Influence of a native legume on soil N and plant response following prescribed fire in sagebrush steppe

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Abstract. Woodland expansion affects grasslands and shrublands on a global scale. Prescribed fire is a potential restoration tool, but recovery depends on nutrient availability and species responses after burning. Fire often leads to long-term losses in total nitrogen, but presence of native legumes can influence recovery through addition of fixed nitrogen. We examined the effects of prescribed fire in the central Great Basin, Nevada, USA, on density, biomass and nutrient content of a native legume, \textit{Lupinus argenteus} (Pursh), and the effects of \textit{Lupinus} presence and prescribed fire on soil inorganic nitrogen and on neighboring plant functional groups. We examined three treatments – 1 year post-burn, 3 years post-burn and unburned control in three replicate blocks. Extractable soil inorganic nitrogen was variable and, despite a tendency towards increased inorganic nitrogen 1 year post-burn, differences among treatments were not significant. Extractable soil inorganic nitrogen was higher in \textit{Lupinus} presence regardless of time since fire. \textit{Lupinus} density increased after fire mainly owing to increased seedling numbers 3 years post-burn. Fire did not affect \textit{Lupinus} tissue N and P concentrations, but cover of perennial grasses and forbs was higher in \textit{Lupinus} presence. The invasive annual grass \textit{Bromus tectorum} had low abundance and was unaffected by treatments. Results indicate that \textit{Lupinus} has the potential to influence succession through modification of the post-fire environment.

Introduction

Woodland expansion is affecting grasslands and shrublands on a global scale (Wessman et al. 2007). As woodlands expand into grasslands and shrublands, they increase shading and reduce resource availability (Breshears et al. 1997; Leffler and Caldwell 2005), leading to elimination of understory shrubs and herbaceous vegetation (Tausch and Tueller 1990; Miller et al. 2000) and depletion of the native understory species seedbank (Konick and Everett 1982; Allen and Nowak 2008). Over time, tree dominance results in higher fuel loads and can increase the risk of severe wildfires that leave areas susceptible to invasion by exotic species (Konick 1985; Chambers et al. 2007). Higher-elevation sagebrush steppe communities throughout the intermountain western US are affected by expansion of pinyon and juniper woodlands. Although fire is a natural, reoccurring disturbance in shrublands that prevents tree dominance, depletion of fine fuels due to overgrazing by livestock coupled with fire suppression has led to increased tree cover and woody fuel loads (Tausch et al. 1981). Prescribed fire has been proposed as a management tool for decreasing pinyon and juniper dominance and restoring sagebrush steppe communities (Miller et al. 2000). Fire return intervals in sagebrush steppe differ depending on community type, but range from ~60 to 110 years (Whisenant 1990). Recovery within sagebrush ecosystems is influenced by the post-fire resource environment and the responses of residual shrubs and herbaceous species.

Nutrients within woodlands are spatially and temporally variable (Chambers 2001). Fire significantly affects the availability of nutrients, especially nitrogen (N) (Blank et al. 2007; Rau et al. 2007). Over the long term, fire can lead to losses in total N through volatilisation and through transfer of organic N from labile to recalcitrant pools (Gonzalez-Perez et al. 2004; Castro et al. 2007). Also, fire can negatively impact microbial biomass and activity that, in turn, can slow the cycling of plant-available N (Choromansk and DeLuca 2002; Certini 2005; Guerrero et al. 2006). Folowing low-severity fires, increases in available nutrients occur owing to deposition of ash onto the soil surface, release of orthophosphate and NH\textsubscript{4}\textsuperscript{+} from organic matter, decomposition of belowground biomass, and further oxidation of NH\textsubscript{4}\textsuperscript{+} to NO\textsubscript{3}\textsuperscript{−} (Raison 1979; Hobb and Schimel 1984; Covington et al. 1991; Blank and Zamudio 1998). For example, in the sagebrush steppe of the central Great Basin, Nevada, USA, inorganic N levels increased after a spring prescribed fire and remained higher than a paired unburned control for 3 years (Rau et al. 2007). Fire also can influence N availability through its effect on N mineralisation (Prieto-Fernandez et al. 1993; Guerrero et al. 2005). High fire temperatures often reduce N mineralisation, whereas low-intensity fires can stimulate mineralisation of N (Serrasolsas and Khanna 1995; Guerrero et al. 2005). For example, N mineralisation increased 1 year after prescribed fire in both shrub
and grassland communities in Colorado (Hobbs and Schimel 1984).

