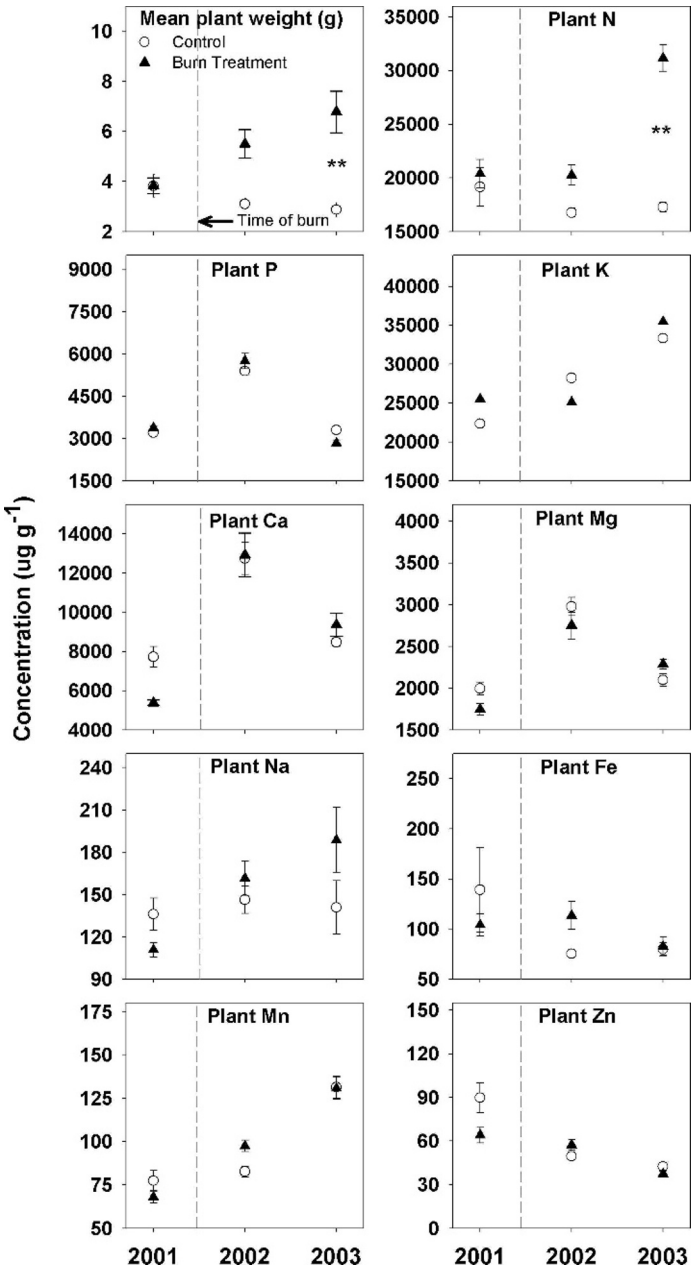

Figure 3. Mean aboveground plant weight (g), tissue nutrient concentrations ($\mu g \cdot g^{-1}$), and standard errors for *Crepis acuminata* in 2001, 2002, and 2003 on the control (2 195 m) and burned (2 225 m) sites. Asterisks indicate differences between sites.

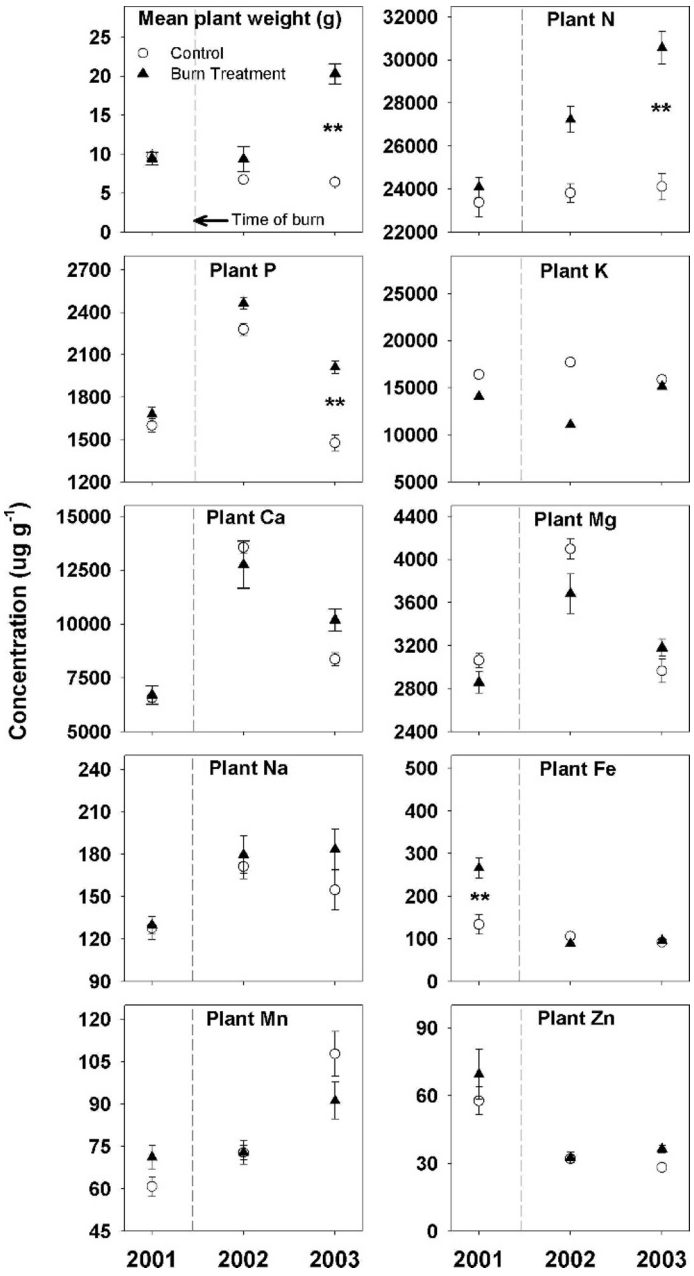

Figure 4. Mean aboveground plant weight (g), tissue nutrient concentrations ($\mu g \cdot g^{-1}$), and standard errors for *Lupinus argenteus* in 2001, 2002, and 2003 on the control (2 195 m) and burned (2 225 m) sites. Asterisks indicate differences between sites.

the burn (Fig. 2). Burning had fewer effects on the soil profile than it did on near-surface soils with increases observed only for NO_3^- and total inorganic N ($P < 0.05$; Fig. 2). The same trend identified for extractable surface Zn^{2+} is also identified for Zn^{2+} in the rest of the profile. Prior to the burn, extractable Zn^{2+} was greater on the control site when compared to the burn site. However, following the burn, extractable Zn^{2+} on the burn site was similar to the control site, possibly indicating that burning increased extracable Zn^{2+} ($P < 0.05$; Fig. 2). Soil profile nutrients that differed by microsite included Mn^{2+}, Fe^{2+}, Zn^{2+}, Ca^{2+}, Mg^{2+}, K^+, NH_4^+, and total inorganic N ($P < 0.05$). Again, nutrient contents were typically greater under trees and shrubs than in interspace microsites (Rau et al. 2007).

