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Facilitation and interference of seedling establishment by a native legume before and after wildfire

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Abstract In semi-arid ecosystems, heterogeneous resources can lead to variable seedling recruitment. Existing vegetation can influence seedling establishment by modifying the resource and physical environment. We asked how a native legume, *Lupinus argenteus*, modifies microenvironments in unburned and burned sagebrush steppe, and if *L. argenteus* presence facilitates seedling establishment of native species and the non-native annual grass, *Bromus tectorum*. Field treatments examined mechanisms by which *L. argenteus* likely influences establishment: (1) live *L. argenteus*; (2) dead *L. argenteus*; (3) no *L. argenteus*; (4) no *L. argenteus* with *L. argenteus* litter; (5) no *L. argenteus* with inert litter; and (6) mock *L. argenteus*. Response variables included soil nitrogen, moisture, temperature, solar radiation, and seedling establishment of the natives *Elymus multisetus* and *Eriogonum umbellatum*, and non-native *B. tectorum*. In both unburned and burned communities, there was higher spring soil moisture, increased shade and reduced maximum temperatures under *L. argenteus* canopies. Adult *L. argenteus* resulted in greater amounts of soil nitrogen (N) only in burned sagebrush steppe, but *L. argenteus* litter increased soil N under both unburned and burned conditions. Although *L. argenteus* negatively affected emergence and survival of *B. tectorum* overall, its presence increased *B. tectorum* biomass and reproduction in unburned plots. However,
L. argenteus had positive facilitative effects on size and survival of *E. multisetus* in both unburned and burned plots. Our study indicates that *L. argenteus* can facilitate seedling establishment in semi-arid systems, but net effects depend on the species examined, traits measured, and level of abiotic stress.

Keywords *Bromus tectorum* · Invasion · *Lupinus argenteus* · Nitrogen · Sagebrush steppe

Introduction

In arid and semi-arid ecosystems, resources are spatially and temporally heterogeneous (Jackson and Caldwell 1993; Schlesinger and Pilmanis 1998) leading to differential seedling recruitment (Maestre et al. 2003; Chesson et al. 2004). In these harsh, low nutrient environments, factors that increase resource availability can enhance seedling establishment of both native (Callaway 1995; Pugnaire et al. 1996; Moro et al. 1997) and non-native species (Lenz and Facelli 2003; Cavieres et al. 2005). At landscape scales, increases in resources are often caused by disturbances such as wildfire. At more local scales, existing vegetation can alter resources directly by modifying the microenvironment or by increasing resource availability, or indirectly via reduced competition, introduction of beneficial soil microorganisms, or protection from herbivores (Bertness and Callaway 1994; Callaway 1995; Bruno et al. 2003; Brooker et al. 2008). Such modifications of resources can alter interactions among seedlings and mature plants. The net outcomes of these interactions depend on current environmental conditions and the life histories and ecophysiological characteristics of the

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interacting species and can be positive, negative, or neutral (Brooker et al. 2008; Maestre et al. 2009). Although it is widely recognized that the prevalence of facilitation often depends on environmental conditions (Pugnaire and Luque 2001; Bruno et al. 2003; Brooker et al. 2008), few studies have investigated the effects of fire on interactions among mature plants and seedlings or the mechanisms involved.

Wildfire is a dominant disturbance in arid and semi-arid systems that can alter environmental conditions and influence facilitative and competitive interactions. After fire, available light and soil moisture increase due to reduced plant presence, and soil temperature increases as a result of blackened soil surfaces (Chambers and Linnerooth 2001). Fire also results in short-term increases in nutrient availability, especially nitrogen (N) (Wan et al. 2001). Although post-fire conditions may favor seedling establishment of certain species, it can also result in harsher conditions that reduce seedling establishment of other species (Chambers and Linnerooth 2001). Species that recover after fire can modify the environment to make it more hospitable. Germination of many legumes is stimulated by heat and chemical cues associated with fire (Bradstock and Auld 1995), and perennial legumes quickly resprout after fire, resulting in increased density (Goergen and Chambers 2009). In the post-fire environment, the functional role of legumes may differ from that of the pre-burned environment due to differences in resources limiting to establishment (Goergen and Chambers 2009).

Like many other species, legumes can facilitate seedling establishment by modifying abiotic microsite conditions or by fostering different microbial communities. Most studies have focused on the capacity of legumes to fix atmospheric N, and, therefore, hypothesize that facilitation by legumes is due to increases in available soil N (Maron and Connors 1996; Maron and Jefferies 1999). The specific mechanisms responsible for this increase are rarely examined, but could occur through a number of pathways. N can be added through decomposition of nutrient-rich tissue following death of the plant (Maron and Connors 1996), "leaking" of fixed N from live plant roots (Goergen et al. 2009), or reduced uptake of soil N due to acquiring N from fixation (N sparing, Trannin et al. 2000).

In sagebrush steppe, the native perennial N_2-fixing legume, *Lupinus argenteus* (Pursh) can comprise a large component of the vegetation, especially after fire (Goergen and Chambers 2009). This species can alter resources by increasing N availability and by modifying environmental conditions that influence seedling establishment. High tissue N concentrations and low C:N ratios indicate that *L. argenteus* can provide substantial amounts of N through rapid litter decomposition (Metzger et al. 2006; Goergen et al. 2009). Also, exudation of organic N into the rhizosphere by *L. argenteus* indicates that this species can influence N availability while actively growing (Goergen et al. 2009). Finally, this herbaceous, bushy perennial can reach a height and diameter of 0.5 m × 0.5 m, and thus has the potential to alter environmental conditions through modification of the microclimate beneath its canopy (light, moisture, temperature).

The ability of legumes to modify resource availability and microsite conditions may promote recruitment of native species, but may also create an avenue for invasion. Modification of resource availability, especially N, is particularly important for promoting establishment and spread of non-native annual grasses (Huenneke et al. 1990). Sagebrush ecosystems are threatened by the widespread invasion of the annual grass, *Bromus tectorum* (L.). Early growth of *B. tectorum* combined with high growth rates can result in pre-emption of resources (Knapp 1996; James 2008a, b). Rapid accumulation of *B. tectorum* biomass can increase fine fuels and result in more frequent and larger fires (D'Antonio and Vitousek 1992). *Bromus tectorum* benefits from additional N (Monaco et al. 2003), and increased nutrient availability after fire combined with N input from legumes may increase both establishment and reproductive output of *B. tectorum*. Although legumes are suggested to have facilitated establishment and invasion of seedlings in other systems (e.g., Morris and Wood 1989; Maron and Connors 1996), facilitation by legumes has not been reported in sagebrush steppe.

We examined the potential of a native legume, *L. argenteus*, to facilitate seedling establishment of *B. tectorum* and native perennial herbaceous species in sagebrush steppe. Because a wildfire burned through the study area during the second year of the study, we were able to examine mechanisms of facilitation in both unburned and burned sagebrush steppe. We addressed three questions: (1) How does *L. argenteus* modify the resource environment in unburned and burned sagebrush steppe, and for N, what is the dominant mechanism? (2) Does resource modification by *L. argenteus* facilitate seedling establishment in unburned and burned sagebrush steppe? (3) Do the effects of *L. argenteus* on seedling establishment differ depending on species life form or nativity in unburned and burned sagebrush steppe?

Materials and methods

Study area

The study area is 25 km NW of Reno, Nevada, USA (39°40′N, 120°03′W, elevation ~1,615 m) at the east face of the Sierra Nevada foothills (slope 2–3%). Study sites were located in three small watersheds on predominantly north-facing aspects. Soils are classified as well draining, very stony, sandy loam Xerollic Durargids of the Trosi

series (Sketchley 1975). Mean temperatures range from −6°C in January to 31°C in July. Mean annual precipitation is 245 mm and arrives mostly in the form of snow or spring rains. Precipitation at the study area was below average for both study years [142 and 176 mm for 2007 and 2008, respectively; Western Regional Climate Center (WRCC) 2008]. The area is grazed during summer, but our study sites were not grazed for a minimum of 1 year prior to our study. Fire is another dominant disturbance, but our sites had not burned in the past 40–50 years (Chris Ross, personal communication).

Vegetation is typical sagebrush steppe dominated by *Artemisia tridentata wyomingensis* and the perennial grasses *Poa secunda* and *Elymus multisetus*. Other dominant herbaceous species include the perennial forbs, *Wyethia mollis*, *Balsamarhiza sagitata*, *Crepis acuminata*, and *Phlox speciosa*. The invasive, annual grass, *B. tectorum*, occurs on the study sites. *Lupinus argenteus* is the most abundant legume although other species, including those in the genera *Astragalus* and *Trifolium*, are present.

Experimental design

We used a manipulative field experiment with a replicated block design. Each of six treatments had five replicate plots located in three separate blocks in unburned (year 1) and burned (year 2) sagebrush steppe ($n = 90$ plots per year). We established blocks in three small watersheds with similar slope, elevation, aspect, soils, vegetation, and fire history. We used six treatments (Table 1) to identify mechanisms by which *L. argenteus* might influence seedling establishment: (1) live *L. argenteus* (LL), (2) dead *L. argenteus* with litter in place (DL), (3) no *L. argenteus* (NL), (4) no *L. argenteus* with *L. argenteus* litter (LLT), (5) no *L. argenteus* with inert, fake litter (FLT), and (6) mock *L. argenteus* (ML). Differences between no *L. argenteus* plots and live *L. argenteus* plots indicated an effect (positive or negative) of *L. argenteus*. When an effect was present, we clarified the likely mechanism(s) responsible for facilitation or interference by examining differences in responses between live *L. argenteus* and remaining treatments.

In spring 2006, we located 20 treatment plots containing 6 or more adult *L. argenteus* and 40 treatment plots without *L. argenteus* within each block. To prevent influence from other N-fixing species present at the field site, we located all plots a minimum of 1 m away from other, non-target N-fixing plants. Dead and live *L. argenteus* treatments were randomly assigned to plots containing adult *L. argenteus*. No *L. argenteus*, fake and *L. argenteus* litter, and mock *L. argenteus* treatments were randomly assigned to plots without *L. argenteus*. Plots consisted of six seeding grids (30 × 30 cm; two per target species) placed directly beneath the treatment (live, dead, or mock *L. argenteus*, *L. argenteus* or fake litter). For no *L. argenteus* treatments, plots were placed in interspaces. Due to limitations associated with the natural distribution of vegetation within sagebrush steppe, plots varied in size but all seeding grids per plot were within a 1 m radius of each other. There was a minimum of 5 m between plots. In DL plots, we treated all *L. argenteus* plants in the plots and within 0.5 m of plots with Round-up^{TM} herbicide during June 2006 and 2007. We added *Lupinus argenteus* litter and inert, fake litter (fabric of similar color and reflective properties as *L. argenteus* tissue cut into 1′ strips) to LLT and FLT plots in October 2006 and 2007 to simulate natural litter fall. For *L. argenteus* litter plots, we added 24 g of *L. argenteus* litter uniformly over top of each seeding grid within the plot (approximately 1 cm deep). This amount was determined by obtaining the average dry mass of *L. argenteus* plants contained within ten randomly located 1-m^2 quadrats and then scaled down to seeding grid size. For fake litter plots, we added 55 g of inert fabric litter to ensure a similar coverage and depth of litter. Litter was kept in place using 1″ vinyl-coated landscaping netting and staples. ML structures (artificial plants of similar size and shape to adult *L. argenteus* staked in place with rebar) were placed in plots in March 2007 and 2008 to correspond with natural resprouting of *L. argenteus* in the field. *Lupinus argenteus* were absent from NL plots, and each LL plot had six or more adult *L. argenteus* plants, averaging 25% cover over each seeding grid.

A wildfire burned all three blocks within the study area in July 2007. The fire consumed most standing vegetation.

Table 1 Experimental treatments and mechanisms being tested by each treatment

Treatment	Mechanism tested
No lupine (NL)	Control—no environmental modification
Live lupine (LL)	Modification of nutrient and physical environment by the whole, live plant
Dead lupine (DL)	Modification of nutrient and physical environment by the decomposing plant
Mock lupine (ML)	Modification of physical environment
Lupine litter (LLT)	Modification of soil surface and nutrient environment by decomposition of aboveground tissue
Fake litter (FLT)	Modification of physical environment at soil surface

Because we were not able to collect 2 years of data for the unburned condition, we examined the same questions, at the same location, for unburned plots in year 1 and burned plots in year 2. In year 2, dead *L. argenteus* (DL) treatments were initiated prior to the fire, but none of the other treatments or seeding had been conducted. We seeded the remaining pre-selected plots in late September of year 2. In year 2, the dead *L. argenteus* treatment only examined the effect of belowground decomposition of plant tissue due to loss of standing dead tissue in the fire. We monitored dead and live *L. argenteus* plots in the spring to verify that *L. argenteus* plants were killed for DL plots and resprouting for LL plots.

Resource environment

Treatment modification of the physical environment was assessed by measuring soil moisture, temperature, and light at the soil surface directly beneath the designated treatment. Within a subsample of plots for each treatment ($n = 3$ per block), we placed an additional, unseeded grid adjacent to our seeding grids. These additional grids were used for soil sampling and allowed us to examine the effect of our treatments on soil water and N without disturbing seedlings. Soil samples for gravimetric soil water content were collected from the 0–10 cm depth monthly over the growing season (March–June 2007 and March–June and August 2008). Soil water content was determined based on wet and oven-dried (100°C) weight. Daily maximum and minimum temperature ($n = 15$ per treatment in year 1 and $n = 9$ in year 2) were recorded with temperature buttons (I button; Maxim, Sunnyvale, CA, USA) buried at 5 cm. Photon flux density (PFD) at the soil surface was recorded in both years during peak plant growth (mid-June) using a LiCor 250 (LICOR, Lincoln, NE, USA) within a subsample of each treatment ($n = 15$ per treatment in year 1 and $n = 9$ in year 2).

Soil extractable inorganic N (NH_4^+–N + NO_3^-–N) status was examined in each treatment on five dates (30 March and 11 June 2007 and 25 March, 17 June, and 19 August 2008). We also characterized soils for potential net N mineralization, and total carbon (C) and N. For all soil nutrient analyses, we collected three samples per treatment per site from the 0–10 cm depth. Samples were air-dried and sieved to <2 mm. Inorganic N (NH_4^+–N + NO_3^-–N) was obtained by extraction with 2.0 M KCl and analyzed colorimetrically (Robertson et al. 1999; LACHAT Instruments, Milwaukee, WI, USA). Rates of potential net N mineralization were assessed by aerobic laboratory incubation. 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 mineralization 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, St. Joseph, MI, USA).

Seedling establishment

Native species with different life form and life history characteristics, a perennial grass and forb, and the invasive annual grass, *B. tectorum*, were chosen to evaluate treatment effects on seedling establishment. *Elymus multisetus* (M. E. Jones), a short-lived perennial grass, has phenology similar to *B. tectorum* (Booth et al. 2003), and can limit *B. tectorum* establishment and reproduction (Humphrey and Schupp 2004). *Eriogonum umbellatum* (Torr.) is a perennial forb with an intermediate life span. Seeds of *E. umbellatum, E. multisetus,* and *B. tectorum* (hereafter *Eriogonum*, *Elymus*, and *Bromus*) were obtained from local Great Basin sources (Comstock Seeds, Gardnerville, NV, USA, for *Eriogonum* and *Elymus*, field collection for *Bromus*). A standard tetrazolium viability test (Moore 1972) indicated that in 2006 and 2007 seeds of *Bromus* were 93 and 99% viable, seeds of *Elymus* were 81 and 82% and *Eriogonum* seeds were 80 and 79% viable. We seeded in late September 2006 and 2007. Each plot contained two seeding grids per species that were planted with 25 filled seeds spaced 4 cm apart. We applied litter treatments over each grid after seeding.

We assessed seedling emergence and survival monthly over the growing season (March–June 2007 and 2008 with an additional sampling of perennials in August 2008). Individual seedlings were marked with toothpicks upon emergence and recorded as alive or dead at each census. Emergence was the cumulative number of seedlings observed in each growing season. Percent survival was the number of seedlings alive at the end of each growing season divided by the total number that emerged. *Bromus* plants were harvested at maturity (mid-June), dried at 60°C for 48 h, sorted by vegetative versus reproductive tissue, and weighed. We recorded height of *Elymus* and number of leaves of *Eriogonum* as a non-destructive estimate of size in mid-June 2007 and 2008 for comparison with *Bromus*.

Data analysis

All analyses were conducted with JMP 5.0.1 (SAS Institute, Cary, NC, USA), and all values are presented as mean ± standard error (SE). Due to differences in baseline condition among years (burned vs. unburned), we analyzed measured variables for each year separately. All data were assessed to verify model assumptions of normality and equality of variance. For environment data (soil moisture, extractable inorganic N, and maximum, minimum, and

temperature difference), we tested for the effect of sampling date (time) and treatment with repeated measures ANOVA. Treatment was a fixed effect, block a random effect, and time a repeated measure. For PFD, we tested for an effect of treatment (block as a random effect). Seedling emergence and survival were assessed with treatment and species as fixed effects and block and plot (nested in treatment and block) as random effects. For significant effects, mean comparisons were assessed using Tukey adjusted least square means for multiple comparisons at the 95% confidence level. Size variables for each species were analyzed separately due to measurement differences.

We quantified the net effect of *L. argenteus* presence using the log response ratio (Ln RR; Pugnaire and Luque 2001). Differences between NL and LL plots for each species response variable (emergence, survival, and size) were assessed using the equation Ln RR = $\mathrm{Ln}(\mathrm{Response}_{\text{live lupine plots}}/\mathrm{Response}_{\text{no lupine plots}})$. Negative values indicated a net negative effect (interference), positive values indicated a net positive effect (facilitation), and values not different from zero indicate a net neutral effect. We used a one-sample *t* test to compare the Ln RR for each species response variable with an expected mean of zero (net neural interaction) to determine the presence of facilitation or inhibition. When facilitation or inhibition occurred, we clarified which environmental variables may potentially be responsible with Spearman's ρ to determine nonparametric correlations between all measured environmental variables and the variable of interest.

Results

Unburned community—year 1

In unburned (2007) sagebrush steppe, soil moisture at 0–10 cm was influenced more by the pattern of precipitation than by treatment ($F_{5,29} = 0.35$, $P < 0.88$) and decreased over the growing season ($F_{3,29} = 219.5$, $P < 0.0001$). Soil moisture rapidly decreased from late March (19.79%) to late April (1.37%) when values were approximately 14 times lower. Aside from the first sampling date, LL plots had 16–45% more soil moisture than NL plots (Fig. 1a), although high variability across the landscape resulted in no significant differences among treatments.

In contrast, both temperature and light reaching the soil surface were affected by treatment. The maximum soil temperature differed among treatments ($F_{5,70} = 4.9$, $P = 0.0007$). NL plots were the warmest and LL plots were the coolest for all but the first month sampled (March) (treatment × time; $F_{15,188} = 3.1$, $P = 0.0002$; Fig. 1b). As the season progressed, the difference between daily minimum and maximum temperatures increased for all treatments ($F_{3,68} = 398.9$, $P < 0.0001$), and differences varied by sampling month (treatment × time; $F_{15,188} = 2.8$, $P = 0.0005$). In general, NL plots experienced the greatest fluctuation between minimum and maximum temperatures and LL plots the least. Light level also differed among treatments in unburned steppe ($F_{5,79} = 109.5$, $P < 0.0001$), with NL plots having twice as much light reaching the soil surface as DL plots, and on average almost four times more than remaining treatments. The least amount of light occurred in ML plots (Fig. 1c).

Total KCl extractable soil inorganic N in unburned sagebrush steppe decreased over the growing season ($F_{1,82} = 166.8$, $P < 0.0001$) and was influenced by treatment ($F_{5,82} = 5.2$, $P = 0.0004$). At both sampling times, LLT plots had the greatest amount of total inorganic N (NH_4^+–N + NO_3^-–N) (Fig. 1d). NO_3^-–N was the dominant form of N present, although the proportion of N as NH_4^+–N increased in June likely in response to precipitation. There was no treatment effect on potential net N mineralization or C:N ratio, but the pattern resembled that of extractable N (data not shown).

All species examined exhibited early emergence with greater than 80% of the seedlings that emerged over the growing season present by the April sampling (Fig. 2a–c). Emergence differed among the seeded species ($F_{2,439} = 123.4$, $P < 0.0001$) with non-native *Bromus* having 9 and 46% higher emergence than *Elymus* and *Eriogonum*, respectively. Emergence was higher in the native grass, *Elymus*, than in the native forb, *Eriogonum* (Fig. 2a, b). The presence of *L. argenteus* resulted in a net neutral effect for natives and a weak, but non-significant, negative effect for *Bromus* (Fig. 2d). Overall, there was no effect of treatment on emergence ($F_{5,75} = 0.34$, $P = 0.88$).

Seeded species also differed in survival ($F_{2,431} = 252.8$, $P < 0.0001$; Fig. 2e–g). *Bromus* had almost twice the number of plants surviving until June compared to either native species (*Bromus* 79%, *Elymus* 43%, and *Eriogonum* 40%). Only *Elymus* survival was directly facilitated by *L. argenteus* (Fig. 2h). *Elymus* survival was not significantly correlated with any single environmental factor, but was likely influenced by a combination of increased moisture ($\rho = 0.37$, $P = 0.17$) and reduced temperature ($\rho = -0.42$, $P = 0.17$) associated with *L. argenteus*. Treatment had a significant effect on survival across species ($F_{5,75} = 2.75$, $P = 0.02$; Fig. 2e–g). *Elymus* had the greatest survival in FLT, LL, and LLT plots (Fig. 2c). In contrast, *Eriogonum* tended to have the highest survival in DL plots (Fig. 2c). The highest survival for *Bromus* was in LLT plots, but survival was reduced in the presence of *L. argenteus* (Fig. 2h).

Relative to plots without *L. argenteus*, the presence of this legume facilitated size of *Elymus* and *Bromus* (Fig. 3d). *Elymus* height most strongly, but not significantly,

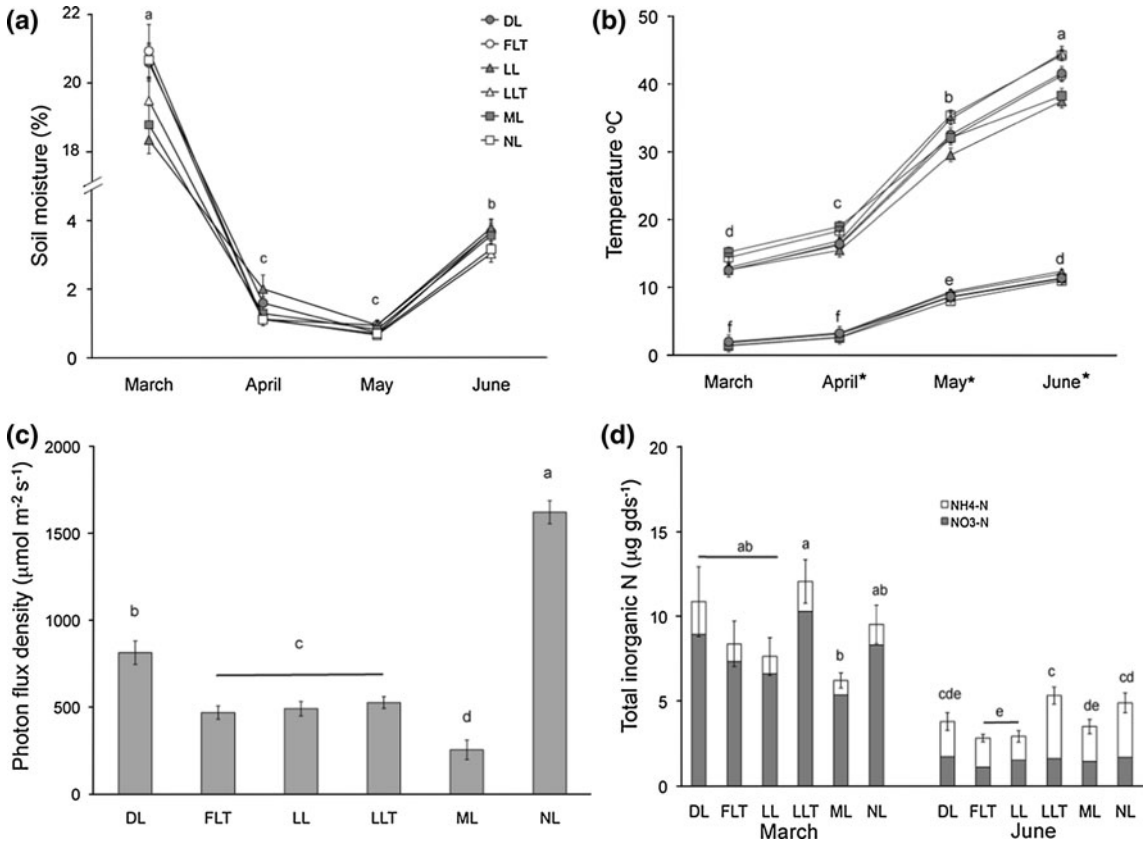

Fig. 1 Differences in **a** % soil moisture, **b** maximum and minimum soil temperature, **c** PFD, and **d** total soil inorganic N (NO_3–N + NH_4–N) among treatments in unburned sagebrush steppe. Values are mean ± SE. $n = 9$–15 per treatment. *Different letters* indicate significant differences among sampling times (**a**, **b**) or treatments (**c**) or treatment and time (**d**) ($P < 0.05$). *Asterisks* on *x axis* indicate significant differences in maximum temperature between live and no *L. argenteus* treatments. Dead *L. argenteus* (*DL*), fake *L. argenteus* litter (*FLT*), live *L. argenteus* (*LL*), *L. argenteus* litter (*LLT*), mock *L. argenteus* (*ML*) and no *L. argenteus* (*NL*)

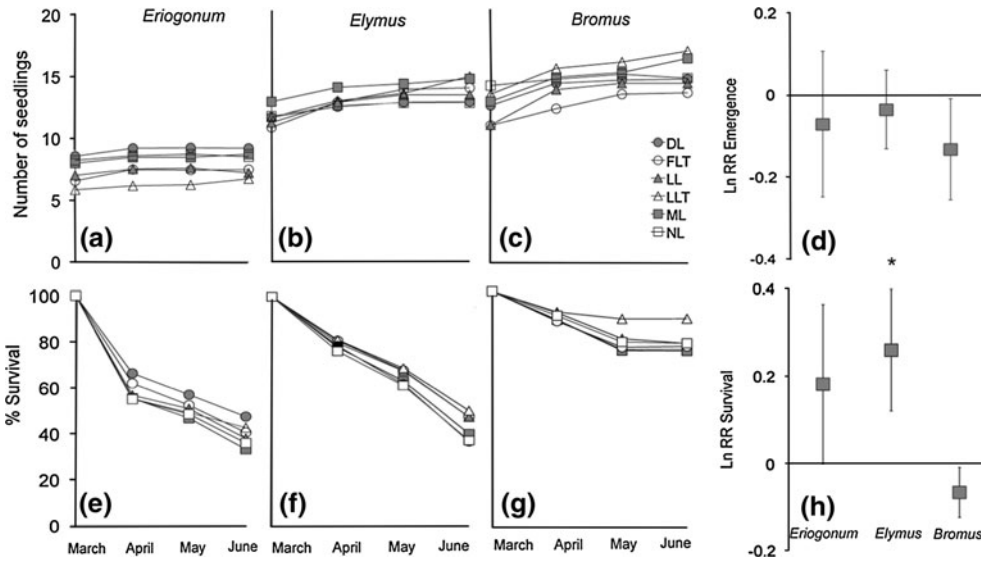

Fig. 2 Differences in **a**–**c** mean cumulative seedling emergence in unburned sagebrush steppe for *Eriogonum, Elymus*, and *Bromus* (out of 25 seeds) and **d** net effect of *L. argenteus* on emergence expressed as Ln RR. Differences in **e**–**g** mean seedling survival and **h** net effect of *L. argenteus* on seedling survival for *Eriogonum*, *Elymus*, and *Bromus* $n = 15$. For net effects, *asterisks* indicate values significantly different from zero at $P < 0.05$; negative values indicate inhibition and positive values facilitation. Treatment abbreviations as in Fig. 1

correlated with reduced PFD ($\rho = -0.48$, $P = 0.069$) and *Bromus* biomass positively correlated with soil moisture ($\rho = 0.54$, $P = 0.037$) associated with live *L. argenteus*. However, treatment influenced measures of size for each species ($F_{5,70} = 2.6$, $P = 0.03$ for *Eriogonum* leaves, $F_{5,72} = 9.2$, $P < 0.0001$ for *Elymus* height, and $F_{5,70} = 3.7$,

$P = 0.005$, and $F_{5,70} = 2.4$, $P = 0.04$ for *Bromus* biomass and seeds, respectively). The forb, *Eriogonum*, produced more leaves in the ML treatment (Fig. 3a), whereas the tallest *Elymus* plants were in the LL, LLT and FLT treatments (Fig. 3b). The greatest amount of *Bromus* biomass and seed production occurred in the LLT plots and least in the NL and ML plots (Fig. 3c).

Burned community—year 2

In burned sagebrush steppe, soil moisture was highest in late March (11.8%) and decreased in late April (5.1%) but was similar in late May, mid-June and mid-August (1.1%). Differences among treatments occurred in all months except May, resulting in a treatment by sampling date interaction ($F_{20,144} = 1.8$, $P = 0.03$). In March, June, and August, LL plots had the greatest amount of soil moisture, with18–32% more moisture than NL plots (Fig. 4a).

Treatment also influenced maximum soil temperatures ($F_{5,38} = 5.8$, $P = 0.0005$; Fig. 4b) and light at the soil surface ($F_{5,46} = 38.2$, $P < 0.0001$; Fig. 4c). At the beginning of the growing season, there were no differences in temperature among treatments; however, from April through August, ML plots had lower maximum temperatures than other treatments (treatment × time; $F_{25,200} = 3.4$, $P < 0.0001$). Differences between daily minimum and maximum temperature follow the same pattern as maximum temperatures, with ML plots having the least fluctuation except in March (treatment × time; $F_{25,200} = 3.2$, $P < 0.0001$). