

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, *Lupinus argenteus* (Pursh), and the effects of *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 *Lupinus* presence regardless of time since fire. *Lupinus* density increased after fire mainly owing to increased seedling numbers 3 years post-burn. Fire did not affect *Lupinus* tissue N and P concentrations, but cover of perennial grasses and forbs was higher in *Lupinus* presence. The invasive annual grass *Bromus tectorum* had low abundance and was unaffected by treatments. Results indicate that *Lupinus* has the potential to influence succession through modification of the post-fire environment.

Additional keywords: community recovery, disturbance, *Lupinus argenteus*, nitrogen.

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 understorey shrubs and herbaceous vegetation (Tausch and Tueller 1990; Miller *et al.* 2000) and depletion of the native understorey species seedbank (Koniak 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 (Koniak 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.* 2006). 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.* 2005). However, in the short term, fire often results in a pulse of available nutrients (Neary *et al.* 1999; Wan *et al.* 2001). Following low-severity fires, increases in available nutrients occur owing to deposition of ash onto the soil surface, release of orthophosphate and NH_4^+ from organic matter, decomposition of belowground biomass, and further oxidation of NH_4^+ to NO_3^- (Raison 1979; Hobbs 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 understorey 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 (Wroblewski 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 *et al.* 2002) by increasing available soil N via higher N mineralisation and nitrification (Vitousek and Walker 1989; Maron and Jefferies 1999; Myrold and Huss-Danell 2003; Johnson *et al.* 2004). If establishment and growth of native N₂-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 arboreus* 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 ceteraceum* 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°35'83"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 Haploxerolls. 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 ranged 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.

Table 1. Climate data for the study period from nearby Reese River, O'Toole, Nevada (station ID 266746)
Values are annual mean $\pm$ standard deviation for 33-year average

	Precipitation (mm) October–June	Maximum temperature (°C) April–June	Minimum temperature (°C) April–June
33-year average	145 $\pm$ 14	19.0 $\pm$ 2.6	−0.8 $\pm$ 1.3
2002	168	20.1	−1.1
2003	97	18.7	−1.3
2004	184	19.9	−1.2
2005	160	17.8	−1.2

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 $\pm$ 24°C in interspaces, 304 $\pm$ 26°C under trees and 369 $\pm$ 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.

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 nested 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 (g 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 ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) 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 ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$). 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 $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$, 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 $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$ 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 $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ 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

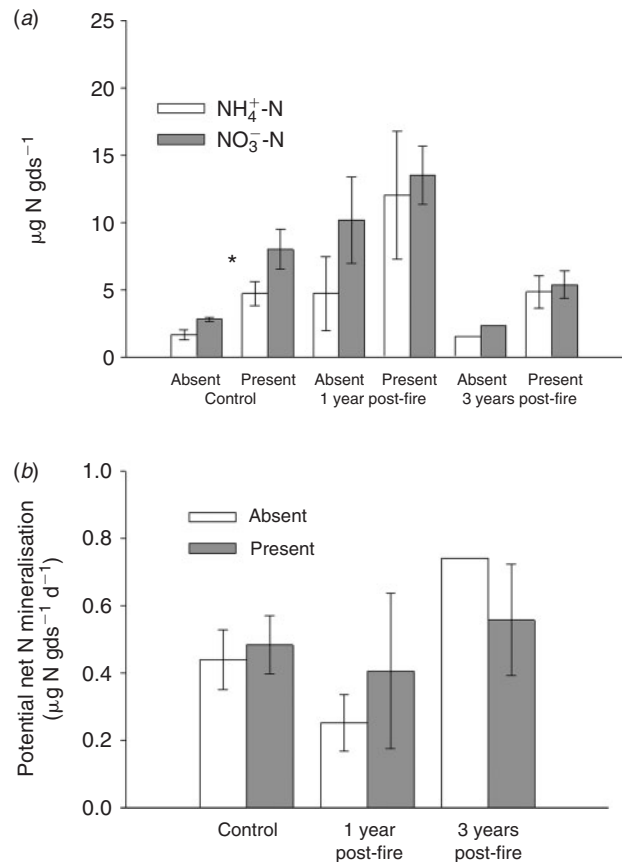


Fig. 1. Extractable soil $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ (a); and potential net N mineralisation (b) with time since fire in the absence and presence of *Lupinus*. The abundance of *Lupinus* at the 3-year post-fire sites led to only one *Lupinus* absent quadrat being sampled. $n = 6$ plots per burn treatment block. Values are means $\pm$ s.e.; asterisk indicates significant differences in inorganic N between *Lupinus* present and absent plots at $P < 0.05$. gds, gram dry soil.

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 $\text{NO}_3^-\text{-N}$ in unburned treatments ($r^2 = 0.2015$, $P = 0.06$). 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).