Spatial, Temporal, and Burning Effects on Plants

The analyses by individual species indicated that plants were similar on control and treatment sites before the burn and that burning had significant effects on all plant species. Burning increased plant weight and tissue N concentration in the forb *C. acuminata* by the second year following fire (Fig. 3). The forb, *L. argenteus* had increased plant weight, tissue N, and P by the second year after burning. Also, *L. argenteus* Fe

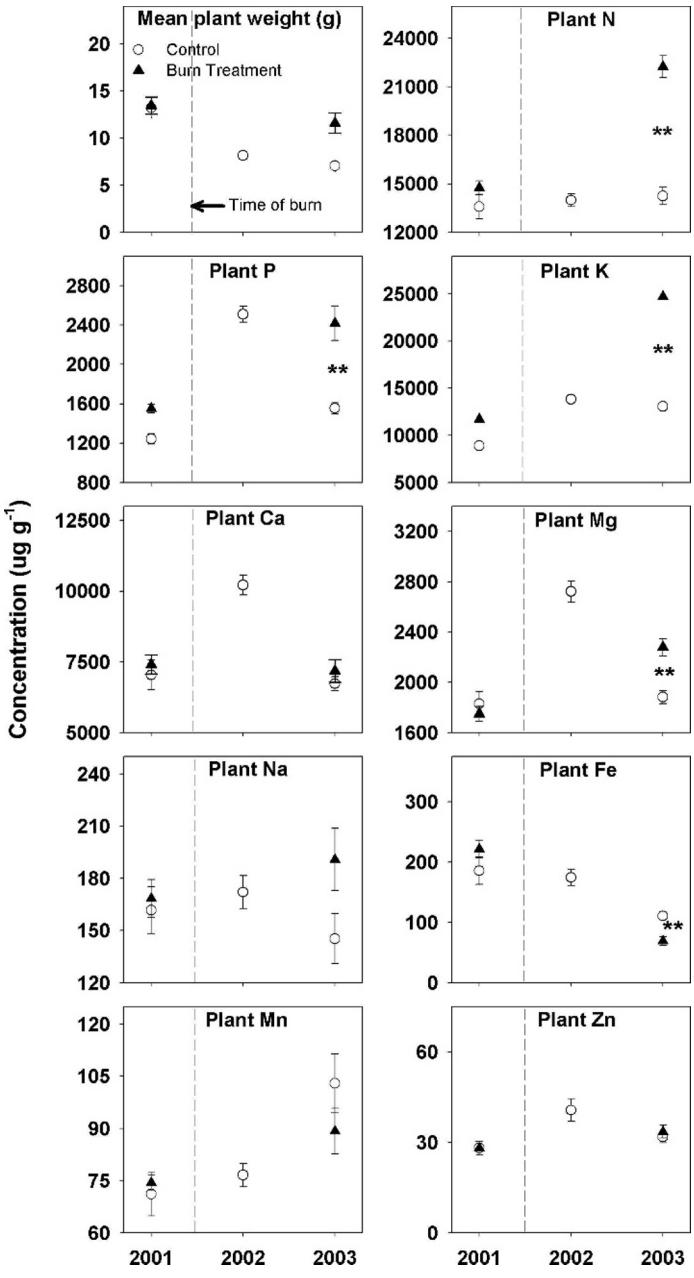

Figure 5. Mean aboveground plant weight (g), tissue nutrient concentrations ($\mu g \cdot g^{-1}$), and standard errors for *Eriogonum umbellatum* in 2001, 2002, and 2003 on the control (2 195 m) and burned (2 225 m) sites. Asterisks indicate differences between sites.

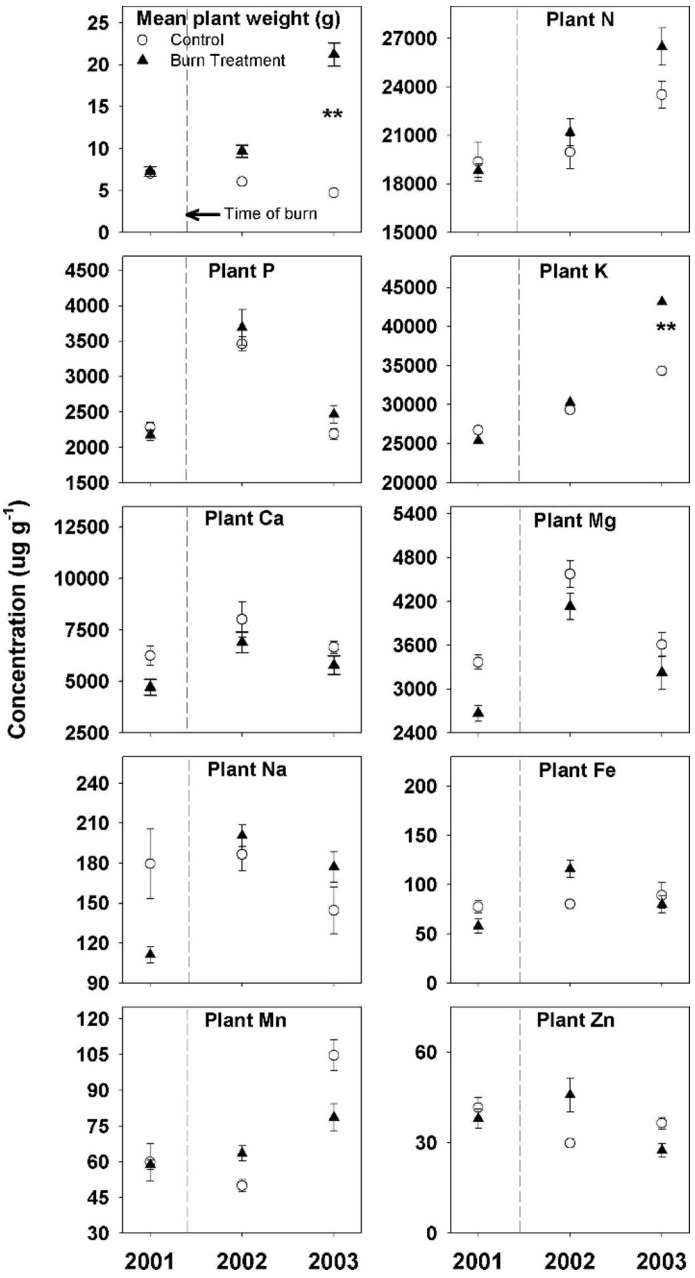

Figure 6. Mean aboveground plant weight (g), tissue nutrient concentrations ($\mu g \cdot g^{-1}$), and standard errors for *Eriogonum elatum* in 2001, 2002, and 2003 on the control (2 195 m) and burned (2 225 m) sites. Asterisks indicate differences between sites.

concentrations decreased in the first and second year after burning (Fig. 4). The woody forb *Eriogonum umbellatum* did not resprout in the first season following the spring prescribed burn on the burned site. However, by the next spring, the forb resprouted and by the next summer had higher tissue N, P, K, and Mg (but lower Fe) on the burned site (Fig. 5). *Eriogonum elatum*, a low growing fleshy forb, resprouted shortly after the prescribed fire on the burned site but had no initial nutritional response. By the second year after burning, plant weight and tissue K had increased on the burned site (Fig. 6). The perennial grass *Poa secunda secunda* was another species that did not resprout on the burned site in the first season following the spring prescribed fire. However, by the second year following the prescribed fire, *Poa secunda secunda* resprouted and had increased plant weight and tissue N and Mg as a result of burning (Fig. 7). *F. idahoensis*, another perennial grass, did resprout the first season after the fire and had immediate increases in tissue N and P (Fig. 8). In the second year after burning, *F. idahoensis* still had increased tissue N and also had increased tissue K, Ca, and Mg (Fig. 8). Tissue Mn had decreased in the second year on the burned site (Fig. 8).

F. idahoensis was the only species with significant microsite effects and microsite × burning interactions. Individual *F. idahoensis* plants were typically larger under tree and shrub

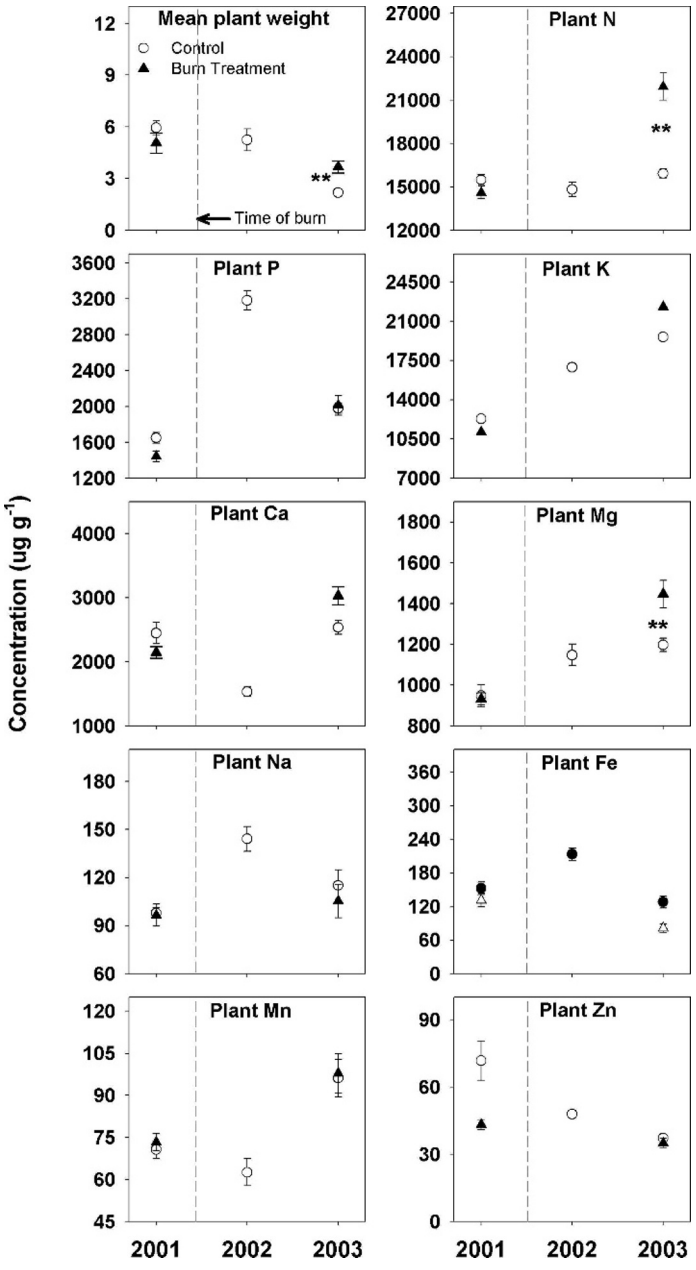

Figure 7. Mean aboveground plant weight (g), tissue nutrient concentrations ($\mu g \cdot g^{-1}$), and standard errors for *Poa secunda* in 2001, 2002, and 2003 on the control (2 195 m) and burned (2 225 m) sites. Asterisks indicate differences between sites.

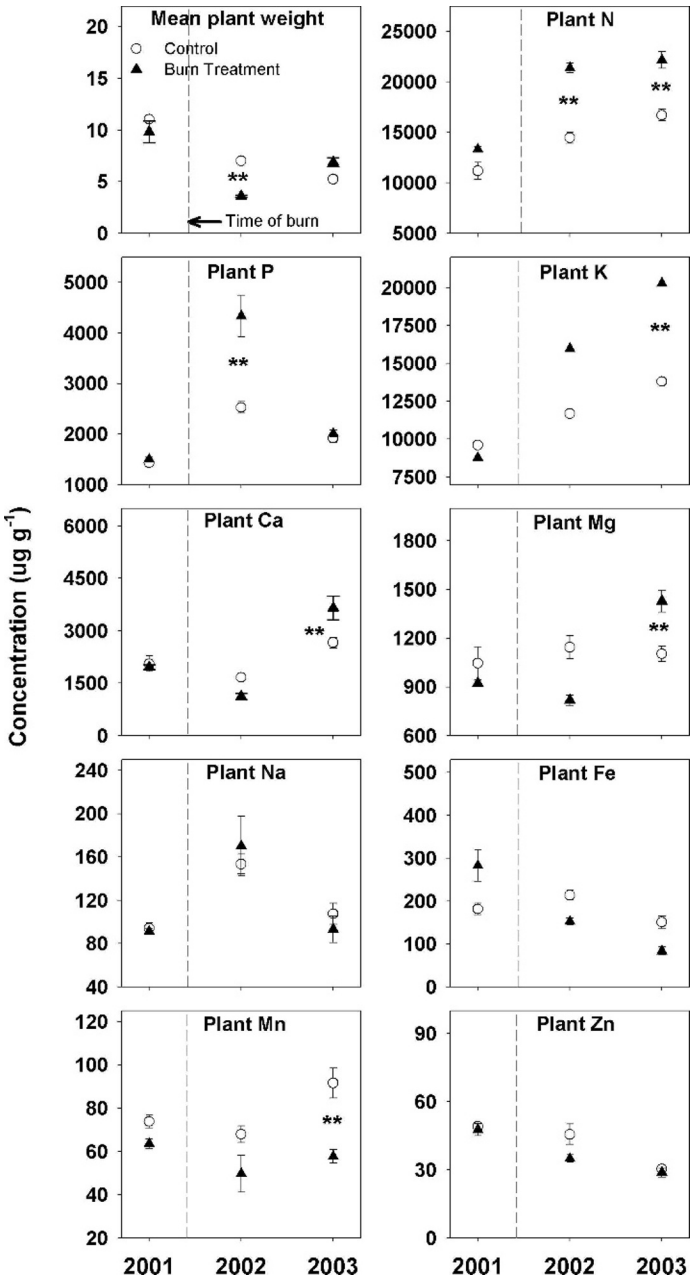

Figure 8. Mean aboveground plant weight (g), tissue nutrient concentrations ($\mu g \cdot g^{-1}$), and standard errors for *Festuca idahoensis* in 2001, 2002, and 2003 on the control (2 195 m) and burned (2 225 m) sites. Asterisks indicate differences between sites.

canopies before burning, but plant weights were similar among microsites after burning ($P < 0.05$). Also, plant tissue Na decreased in under tree and interspace microsites but increased in undershrub canopy microsites by the second season after burning as indicated by mean comparisons of the year × site × microsite interaction ($P < 0.05$).

Soil Relationship to Plants

Although plants differed in their relative nutrient concentrations, there were common trends in response to burning. Therefore, to simplify the results and discussion of the canonical correspondence analysis (CCA), we limited the plant response variables to those most commonly affected by burning, that is, plant weight and tissue N, P, K, and Mg (Fig. 9). This allowed us to include all plant species in the same CCA. Results from the CCA indicate there are three significant eigenvalues in the data set (Table 1). The first axis indicates positive relationships among all the plant variables, which commonly responded to burning and the binary variable "treatment," soil surface K^+, NO_3^-, and inorganic N (Table 2). The second axis indicates moderate positive association between plant tissue Mg and soil surface Mn^{2+}, Ca^{2+}, and Mg^{2+} (Table 2). There also is a moderate negative association between plant Mg and soil surface ortho-P and soil profile

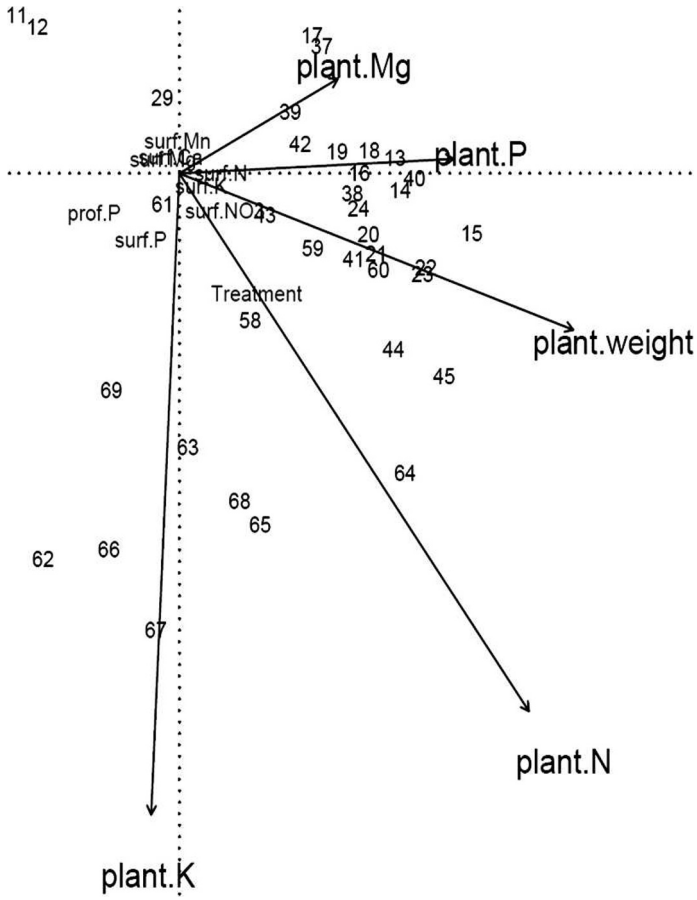

Figure 9. Canonical correspondence analysis ordination diagram with observation numbers, relevant soil nutrients and treatments, and relevant plant nutrients and weight (arrows). The first axis is horizontal (soil nutrients and treatment), and the second axis is vertical (plant nutrients and weight). Observations far from the origin are not shown so that more detail can be seen on this figure.

ortho-P (Table 2). The third axis uniquely relates plant weight with soil surface Mn^{2+} (Table 2).

DISCUSSION

Spatial, Temporal, and Burning Effects on Soils

Burning resulted in increases in soil surface NH_4^+, NO_3^-, and total inorganic N as observed in other semiarid systems (Hobbs and Schimel 1984; DeBano and Klopatek 1988; Covington et al. 1991; Blank and Zamudio 1998). The increases in NO_3^- and inorganic N occurred throughout the entire soil profile. Release of NH_4^+ from organic matter occurs during burning and decomposition of incompletely consumed above- and belowground biomass, and then NH_4^+ is converted to NO_3^- by soil microorganisms (Covington et al. 1991). The NO_3^- ion is highly mobile and easily moves down through the soil profile (Chorover et al. 1994). The observed increases in the mineral cations Ca^{2+}, Mn^{2+}, and Zn^{2+} likely were due to deposition of ash onto the soil surface after combustion and incorporation into the mineral soil (Neary et al. 1999). Micronutrients are seldom sampled following fire, and the increases in Mn^{2+} and Zn^{2+} rarely have been documented (Neary et al. 1999). Differences in nutrient contents among microsites can be attributed to variations in plant uptake, litter fall, and microbial communities (Chambers 2001; Compton and Boone 2002; Booth et al. 2003; Rau et al. 2007). These differences often persist following fire (Blank et al. 1994a; Blank and Zamudio 1998; Rau et al. 2007).

Spatial, Temporal, and Burning Effects on Plants

The effect of microsite on aboveground plant characteristics was minimal in this study. Although soil nutrients differed statistically by microsite, the absolute magnitude of that difference may not be large enough to affect plant nutrient uptake (Rau et al. 2007). More investigation may be necessary to determine the interactions between nutrient availability and plant physiological parameters at the microsite scale.

Burning had a significant effect on all the plant species studied, and this effect increased over time. For plants that resprouted the first season after the burn (June 2002), there were few differences in aboveground plant biomass or nutrients on control vs. burned sites. Only *F. idahoensis* had higher plant N and P concentrations the first season after burning, and *L. argenteus* had decreased Fe on the burn site the first season after the burn (June 2002). Increases in plant nutrients have been reported in the first growing season following spring burns in more mesic environments (Cook et al. 1994; Anderson and Menges 1997; Bennett et al. 2002). The general lack of response during the first growing season in this semiarid environment likely occurred because of the short growing season and a delayed increase in soil nutrient availability within the rooting zone. Although increases in NH_4^+ were observed in the 0–3-cm depth immediately after the burn, increases in NO_3^- and in total inorganic N were not seen in the soil profile until the first fall after the burn (Rau et al. 2007). The increased nutrient response of *F. idahoensis* to burning in the first season may be because of lower aboveground biomass on the burned location (Fig. 8). Smaller and younger plants have been documented to have higher aboveground concentrations of mineral nutrients because of the low percentage of structural tissues in smaller younger plants (Schaffers 2002). By the second year after burning, increases in plant biomass and nutrient concentrations were evident for all species. Soil content of NH_4^+, NO_3^-, and total inorganic N were all higher on the burned than control site by the first year after the burn at the 0–3-cm depth, and NO_3^- and total inorganic N were elevated in the soil profile.

Some variation in individual species responses to burning were observed and are likely due to differences in burn tolerance, root characteristics, mycorrhizal associations, and ecophysiological characteristics (Steuter and McPherson 1995; Anderson and Menges 1997). Species dependent responses to burning have been documented elsewhere (Cook et al. 1994; Anderson and Menges 1997). In this study, two of the plant species, *Eriogonum umbellatum* and *Poa secunda secunda*, did not resprout the first summer after the spring prescribed burn. *Eriogonum umbellatum* is a large woody forb with extensive belowground biomass allocation. A larger fuel component at the time of burning may have increased temperatures at the root crown and delayed vegetative recovery (Steuter and McPherson 1997). *Poa secunda secunda* is a cool-season grass and likely did not resprout in the first year because conditions were not favorable in the weeks following the burn.

Table 1. Eigenvalues, correlation coefficients, proportion of variance, and *P* values for the canonical correspondence analysis of soil and plant nutrient data. Results for axes 1 through 3 are shown.

	Axis		
	1	2	3
Eigenvalues	7.2748	2.1643	0.8739
Correlation coefficients	0.9376	0.8270	0.7422
Proportion of variance	0.6214	0.1849	0.1048
P value	<0.0001	<0.0001	0.0091

Soil Relationship to Plants

Although each plant species in our study had variable responses to fire, most of the species exhibited an increase in plant weight in response to burning (*C. acuminata*, *L. argenteus*, *Eriogonum elatum*, and *Poa secunda secunda*) and in tissue N concentrations (*C. acuminata*, *L. argenteus*, *Eriogonum umbellatum*, *Poa secunda secunda*, and *F. idahoensis*). In our study, plant weight and tissue N were most closely related to the blanket variable "treatment," soil surface NO_3^-, total inorganic N, and K^+ concentrations. Other observed responses to burning, including increased tissue Mg (*Eriogonum umbellatum*, *Poa secunda secunda*, and *F. idahoensis*), increased tissue K (*Eriogonum umbellatum*, *Eriogonum elatum*, and *F. idahoensis*), and increased tissue P (*L. argenteus*, *Eriogonum umbellatum*, and *F. idahoensis*), also were most closely related to "treatment," surface NO_3^-, inorganic N, and K^+. The canonical soil variable "treatment" comprises a complex set of variables not measured in this study. It could be argued the influence of treatment resulted from reduced competition and increased available soil moisture due to reduction of woody biomass following burning. Removal of woody biomass has been shown to increase soil moisture and herbaceous vegetation in arid rangelands (Chambers and Linerooth 2001; Wright and Chambers 2002). Sturgis (1993) documented that herbaceous biomass doubled the first three years following shrub removal and that effects of shrub removal were evident 20 years

Table 2. Canonical coefficients and intraset correlations for the plant and soil variables from the canonical correspondence analysis. Results for axes 1 through 3 are shown.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Plant						
Weight	0.497	0.288	0.800	0.466	0.238	0.594
Tissue Mg	0.528	0.517	−0.570	0.495	0.427	−0.423
Tissue K	0.731	−0.480	−0.253	0.686	−0.397	−0.188
Tissue P	0.554	0.289	−0.621	0.520	0.239	−0.461
Tissue N	0.826	−0.183	−0.008	0.774	−0.151	−0.006
Soil						
Treatment	0.941	−0.024	0.035	0.882	−0.020	0.026
Surface Mn^{2+}	0.137	0.423	0.663	0.129	0.350	0.492
Surface Fe^{2+}	0.014	0.399	0.389	0.013	0.330	0.289
Surface Zn^{2+}	0.303	0.318	0.159	0.284	0.263	0.118
Surface Ca^{2+}	0.330	0.427	0.404	0.309	0.353	0.300
Surface Mg^{2+}	0.476	0.427	0.190	0.446	0.353	0.141
Surface K^+	0.577	0.177	0.382	0.541	0.147	0.284
Surface Na^+	0.352	0.045	0.267	0.330	0.037	0.198
Surface ortho-P	0.432	−0.436	0.207	0.405	−0.360	0.154
Surface NH_4^+	0.354	0.397	0.258	0.332	0.328	0.192
Surface NO_3^-	0.738	0.192	0.298	0.692	0.159	0.221
Surface inorganic N	0.568	0.361	0.309	0.532	0.298	0.230
Profile Mn^{2+}	−0.312	0.399	0.432	−0.293	0.330	0.320
Profile Fe^{2+}	−0.233	0.329	0.284	−0.218	0.272	0.211
Profile Zn^{2+}	−0.073	0.153	0.038	−0.068	0.127	0.028
Profile Ca^{2+}	0.319	0.398	0.346	0.299	0.329	0.257
Profile Mg^{2+}	0.225	0.367	0.239	0.211	0.303	0.177
Profile K^+	0.477	0.241	0.396	0.447	0.199	0.294
Profile Na^+	0.425	0.150	0.344	0.399	0.124	0.256
Profile ortho-P	−0.024	−0.514	0.072	−0.023	−0.425	0.054
Profile NH_4^+	−0.143	0.146	−0.028	−0.134	0.121	−0.021
Profile NO_3^-	0.334	0.063	0.014	0.313	0.052	0.011
Profile inorganic N	0.138	0.133	−0.008	0.129	0.110	−0.006

following treatment. Similarly, increasing near-surface-soil N has been documented to increase plant weight and N content in agricultural studies (Marschner 1995). Nitrogen is typically limiting in most systems, and plants increase uptake, have a higher photosynthetic rate, and grow larger when nitrogen availability is increased (Marschner 1995). The relationship between plant weight, plant tissue nutrients, and soil surface K^+ may be confounded by the fact that the burn site initially had higher K^+ than the control site.

The relationships among fire-induced increases in plant tissue Mg, P, and K and soil properties are not well understood, and the timing of plant and soil collections in this study may make the interpretation of these results more complex. However, it is possible that increases in plant Mg, P, and K are directly and indirectly related to reduced competition, increased soil inorganic N, and soil cations. Plant uptake of cations has been positively and directly correlated with the concentration of the corresponding cation in soil (Schaffers 2002). Also, it has been observed that cation concentrations in soil do not necessarily affect plant uptake of the corresponding cation but rather influence the uptake of a different nutrient (Hayati and Proctor 1990). It also is possible that increases in plant tissue P and cations are necessary to balance increases in plant tissue N (Marschner 1995). Thus, these relationships may be a result of simultaneous and complex nutrient limitation in native soils (Hayati and Proctor 1990).

IMPLICATIONS

Plant nutritional response to fire has been documented by several authors, yet few attempts have been made to quantify the direct influence of wildland soil chemical changes on plant nutrition (Carreira and Niell 1992; Blank et al. 1994b; Cook et al. 1994; Anderson and Menges 1997; Bennett et al. 2002). Results from our study indicate that fire increased soil nitrogen and metal cations immediately following fire and for at least one year postburn. Vegetation that resprouted or germinated on burned locations responded not only to changes in soil nutrients but also to possible changes in plant competition, soil water content, organic compounds, and microbial communities (Carreira and Niell 1992; Blank et al. 1994b; Cook et al. 1994; Anderson and Menges 1997; Bennett et al. 2002).

The direct influence of soil nutrients on plant nutrition in wild systems is not well understood but appears to be species specific. Previous studies have found that soil nutrient supply or content has direct positive or negative relationships with plant tissue concentrations of that nutrient or other related nutrients (Hayati and Proctor 1990; Schaffers 2002). In our system, the effects of burning and changes in soil surface NO_3^- and inorganic N concentrations as measured in the fall had dramatic influences on plant weight and tissue N concentrations. Plants in our study responded better to changes that affected the soil surface because of the immediate and persistent increase in soil nutrients.

It appears that spring prescribed burning was a plausible option for slowing pinyon–juniper expansion on our demonstration area and may be applicable to other areas as long as sufficient understory vegetation is present on locations to be treated (Chambers et al. 2007). Spring burning increased understory plant biomass or nutrient concentration for all species in our study. Fall burning in these woodlands may not have the same beneficial effects because of decreased soil and fuel moisture and increased fire severity (Cook et al. 1994).

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LITERATURE CITED

Anderson, R. C., and E. S. Menges. 1997. Effects of fire on sandhill herbs: nutrients, mycorrhizae, and biomass allocation. *American Journal of Botany* 84(8):938–948.

Barnett, J. K., and J. A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. *Journal of Range Management* 47(2):114–118.

Bennett, L. T., T. S. Judd, and M. A. Adams. 2002. Growth and elemental content of perennial grasslands following burning in semi-arid, sub-tropical Australia. *Plant Ecology* 164:185–199.

Blank, R. R., F. Allen, and J. A. Young. 1994a. Extractable anions in soils following wildfire in a sagebrush-grass community. *Soil Science Society of America Journal* 58:564–570.

Blank, R. R., F. Allen, and J. A. Young. 1994b. Growth and elemental content of several sagebrush-steppe species in unburned and post-wildfire soil and plant effects on soil attributes. *Plant and Soil* 164:35–41.

Blank, R. R., F. Allen, and J. A. Young. 1996. Influence of simulated burning of soil-litter from low sagebrush, squirreltail, cheatgrass, and medusahead on water-soluble anions and cations. *International Journal Wildland Fire* 6(3):137–143.

Blank, R. R., and D. C. Zamudio. 1998. The influence of wildfire on aqueous-extractable soil solutes in forested and wet meadow ecosystems along the eastern Sierra-Nevada range, California. *International Journal of Wildland Fire* 8(2):79–85.

Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91:36–48.

Carreira, J. A., and F. X. Niell. 1992. Plant changes in a semi-arid Mediterranean shrubland after fire. *Journal of Vegetation Science* 3:457–466.

Certini, G. 2005. Effects of fire on properties of forest soil: a review. *Oecologia* 143:1–10.

Chambers, J. C. 2001. *Pinus monophylla* establishment in an expanding *Pinus-Juniperus* woodland: environmental conditions, facilitation and interacting factors. *Journal of Vegetation Science* 12:27–40.

Chambers, J. C., and A. R. Linnerooth. 2001. Restoring sagebrush dominated riparian corridors using alternative state and threshold concepts: environmental and seedling establishment response. *Applied Vegetation Science* 4:157–166.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes great basin sagebrush ecosystems invasible by Bromus tectorum? *Ecological Monographs* 77:117–145.

Chorover, J., P. M. Vitousek, D. A. Everson, A. M. Esperanza, and D. Turner. 1994. Solution chemistry profiles of mixed-conifer forests before and after fire. *Biogeochemistry* 26:115–144.

Compton, J. E., and R. E. Boone. 2002. Soil nitrogen transformations and the role of light fraction organic matter in forest soils. *Soil Biology and Biochemistry* 34:933–943.

Connelly, J. W., S. T. Knick, M. A. Schroeder, and S. J. Stiver. 2004. Conservation assessment of greater sage-grouse and sagebrush habitats. Cheyenne, WY, USA: Western Association of Fish and Wildlife Agencies. Unpublished report. 20 p.

Cook, J. G., T. J. Hershey, and L. L. Irwin. 1994. Vegetative response to burning on Wyoming mountain-shrub big game ranges. *Journal of Range Management* 47:296–302.

Covington, W. W., and L. F. DeBano. 1988. Effects of fire on pinyon-juniper soils. Panel paper presented at the Effects of Fire in Management of Southwestern Natural Resources conference; 14–17 November 1988; Tucson, AZ, USA. 8 p.

Covington, W. W., L. F. DeBano, and T. G. Huntsberger. 1991. Soil nitrogen changes associated with slash pile burning in pinyon-juniper woodlands. *Forest Science* 37:347–355.

DeBano, L. F., and J. M. Klopatek. 1988. Phosphorus dynamics of pinyon-juniper soils following simulated burning. *Soil Science Society of America Journal* 52:271–277.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994. Diets and food selection of sage grouse chicks in Oregon. *Journal of Range Management* 47:90–93.

Fischer, R. A., K. P. Reese, and J. W. Connelly. 1996. Influence of vegetal moisture content and nest fate on timing of female sage grouse migration. *Condor* 98:868–872.

Gruell, G. E. 1999. Historical and modern roles of fire in pinyon-juniper. *In:* S. B. Monsen and R. Stevens [comps.]. Proceedings: ecology and management of pinyon-juniper communities in the interior west. Proceedings RMRS-P-9. Ogden, UT: US Department of Agriculture Forest Service Rocky Mountain Research Station. p. 24–28.

Hainds, M. J., R. J. Mitchell, B. J. Palik, L. R. Boring, and D. H. Gjerstad. 1999. Distribution of native legumes (legumioseae) in frequently burned longleaf pine (pinaceae)-wiregrass (Poaceae) ecosystems. *American Journal of Botany* 86(11):1606–1614.

Hayati, A. A., and M. C. F. Proctor. 1990. Plant distribution in relation to mineral nutrient availability and uptake on a wet-heath site in south-west England. *Journal of Ecology* 78:134–151.

Hendricks, J. J., and L. R. Boring. 1999. N_2-fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *Forest Ecology and Management* 113:167–177.

Hobbs, N. T., and D. S. Schimel. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. *Journal of Range Management* 37(5):402–404.

Horneck, D. A., and R. O. Miller. 1998. Determination of total nitrogen in plant tissue. *In:* Y. P. Karla [ed.]. Handbook of reference methods for plant analyses. Boca Raton, FL, USA: CRC Press. p. 75–83.

Keeney, D. R., and D. W. Nelson. 1982. Nitrogen—inorganic forms. Methods of soil analyses, part 2. *In:* Chemical and microbiological properties. Agronomy Monograph no. 9. 2nd ed. Madison, WI: Soil Science Society of America. p. 645–649.

Lindsay, W. L., and W. A. Norvell. 1978. Development of a DTPA soil test for zinc, iron, manganese, and copper. *Soil Science Society of America Journal* 42:421–428.

Marschner H. 1995. Mineral nutrition of higher plants. 2nd ed. San Diego, CA, USA: Academic Press. 889 p.

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. *Journal of Range Management* 52:550–559.

Miller, R. F., and R. J. Tausch. 2001. The role of fire in juniper and pinyon woodlands: a descriptive analysis. *In:* K. E. M. Gallet and T. P. Wilson [eds.]. Proceedings of the Invasive Species Workshop: the role of fire in the control and spread of invasive species. Tallahassee, FL, USA: Tall Timbers Research Station. Miscellaneous Publication No. 11. p. 15–30.

Miller, R. F., and P. E. Wigand. 1994. Holocene changes in semi arid pinyon-juniper woodlands: response to climate, fire, and human activities in the U.S. Great Basin. *Bioscience* 44:465–474.

Miller, R. O. 1998. High-temperature oxidation: dry ashing. *In:* Y. P. Karla [ed.]. Handbook of reference methods for plant analyses. Boca Raton, FL, USA: CRC Press. p. 53–56.

Neary, D. G., C. C. Klopatek, L. F. DeBano, and P. F. Ffolliot. 1999. Fire effects on below ground sustainability: a review and synthesis. *Forest Ecology and Management* 122:51–71.

Olsen, S. R., and L. E. Sommers. 1982. Phosphorus. Methods of soil analyses, part 2. *In:* Chemical and microbiological properties. Agronomy Monograph no. 9. 2nd ed. Madison, WI: Soil Science Society of America. p. 421–422.

Rau, B. M., R. R. Blank, J. C. Chambers, and D. W. Johnson. 2007. Prescribed fire and time: Soil extractable nitrogen and phosphorus dynamics in a Great Basin sagebrush ecosystem. *Journal of Arid Environments* 71:362–375.

Rau, B. M., J. C. Chambers, R. R. Blank, and W. W. Miller. 2005. Hydrologic response of a central Nevada pinyon-juniper woodland to prescribed fire. *Rangeland Ecology and Management* 56:614–622.

Reiner, A. L. 2004. Fuel load and understory community changes associated with varying elevation and pinyon-juniper dominance [master's thesis]. Reno, NV, USA: University of Nevada Reno. 63 p.

Schaffers, A. P. 2002. Soil, biomass, and management of semi-natural vegetation. *Plant Ecology* 158:229–246.

Stueter, A. A., and G. R. McPherson. 1997. Fire as a physical stress. *In:* D. J. Bedunah [ed.]. Wildland plants: physiological ecology and developmental morphology. Denver, CO, USA: Society for Range Management. p. 550–579.

Sturgis, D. L. 1993. Soil-water and vegetation dynamics through 20 years after big sagebrush control. *Journal of Range Management* 46:161–169.

Tausch, R. J., and N. E. West. 1995. Plant species composition patterns with differences in tree dominance on a southwestern Utah pinon-juniper site. Fort Collins, CO, USA: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. General Technical Report RM-258. 226 p.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179.

Thomas, G. W. 1982. Exchangeable cations. Methods of Soil Analyses, part 2. *In:* Chemical and microbiological properties. Agronomy Monograph no. 9. 2nd ed. Madison, WI: Soil Science Society of America. p. 159–161.

Wright, J. M., and J. C. Chambers. 2002. Restoring sagebrush dominated riparian corridors using alternative state and threshold concepts: biomass and species response. *Applied Vegetation Science* 5:237–246.

Appendix A. Results for the analysis of variance comparing measured soil variables at all sites, microsites, years, and soil depths.

		Mn^{2+}		Fe^{2+}		Zn^{2+}		Ca^{2+}		Mg^{2+}		K^{+}	
Effect	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Treatment	1	6.2	0.0471	6.55	0.0429	12.47	0.0123	64.81	0.0002	9.32	0.0224	115.18	< .0001
Replicate (treatment)	6												
Microsite	2	26.91	< .0001	11.43	0.0017	6.83	0.0105	21.08	0.0001	3.65	0.0576	15.46	0.0005
Treatment × microsite	2	2.87	0.0956	0.78	0.4808	0.1	0.9013	2.78	0.1021	1.29	0.3105	6.91	0.0101
Microsite × replicate (treatment)	12												
Depth	3	35.87	< .0001	7.29	0.0003	44.03	< .0001	105.01	< .0001	49.22	< .0001	65.34	< .0001
Microsite × depth	6	2.62	0.0264	1.85	0.107	4.36	0.0012	2.86	0.0171	6.74	< .0001	3.14	0.0103
Treatment × depth	3	6.67	0.0007	1.73	0.1724	0.39	0.7634	8.98	< .0001	0.69	0.5601	11.67	< .0001
Treatment × microsite × depth	6	0.54	0.7762	2.85	0.0174	1.12	0.364	0.69	0.6594	0.26	0.9525	1	0.433
Depth × microsite × replicate(treatment)	54												
Year	2	40.74	< .0001	3.65	0.0284	3.16	0.0453	2.22	0.1118	5.77	0.0039	1.35	0.2636
Year × depth	6	1.43	0.2068	0.89	0.5067	1.34	0.2444	0.33	0.9226	1.33	0.2483	0.37	0.8997
Year × microsite	4	0.43	0.7863	0.91	0.4581	2.19	0.0725	1.04	0.3885	0.66	0.621	0.31	0.8737
Year × treatment	2	0.58	0.5612	1.2	0.3046	3.6	0.0298	0.53	0.5874	1.34	0.266	0.02	0.9794
Year × microsite × depth	12	0.94	0.506	1.89	0.0397	2.95	0.0011	0.85	0.5967	0.7	0.7539	0.5	0.9134
Year × treatment × depth	6	1.45	0.2006	1.55	0.1672	0.95	0.4631	0.17	0.9834	0.77	0.5972	0.13	0.9929
Year × treatment × microsite	4	0.76	0.55	0.29	0.8827	0.96	0.4311	2.01	0.096	0.83	0.5094	0.32	0.8655
Year × treatment × microsite × depth	12	1.02	0.4354	1.37	0.1864	0.65	0.7975	0.55	0.8752	0.42	0.953	0.37	0.9722
Year × depth × microsite × replicate (treatment)	144												

		Na^{+}		Ortho-P		NH_4^+		NO_3^-		Inorganic N	
Effect	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Treatment	1	89.38	< .0001	5.43	0.0587	0.01	0.9274	30.2	0.0015	8.2	0.0287
Replicate (treatment)	6										
Microsite	2	0.5	0.6179	5.74	0.0179	6.39	0.0129	4.16	0.0424	5.06	0.0255
Treatment × microsite	2	0.09	0.911	0.18	0.8356	1.33	0.3001	0.32	0.7355	1.08	0.3707
Microsite × replicate (treatment)	12										
Depth	3	61.93	< .0001	4.36	0.008	8.56	< .0001	3.85	0.0144	7.68	0.0002
Microsite × depth	6	0.66	0.6786	0.64	0.6963	1.37	0.2454	1.16	0.3396	1.62	0.1594
Treatment × depth	3	23.95	< .0001	2.83	0.0471	6.81	0.0006	3.69	0.0173	4.5	0.0069
Treatment × microsite × depth	6	0.76	0.6078	0.9	0.5021	3	0.0132	1.66	0.1477	2.43	0.0375
Depth × microsite × replicate (treatment)	54										
Year	2	0.52	0.5947	60.05	< .0001	0.73	0.4813	20.94	< .0001	8.62	0.0003
Year × depth	6	0.37	0.8961	1.63	0.1431	1.42	0.2116	0.45	0.8469	1.1	0.3645
Year × microsite	4	1.51	0.2026	1.58	0.1818	6.16	0.0001	0.33	0.8547	2.54	0.0426
Year × treatment	2	1.57	0.2115	1.2	0.3045	4.07	0.019	6.77	0.0016	4.23	0.0163
Year × microsite × depth	12	0.86	0.5934	0.36	0.9756	1.62	0.0928	1.58	0.1049	1.76	0.0599
Year × treatment × depth	6	0.29	0.9421	1.78	0.1066	2.42	0.0292	1.64	0.1391	1.75	0.1137
Year × treatment × microsite	4	2.07	0.0871	0.68	0.6056	1.37	0.2461	1.6	0.1773	1.63	0.1709
Year × treatment × microsite × depth	12	0.84	0.6132	0.57	0.8644	2.6	0.0037	2.34	0.0091	2.76	0.0021
Year × depth × microsite × replicate (treatment)	144										

Appendix B. Results for the analysis of variance comparing plant variable for all locations, microsites, years, and species.

		Mn		Fe		Zn		Ca		Mg	
Effect	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Treatment	1	0.63	0.4592	0.04	0.8402	0.03	0.8596	0.59	0.473	2.08	0.1996
Replicate (treatment)	6										
Microsite	2	0.8	0.4721	0.6	0.5642	2.17	0.1566	1.25	0.3218	2.22	0.1516
Treatment × microsite	2	2.15	0.1596	0.23	0.7965	0.33	0.7286	0.4	0.6771	0.63	0.5493
Microsite × replicate (treatment)	12										
Species	5	12.27	<.0001	14.14	<.0001	6.67	<.0001	172.4	<.0001	336.23	<.0001
Treatment × species	5	1.84	0.1151	1.6	0.1692	1.45	0.2145	0.86	0.5111	4.14	0.0022
Microsite × species	8	1.49	0.1759	1.18	0.319	1.24	0.2871	0.78	0.6174	1.24	0.2847
Treatment × microsite × species	8	0.18	0.9932	1.05	0.4057	0.51	0.8471	1.46	0.187	0.71	0.684
Species × microsite × replicate (treatment)	78										
Year	2	73.91	<.0001	35.16	<.0001	35.6	<.0001	35.48	<.0001	49.18	<.0001
Year × treatment	2	4.63	0.0102	12.79	<.0001	1.59	0.2059	3.85	0.022	7.45	0.0007
Year × microsite	4	0.56	0.6884	0.8	0.5254	1.1	0.3558	0.24	0.914	2.94	0.0204
Year × species	10	4.42	<.0001	5.98	<.0001	4.03	<.0001	13.58	<.0001	7.39	<.0001
Year × treatment × microsite	4	3.57	0.007	1.71	0.1477	0.46	0.7644	1.07	0.3712	0.77	0.5449
Year × treatment × species	8	1.27	0.2546	4.41	<.0001	1.54	0.1414	1.67	0.1021	0.44	0.8993
Year × microsite × species	16	1.81	0.0274	0.91	0.5604	1.75	0.0353	1.32	0.1804	3.16	<.0001
Year × treatment × microsite × species	11	0.47	0.9212	1.58	0.1006	1.31	0.2176	0.62	0.8161	0.7	0.7345
Year × species × microsite × replicate (treatment)	487										

		K		Na		P		N		Weight	
Effect	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Treatment	1	4.44	0.0798	0.14	0.7223	14.44	0.009	30.73	0.0015	16.28	0.0068
Replicate (treatment)	6										
Microsite	2	10.36	0.0024	2.7	0.1079	4.8	0.0294	0.33	0.7227	9.42	0.0035
Treatment × microsite	2	0.48	0.63	1.84	0.2012	3.34	0.0701	1.28	0.3123	1.06	0.3782
Microsite × replicate (treatment)	12										
Species	5	178.56	<.0001	15.5	<.0001	132.79	<.0001	67.87	<.0001	40.28	<.0001
Treatment × species	5	6.08	<.0001	0.64	0.6686	4.28	0.0017	2.58	0.0326	12.02	<.0001
Microsite × species	8	0.7	0.6878	1.02	0.4257	1.07	0.3914	2.06	0.0497	4.4	0.0002
Treatment × microsite × species	8	0.75	0.6475	0.79	0.6093	1.46	0.1855	0.64	0.7421	0.61	0.7672
Species × microsite × replicate (treatment)	78										
Year	2	157.3	<.0001	14.44	<.0001	126.45	<.0001	55.97	<.0001	11.26	<.0001
Year × treatment	2	13.23	<.0001	3.07	0.0472	4.29	0.0143	16.21	<.0001	66.35	<.0001
Year × microsite	4	1.02	0.3989	2.75	0.0277	1.63	0.1653	2.21	0.0669	2.4	0.0496
Year × species	10	8.21	<.0001	1.37	0.1906	9.64	<.0001	3.36	0.0003	15.66	<.0001
Year × treatment × microsite	4	0.9	0.4637	0.53	0.7163	0.63	0.6424	2.44	0.0465	1.94	0.1029
Year × treatment × species	8	2.39	0.0154	1.49	0.1597	2.97	0.003	1.01	0.4303	10.82	<.0001
Year × microsite × species	16	1.48	0.1019	1.59	0.0667	0.54	0.924	0.97	0.4899	1.78	0.0304
Year × treatment × microsite × species	11	0.9	0.541	1.66	0.08	0.5	0.9048	0.64	0.7913	1.94	0.0321
Year × species × microsite × replicate (treatment)	487										