Reduction of competition and temporary increase of available soil nutrients associated with prescribed fires may help promote increased growth of native understory vegetation (Moore et al. 1982; Rau et al. 2008). Biomass of perennial herbaceous sagebrush species was twice as high in burned plots as unburned controls in both Nevada (Rau et al. 2008) and Wyoming (Cook et al. 1994). In addition to increasing biomass production, post-fire conditions often increase N concentration of plant tissue (Grogan et al. 2000; Metzger et al. 2006; Rau et al. 2008), plant reproductive potential (Wrobleski and Kauffman 2003), seed viability (Dyer 2002) and seed germination (Bradstock and Auld 1995; Romme et al. 1995; Williams et al. 2004). In combination, these factors influence post-fire succession and nutrient retention within sagebrush ecosystems.

Succession after fire can be strongly influenced by the identity of early seral plant species, especially if they are able to modify soil properties (Blank et al. 1994). One plant functional group with the ability to modify soil nutrient availability is legumes. Legumes can alter successional trajectories (Ritchie and Tilman 1995) by modifying the resource environment after disturbance (Morris and Wood 1989) or via facilitation and inhibition (Maron and Connors 1996). Legumes have the potential to affect community N budgets (Spehn 2002) by increasing available soil N via higher N mineralisation and nitrification (Vitousek and Walker 1989; Maron and Jeffries 1999; Myrold and Huss-Danell 2003; Johnson et al. 2004). If establishment and growth of native N$_2$-fixing species is promoted by fire, they may be able to replace N lost owing to fire and facilitate community succession and stability over time. Also, input of organic N from legumes can stimulate recovery of microbial activity and N cycling.

However, disturbance and increased nutrient availability after fire combined with additional N input associated with legumes can provide conditions favorable for invasion by exotic species. N-rich patches created by *Lupinus arboresus* in California led to conversion of native shrubland to exotic annual grassland (Maron and Connors 1996). Similarly, facilitation by an exotic legume is believed to play a role in invasion by the exotic grass *Pennisetum cetaceum* in Hawaii (Carino and Daehler 2002). Although legumes are common in sagebrush steppe communities, little is known about their effects on N availability or how their functional role changes following disturbance. Identifying the effect of legumes on N availability and retention in the post-fire environment can clarify the long-term effects of prescribed fire and the implications for maintenance and renewal of sagebrush systems.

Within the sagebrush steppe, one of the most common native legumes is *L. argenteus* (Pursh), silver lupine (hereafter *Lupinus*). This species exhibits increases in cover and productivity in response to fire (Rau et al. 2008), and the amounts of N fixed can be substantial (Kenny and Cuany 1990; Rumbaugh and Johnson 1991), even in disturbed sites (Johnson and Rumbaugh 1986). This indicates that *Lupinus* may be important in influencing N availability, species interactions and community recovery after disturbance. The objectives of the present study were to examine the interacting effects of the normal increase in mineral N after fire and *Lupinus* presence on N availability and community recovery in a sagebrush steppe ecosystem exhibiting pinyon–juniper expansion. Prescribed burns conducted in 2002 and 2004 at multiple locations along an elevation gradient within a Joint Fire Sciences Program demonstration watershed in the central Great Basin, Nevada, USA, allowed us to develop a fully replicated study. We used a completely randomized design to examine replicate sites 1 year (2004) and 3 years (2002) post-burn and to compare them with unburned controls. We addressed three specific questions. (1) How does time since prescribed fire affect *Lupinus* density, biomass and tissue nutrient concentration? (2) How is soil N affected by the separate and interacting effects of fire and *Lupinus* presence? (3) How are time since fire and *Lupinus* presence related to the response of other plant functional groups? We discuss the implications of these effects for the recovery of sagebrush ecosystems after prescribed fire.

**Methods**

**Study area**

The study was part of a Joint Fire Sciences Program Demonstration Area established to examine the effects of prescribed fire on the soil and plant responses of sagebrush ecosystems exhibiting pinyon and juniper expansion (Chambers 2005; Rau et al. 2005, 2007, 2008). The study area is in Underdown Canyon (39°15′11″N 117°35′33″W) and is located in the Shoshone Mountain Range on the Humboldt–Toiyabe National Forest (Austin Ranger District) in Nye and Lander Counties, Nevada. Parent material at our sites in Underdown Canyon consist of welded and non-welded, Rhyolitic ash flow tuffs (Blank et al. 2007). The weathered parent rock itself is low in clay and therefore minimizes the potential for the host rock to contribute inorganic N (R. Blank, pers. comm.). Alluvial soils dominate the study sites and soils are classified as coarse loamy, mixed frigid, Typic Hapluxerolls. Coarse mineral particles in the 0–15-cm depth decrease from 73.7 to 42.8% and clay and sand particles generally increase with increasing elevation (Rau et al. 2005). Study sites were located on predominantly north-facing aspects and slopes ranging from 5 to 15%. Precipitation is mostly in the form of snow or spring rains, with mean annual amounts ranging from 230 mm at the bottom to 500 mm at the top of the drainage. Climate variables for the study period fell within the 33-year average (Table 1; WRCC 2007).

Dominant vegetation within the study area is mainly sagebrush (*Artemisia tridentata vaseyana*) and single-leaf pinyon (*Pinus monophylla*), but Utah juniper (*Juniperus osteosperma*) is also present. Based on vegetation structure and tree fire scars, it had been more than 100 years since a wildfire burned within the study area (Miller et al. 2008). Tree cover values ranged from 20 to 75% (Reiner 2004). Herbaceous species include perennial grasses (*Poa secunda, Elymus elymoides, Stipa commata, Festuca idahoensis* and *Pseudoroegneria spicata*), perennial forbs (*Eriogonum species, Crepis acuminata, Phlox longifolia, Agoseris glauca* and *Penstemon* species) and annual forbs (*Collinsia parviflora, Gayophytum ramosissimum* and *Phlox gracilis*). The invasive annual grass *Bromus tectorum* is present but its distribution is patchy. Cryptobiotic soil crusts are rare within this canyon. Legumes are present, with *Lupinus argenteus* being the most abundant species.
Variables related to Lupinus spaces, each 1-m² quadrat was recorded (Lupinus line in tree interspaces. The number of 2004 and averaged 5–8 ha in size. The fires were cool burns that 50%). Prescribed burns were conducted in spring 2002 and 2004 and contained trees, shrubs and herbaceous vegetation in a patchy nature. Surface fire temperatures averaged 206 ± 24°C in interspaces, 304 ± 26°C under trees and 369 ± 33°C under shrubs, and decreased with soil depth to an average of 41°C at 5 cm for all microsites (Rau et al. 2005).

For the current study, three replicate blocks were established in June 2005 along the elevation gradient within the watershed. Each block had similar vegetation and the same soil type, and contained one replicate of each of the three treatments: (1) an unburned control site; (2) a site that was burned in 2002 (3 years post-burn); and (3) a site that was burned in 2004 (1 year post-burn). Blocks were separated by a minimum of 1 km. Within each treatment block, plots with and without Lupinus were surveyed, resulting in a completely randomized, split-plot block design with subsampling.

Sampling methods and analysis

Variables related to Lupinus abundance, nutrient contribution, and community composition and biomass were sampled during peak growth using a restricted random sampling design. Two 50-m transects placed 25 m apart were established within each treatment–block combination in areas with similar vegetation, soils and elevation. Location of the first quadrat for each transect was randomly assigned and additional quadrats were placed every 2 m thereafter along the transect. Variables were surveyed by placing a 1-m² quadrat on the upslope side of the transect line in tree interspaces. The number of Lupinus plants within each 1-m² quadrat was recorded (n = 28–35 quadrats per treatment block depending on placement of first quadrat). Within a subsample of these quadrats (n = 10–25 per treatment block depending on the number of Lupinus-present plots), the number of seedlings versus resprouting individuals was recorded. This sampling design captured the range of Lupinus density within blocks, but variation in Lupinus density and distribution among blocks led to an unequal number of Lupinus-present and -absent plots.

Experimental design

In 2002, three replicate burn sites (2103, 2225 and 2347 m) and paired control sites (2073, 2195 and 2347 m) were located along the elevation gradient within the canyon. In 2004, three additional burn sites were located adjacent to the previously established burn and control sites. All sites were located on north-facing alluvial fans with intermediate tree cover (30 to 50%). Prescribed burns were conducted in spring 2002 and 2004 and averaged 5–8 ha in size. The fires were cool burns that consumed trees, shrubs and herbaceous vegetation in a patchy nature. Surface fire temperatures averaged 206 ± 24°C in interspaces, 304 ± 26°C under trees and 369 ± 33°C under shrubs, and decreased with soil depth to an average of 41°C at 5 cm for all microsites (Rau et al. 2005).

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To investigate community changes with time since fire, ocular estimates of Lupinus aerial cover and the cover of all other functional groups (annual grass and forb, perennial grass and forb, shrub) present within the 1-m² quadrat were made to the nearest percentage. To minimize variation due to the individual observer, cover-estimates were first calibrated using a test plot. Standing biomass of Lupinus and each functional group was harvested in a subsample of the quadrats (n = 6 per treatment block). Within three randomly selected quadrats along each transect, a 0.1-m² quadrat was placed within the 1-m² survey quadrat. Vegetation is fairly uniform across sites; therefore, this size of quadrat provided a representative sample of herbaceous vegetation. For quadrats lacking Lupinus, the 0.1-m² quadrat was placed in the center of the plot to create a buffer area of at least 1 m² with no Lupinus plants. For quadrats containing Lupinus, the 0.1-m² quadrat was centered on a Lupinus plant to ensure that sampling was within the area affected by Lupinus. Within these quadrats, biomass was clipped to the ground, sorted by functional group, dried at 65°C for 48 h and weighed. Lupinus plants from each quadrat were composited, ground in a Wiley mill (UDY Corp, Fort Collins, CO) and analyzed for N, carbon (C) and phosphorus (P) concentrations. Percentage of C and N were assessed by combustion of a 0.15-g subsample of ground tissue (LECO TruSpec CN analyzer, St Joseph, MI). Phosphorus concentrations (µg g⁻¹) were obtained by ashing a 0.5-g subsample in a muffle furnace at 500°C for 4 h. Ashed material was solubilized with 20 mL of 0.1 M HCl and 0.5 mL nitric acid, diluted with de-ionized water in a 100-mL volumetric flask (Miller 1998) and analyzed colorimetrically (Lachat Instruments, Milwaukee, WI). Plant N, C and P content were calculated by multiplying tissue concentration by plant weight. No individual forb species was present in enough sampling plots for an adequate comparison; therefore, tissue of another common species, Poa secunda (hereafter Poa), also was ground and analyzed for total C and N to serve as a non-legume comparison.

To determine if Lupinus is altering extractable inorganic soil N, a soil sample was collected from the center of biomass quadrats (n = 6 per treatment block). All soil samples were located in tree and shrub interspaces and included the 0–10-cm depth. Samples were homogenized, air-dried and sieved to remove particles >2 mm. Inorganic N (NH₄⁺-N + NO₃⁻-N) levels were obtained by extraction with 2.0 M KCl and analyzed colorimetrically (Robertson et al. 1999; Lachat Instruments). Although measuring amounts of extractable inorganic N may suggest whether Lupinus presence and fire are influencing the
amount of extractable inorganic soil N at this sampling period, it is only a static, one-time measure of N levels. Therefore, rates of potential net N mineralisation were assessed with an aerobic lab incubation to examine the relative effect of Lupinus and fire on available soil N. A 10-g subsample of air-dried, sieved soil was wet to 55% field capacity and incubated in the dark at 25°C for 30 days. Inorganic N (NH$_4^+$-N + NO$_3^-$-N) levels after the 30-day incubation were obtained as above. Potential net N mineralisation was calculated as final minus initial concentration of extractable inorganic N (NH$_4^+$-N + NO$_3^-$-N). To determine total soil C and N, a 0.25-g subsample was ground and combusted (Sollins et al. 1999; LECO TruSpec CN analyzer).

Data analysis

Differences in Lupinus density, cover, size and tissue P concentration and content data were analyzed as a completely randomized block design with three treatments (control, 1 year post-burn and 3 years post-burn) and subsampling. A mixed effects model was used in which treatment was a fixed effect, and block and treatment by block were random effects. Differences in tissue C and N concentration and content between Lupinus and Poa were analyzed with species as an additional fixed factor. To examine differences in soil ammonium, nitrate, potential net N mineralisation and total C and N, as well as differences in cover of functional groups, Lupinus presence or absence was included as a split plot within treatment and treated as a fixed factor. Owing to differences in sampling, treatment effects on biomass were analyzed separately for Lupinus-present and -absent quadrats. In addition, relationships between Lupinus variables and soil variables also were examined using regression. All data were assessed and transformed as necessary to meet assumptions of normality and equality of variance. For results with significant effects, mean comparisons were assessed using Tukey adjusted least square means for multiple comparisons and considered significant at the 95% confidence level ($\alpha = 0.05$). All analyses were conducted using SAS ver. 9.1.

Results

Soil nitrogen

We measured interspace environments and, although the 1-year-old burn treatment tended to have higher concentrations of extractable soil NH$_4^+$-N and NO$_3^-$-N, neither inorganic N nor rates of potential net N mineralisation differed among burn treatments (F$_2,4 = 0.36$, P = 0.716, F$_2,4 = 2.28$, P = 0.218 and F$_2,4 = 1.47$, P = 0.338 for NH$_4^+$-N, NO$_3^-$-N and N mineralisation respectively). However, combining data across treatments indicated that higher levels of inorganic N occurred in quadrats that contained Lupinus than quadrats without Lupinus (F$_1,33 = 4.13$, P = 0.05 and F$_1,33 = 9.32$, P = 0.005 for NH$_4^+$-N and NO$_3^-$-N respectively). Although this trend is apparent in both control and burned treatments (Fig. 1a), differences between Lupinus presence and absence within treatment were only significant in the unburned control plots (P < 0.05). This trend also was present for rates of potential net N mineralisation (Fig. 1b), although differences were not significant (F$_1,33 = 0.12$, P = 0.739). For both inorganic N amounts and N mineralisation, differences for the 3-year post-fire treatment should be treated with caution, as the high abundance of Lupinus led to only one Lupinus-absent quadrat being sampled in this treatment–block combination (Fig. 1a, b).

To determine what aspect of Lupinus presence may be influencing these results, the effects of Lupinus variables on soil variables were examined. Although Lupinus presence influenced the amount of extractable inorganic N, no measured Lupinus variable was significantly correlated with soil extractable N across all burn treatments. However, examining burn treatments individually indicated that Lupinus biomass was positively correlated with extractable NO$_3^-$-N in unburned treatments ($r^2 = 0.205$, P = 0.06). In contrast, Lupinus presence did not have a significant effect on N mineralisation rates, but Lupinus biomass was positively correlated with N mineralisation rates across both burned and unburned treatments ($r^2 = 0.2425$, P = 0.0106).

Percentage total N in the soils followed a similar pattern to extractable inorganic N, although there were no significant differences related to time since burn or Lupinus presence (Table 2). Soil C : N ratios did not differ with time since fire or Lupinus presence and averaged 13 for all sites (Table 2).
Lupinus density, size distribution, cover and standing biomass

Total Lupinus density was not affected by time since fire ($F_{2,4} = 4.26, P = 0.102$), although there was an increase in the proportion of seedlings to adults ($F_{2,4} = 60.11, P = 0.001$). Three years after fire, average Lupinus density was four times greater than in controls or the 1-year post-fire treatment and approximately 40% of plots contained 10 or more Lupinus plants per m². The greatest density of seedlings occurred in the 3-year post-fire treatment (Fig. 2a).

Plants tended to increase in size with time since fire, but there was large variability in Lupinus standing biomass among treatments ($F_{2,4} = 0.45, P = 0.6663$) (Fig. 2b). One year post-fire, Lupinus biomass averaged greater than 50 g m⁻² and made up 61% of herbaceous plant biomass. This amount was nearly twice that in unburned control treatments (25 g m⁻², 39%). Three years post-fire, Lupinus biomass averaged 150 g m⁻². All plant functional groups tended to have greater standing biomass production 3 years after fire (see Community productivity and composition section), but Lupinus still comprised greater than 50% of the total herbaceous plant biomass.

Lupinus cover also tended to increase with prescribed fire but differences were not significant ($F_{2,4} = 2.63, P = 0.187$, Fig. 2c). One year after fire, Lupinus cover averaged 5% m⁻² and made up 22.7% of total plant cover. This was almost twice that of unburned controls (3.5% cover m⁻², 11.6% of total). By 3 years after fire, mean Lupinus cover was more than double that in 1-year post-fire treatment. In these older burns, cover of all plant functional groups was greater, but Lupinus cover still made up roughly a quarter of the total plant cover (23.4%).

Tissue chemistry

Concentration of total C, N and P in Lupinus tissue did not differ among treatments (Fig. 3a, b, c). Lupinus tissue from all sites had high concentrations of N, leading to low C : N ratios (mean of 16) for all treatments (Fig. 4). The increase in standing biomass increased C, N and P content with time since fire, although differences were not significant ($F_{2,4} = 4.42, P < 0.097, F_{2,4} = 5.17, P < 0.078$ and $F_{2,4} = 6.52, P < 0.055$ for C, N and P respectively) (Fig. 3a, b, c). In contrast to Lupinus, Poa tissue N concentration followed the pattern for extractable soil N and was highest 1 year post-burn. Tissue N concentrations from Poa in the 1-year post-burn treatment contained almost twice as much N as those from the control and 3-year post-burn treatments (Fig. 3c).

The N concentrations of Lupinus were almost two times higher than those for Poa in all but the 1-year post-fire treatment. Owing to higher plant biomass, Lupinus had a 2–13 times higher N content than Poa for all treatments ($F_{1,23} = 59.57$,
Fig. 3. Tissue concentrations and content with time since fire, including Lupinus (a) carbon; (b) nitrogen; (c) phosphorus; and Poa (d) carbon; (e) nitrogen. Owing to small amounts of tissue, phosphorus analysis was only conducted on Lupinus. Phosphorus concentration is in different units owing to analysis method. Values are mean ± s.e. n = 9 per burn treatment.

Greater standing biomass in Lupinus led to higher C content in Lupinus than Poa for all treatments (F_{1,23} = 31.61, P < 0.0001). Lupinus had significantly lower C:N ratios than Poa for all treatment combinations except the 2004 burn (F_{2,23} = 14.71, P < 0.0001, Fig. 4).

Community standing biomass and composition

Total herbaceous standing biomass tended to be greater with time since fire and in the presence of Lupinus. However, much of the observed increase in total biomass between the unburned control and the two burns was due to the increased growth of Lupinus. Community composition also was affected by prescribed fire (Fig. 5). Most functional groups tended to increase in cover with time since fire, but Lupinus became the dominant functional group after fire. Among the other functional groups, the most notable change was the decrease in shrub cover following prescribed fire (14.5 to <1% 1 year after fire, F_{2,4} = 6.36 P = 0.057). The cover of perennial grasses also tended to be influenced by time since fire (F_{2,4} = 6.23, P = 0.059). Cover of this functional group decreased by almost half in the year following fire (4.3 to 2.6%), but was more than triple that of the 1-year post-fire treatment by 3 years after fire (2.6 to 8%, mean comparison, P = 0.069). Cover of perennial grasses also tended to increase in Lupinus-present plots (F_{2,4} = 3.22, P = 0.0739) and differences were greatest 3 years after fire (Fig. 5). The cover of both annual and perennial forbs tended to increase with time since fire although differences were not significant. Cover of perennial forbs did increase in the presence of Lupinus (F_{2,4} = 8.73, P = 0.0034), with differences being greatest 1 year after fire. The only annual grass in the study watershed
Control

\[ \text{Lupinus} \]
\[ \text{Poa} \]

1 year post-fire

3 years post-fire

\[ \text{C : N ratio} \]

0
10
20
30
40
50
60

Fig. 4. C : N ratio of both Lupinus and Poa. Values are mean ± s.e. \( n = 9 \) per burn treatment; asterisks indicate significant differences between species within burn treatment at \( P < 0.001 \).

was Bromus tectorum. The cover of this exotic, annual grass was highest on older burned sites, although the low frequency of occurrence led to no significant differences for treatment or Lupinus presence.

**Discussion**

The presence of Lupinus had a greater effect on extractable inorganic and mineralisable soil N than time since fire at our site. Most studies investigating the effect of fire on soil N find a pulse in inorganic N after fire (Certini 2005) and an increase in available N was observed in a different study within the same watershed (Rau et al. 2007). Although our soils exhibited this characteristic trend of increased inorganic N after fire, only the effect of Lupinus presence was significant. The lack of a significant fire effect was likely due to the fact that we examined interspace soils, which typically exhibit smaller differences in post-fire extractable inorganic N than under shrub and under tree microsites (Chambers et al. 2007; Rau et al. 2007). Numerous other studies, in a variety of systems, have found that the presence of N\textsubscript{2}-fixing species results in elevated soil inorganic N (Vitousek and Walker 1989; Maron and Jefferies 1999; Johnson et al. 2004). However, few studies have examined the combined effect of fire on soil N and the presence or absence of N\textsubscript{2}-fixing species. Our study showed that the presence of Lupinus increased inorganic soil N and N mineralisation regardless of time since fire. This suggests that the combined effects of fire and legumes on soil N are greater than the effects of either fire or Lupinus alone. Thus, comparisons of soil N in relation to fire need to consider the presence of N\textsubscript{2}-fixing species like Lupinus.

Fire did not directly influence the amount of extractable inorganic N in the soil, but it did have an indirect influence via its effect on Lupinus. Density of Lupinus tended to increase following fire and was greatest 3 years after fire. In other ecosystems, including the tallgrass prairie and pine forests of the southeastern US, legumes also respond positively to fire (Towne and Knapp 1996; Hendricks and Boring 1999; Newland and DeLuca 2000). In our study, recently burned sites consisted mostly of resprouting individuals. Germination of many legumes is stimulated by the heat and chemical cues associated with fire.
Although we did not directly measure N2 fixation in the present study, the high concentrations of N in atmospheric N. Although Lupinus may have benefited Lupinus. Also, N2 fixation is not always negatively affected by increases in soil N following fire (Hiers et al. 2003). Casals et al. (2005) found that both seedling and resprouting legume species derived 52–99% of their N from fixation after fire, despite increased amounts of mineral N in burned plots. Similarly, N2 fixation rates of Macrozamia riedlei in south-western Australia were greatest the year following fire and gradually decreased with time since fire (Grove et al. 1980).

Although we did not directly measure N2 fixation in the present study, the high concentrations of N in Lupinus tissue suggest that fixation was occurring.

The ability of legume species to fix N2 in the presence of elevated soil inorganic N may allow them to maintain high levels of tissue N concentration in the face of fluctuating resource availability (Marschner 1986). Although Lupinus biomass increased in burned treatments, tissue N concentrations did not decrease. It is possible that Lupinus tissue N is mostly derived from fixed N, making the amount of available soil N less influential than for other species. The 3-year post-fire treatment had the greatest amount of biomass production for Lupinus (and most other functional groups), but also the lowest amounts of available soil N. Although numerous studies have shown that tissue nutrient concentrations increase after fire (Anderson and Menges 1997; Bennett et al. 2002; Rau et al. 2008), studies examining response of legumes often find results similar to ours. Legume tissue N concentration was not affected by fire in pine forests, although other species did show an increase in tissue N concentrations (Lajeunesse et al. 2006; Metzger et al. 2006). In the present study, only Poe tissue concentrations followed a pattern that resembled that of available soil N, again suggesting that Lupinus is supplementing its N requirement through fixation of atmospheric N.

Total standing biomass and plant cover tended to increase with time since fire, especially where Lupinus was present. Higher overall resource availability in the post-fire environment typically results in increased biomass and cover of most functional groups. In a companion study, Rau et al. (2008) found that biomass of five out of six native species increased within 2 years after prescribed fire. Similarly, Hobbs and Schimel (1984) reported an increase in aboveground biomass within 2 years after fire in shrub and grassland ecosystems of Colorado, USA. In our study, much of the increase in standing biomass and cover after the fire could be attributed to Lupinus itself. In a high-elevation ecosystem, biomass in patches of the N2-fixing species Trifolium dasyphyllum was two times greater than in surrounding patches owing to greater biomass of Trifolium rather than differences in the biomass of other plants (Thomas and Bowman 1998).

We found that the presence of Lupinus was associated with higher cover of certain functional groups. This association could be due to similar preferences for growing conditions; however, it also could indicate that Lupinus is facilitating the growth of neighboring plants in sagebrush ecosystems. Legumes often act as facilitators in harsh environments (Morris and Wood 1989; Pugnaire and Haase 1996; Gosling 2005). In our system, Lupinus may facilitate other functional groups by modifying various aspects of the resource environment depending on time since fire. On both unburned and older burned sites with relatively low levels of N, Lupinus may be decreasing competition for soil N if it is fixing its own N. Decreased competition could result from reduced N uptake by Lupinus or from release of N due to decomposition of N-rich litter (Kenny and Cuany 1990; Hendricks and Boring 1992; Maron and Connors 1996), which may be increased by fire. Further, inputs of organic N by Lupinus via rhizodeposition (Goergen et al. 2009) and turnover of belowground tissue, especially nodules, can promote recovery of microbial biomass and activity, which are strongly related to soil nutrient availability (Coleman et al. 2004; Booth et al. 2005). On recently burned sites with relatively high levels of extractable inorganic N, rapidly resprouting Lupinus also may modify microenvironmental conditions (light and temperature), facilitating seedling establishment and plant growth.

Results of the present study indicate that Lupinus has the potential to both modify available soil N and increase productivity in sagebrush ecosystems like elsewhere (Vitousek and Walker 1989; Jacob et al. 2000; Spehn et al. 2002). The apparent independence of Lupinus tissue N concentrations from soil N concentrations suggests that the functional role of this species may be especially important in low-nutrient systems. The ability of Lupinus to increase N availability can serve to promote resilience of native ecosystems, but also may create an avenue for invasion. Although B. tectorum was not yet a dominant component at our sites, differential resource use, faster growth rate, superior competitive ability and greater seed production of this aggressive annual grass under increased N availability compared with native species can influence recruitment into these systems (Melgoza et al. 1990; Lowe et al. 2002; Monaco et al. 2003). Although the increased N associated with Lupinus has the potential to shift community composition from native to alien dominance, ultimately, the effect of Lupinus presence will depend on the relative degree of competition and the composition of native perennial herbaceous species following fire.

Lupinus appears to affect compositional change through rapid establishment in open microsites following fire and facilitation
of particular plant functional groups. Perennial grass and forb cover exhibited the greatest response to the presence of Lupinus. Recent studies suggest that relatively high cover of perennial herbaceous species can increase the resilience of sagebrush ecosystems following fire and increase resistance to invasion by exotics such as Bromus tectorum (Booth et al. 2003; Chambers et al. 2007). Further experimentation in this area is needed to gain a better understanding of the effects of Lupinus facilitation on community composition and invasion events in sagebrush systems.

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