Table 2. Total C, N and C : N ratio for control, 1-year post-fire, and 3-year post-fire soils in the presence and absence of *Lupinus*
Values are mean $\pm$ s.e.

	Total C (%)	Total N (%)	C : N
Control			
+ <i>Lupinus</i>	3.78 $\pm$ 0.05	0.27 $\pm$ 0.01	13.9 $\pm$ 0.4
- <i>Lupinus</i>	2.31 $\pm$ 0.37	0.18 $\pm$ 0.04	13.2 $\pm$ 1.1
1 year after fire			
+ <i>Lupinus</i>	4.97 $\pm$ 1.11	0.40 $\pm$ 0.10	12.8 $\pm$ 0.2
- <i>Lupinus</i>	3.44 $\pm$ 1.73	0.27 $\pm$ 0.14	13.4 $\pm$ 0.7
3 years after fire			
+ <i>Lupinus</i>	3.62 $\pm$ 0.58	0.28 $\pm$ 0.05	13.2 $\pm$ 0.3
- <i>Lupinus</i>	5.07 $\pm$ 0.0	0.35 $\pm$ 0.0	14.7 $\pm$ 0.0

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 m^2 . 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 $5\% \text{ m}^{-2}$ and made up 22.7% of total plant cover. This was almost twice that of unburned controls ($3.5\% \text{ cover m}^{-2}$, 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

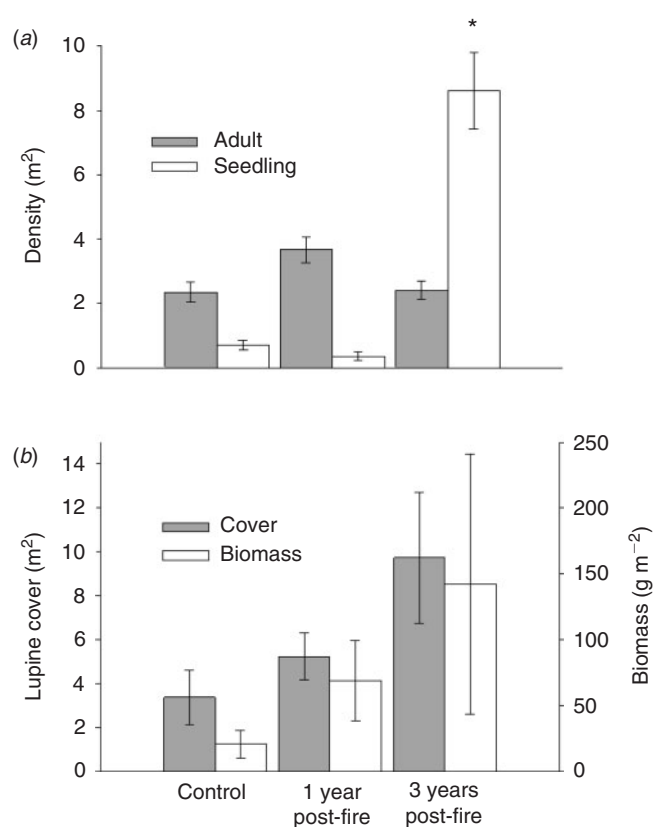


Fig. 2. *Lupinus* response to time since fire as measured by (a) density of adult and seedlings (m^2 ; $n = 18$ per treatment); (b) biomass production ($n = 18$ per treatment) and cover ($n = 25\text{--}38$ per treatment). Values are means $\pm$ s.e.; asterisk indicates significant differences in seedling density among burn treatments at $P < 0.05$.

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. 3e).

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 ($F_{1,23} = 59.57$,

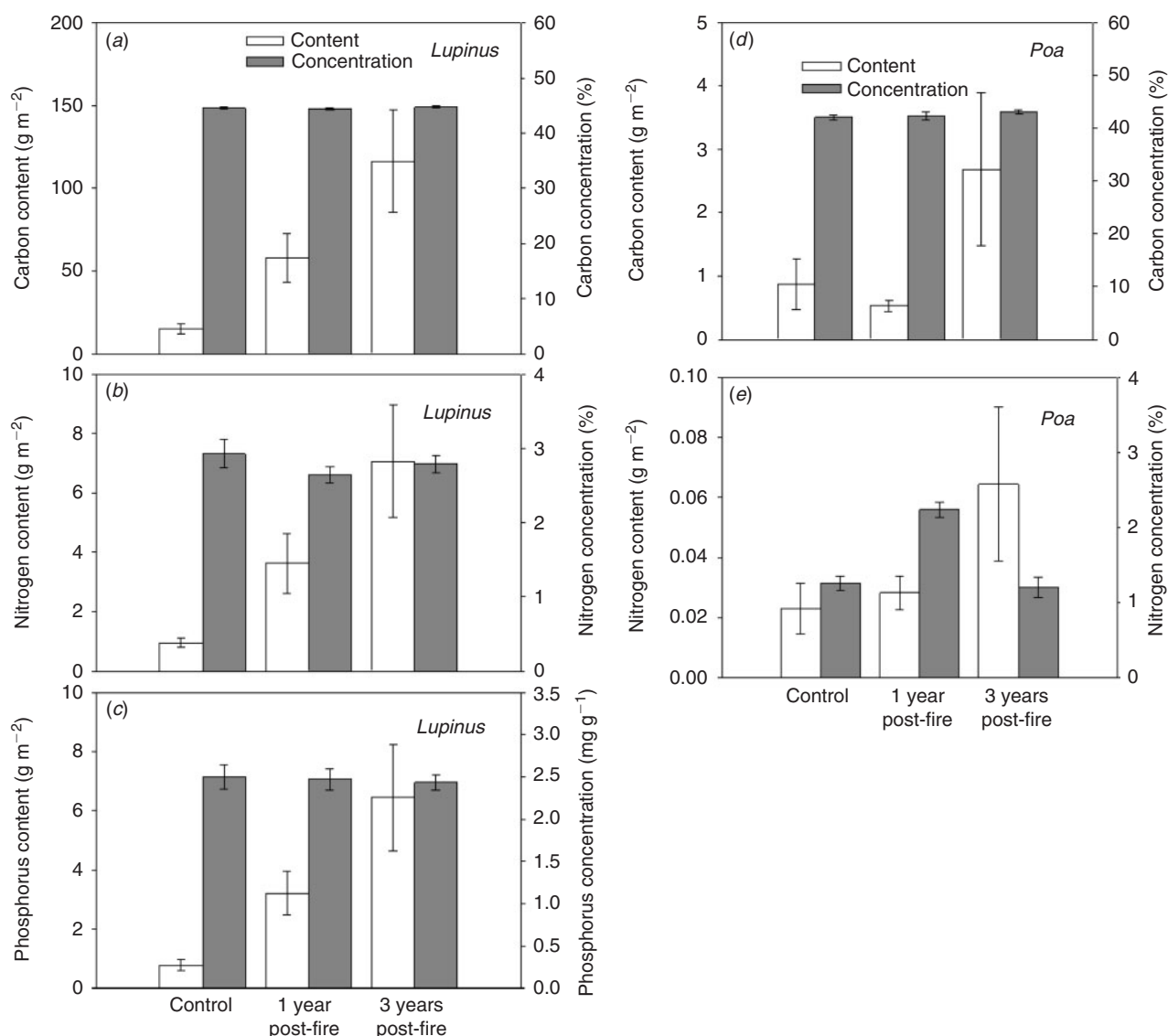


Fig. 3. Tissue concentrations and content with time since fire, including *Lupinus* (a) carbon; (b) nitrogen; (c) phosphorus; and *Poa* (d) carbon; (e) nitrogen. Owing to small amounts of tissue, phosphorus analysis was only conducted on *Lupinus*. Phosphorus concentration is in different units owing to analysis method. Values are mean $\pm$ s.e. $n = 9$ per burn treatment.

$P < 0.0001$). 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

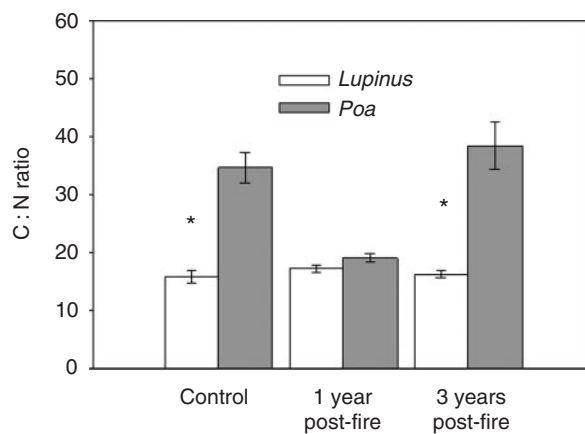


Fig. 4. C:N ratio of both *Lupinus* and *Poa*. Values are mean $\pm$ s.e. $n = 9$ per burn treatment; asterisks indicate significant differences between species within burn treatment at $P < 0.001$.

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_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_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_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 south-eastern 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

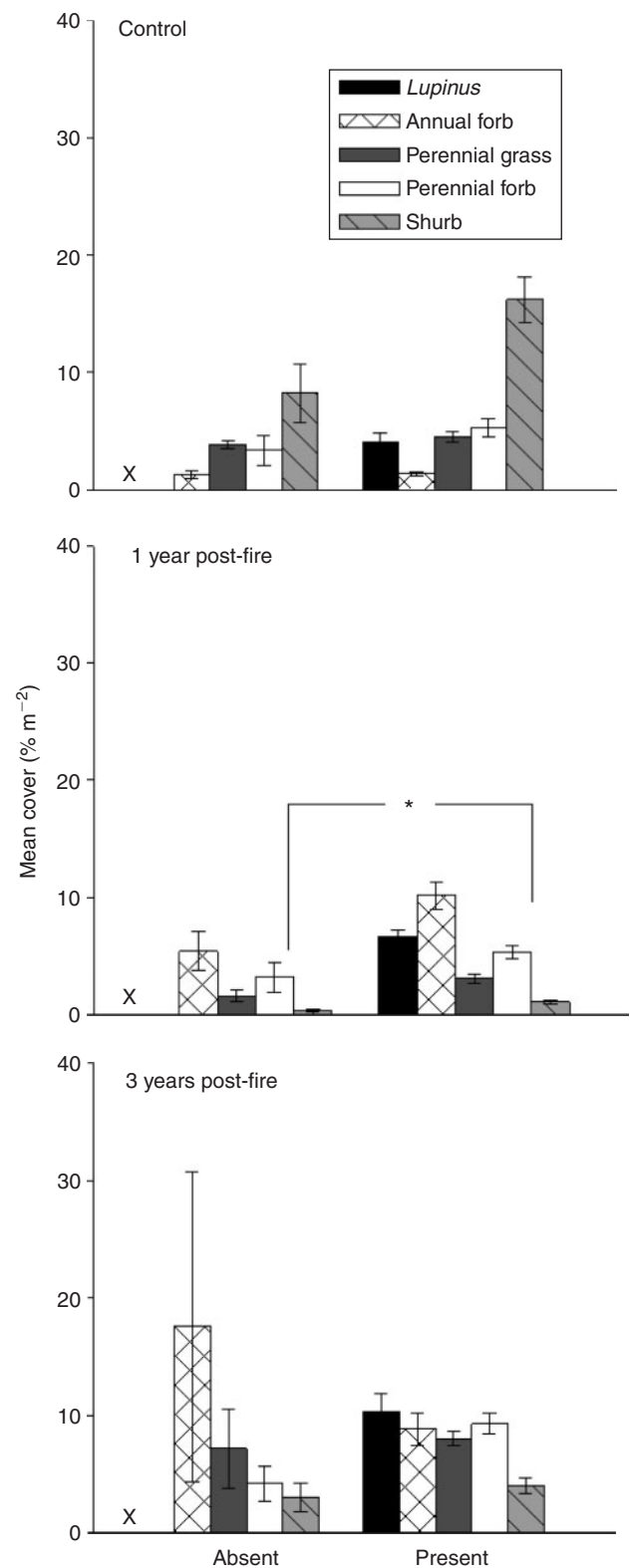


Fig. 5. Functional group response to time since fire in the absence and presence of *Lupinus* for the unburned control, 1-year post-fire and 3-years post-fire treatments. Values are mean cover $\pm$ s.e. $n = 28$ –35 plots per treatment per block; asterisk indicates significant differences between *Lupinus* absence or presence within burn treatment at $P < 0.05$.

(Martin *et al.* 1975; Bradstock and Auld 1995; Hendricks and Boring 1999; Williams *et al.* 2004), but burning can result in seed mortality and harsher conditions for seedling establishment (Chambers and Linnerooth 2001; Williams *et al.* 2003). An increase in seed production the year following fire and favorable conditions for establishment likely resulted in high numbers of seedlings by the third year after fire. Prescribed fire in the Great Basin increased reproductive output of five out of nine species (Wroblewski and Kauffman 2003). Similarly, higher plant density, seed production and reduced seed predation in recently burned areas increased rates of seedling establishment of *Liatris scariosa* in north-eastern grasslands (Vickery 2002).

The increase of *Lupinus* after fire may be in response to changes in availability of limiting resources other than N such as light, water, or P (Vitousek and Field 1999; Casals *et al.* 2005). In a companion study conducted at our field sites, Rau *et al.* (2007) found that P increased in burned plots within 2 years after the prescribed burn. Legumes are often limited by P (Vitousek and Field 1999) and increased availability of P by 3 years post-burn may have contributed to the increased density, biomass and cover of *Lupinus*. In contrast, increased soil N often reduces the competitive advantage to legumes and, therefore, their abundance (Lauenroth and Dodd 1979; Zahran 1999). In our study, we observed slightly lower N mineralisation 1 year after fire, which 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 *Poa* 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; Jacot *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 plant 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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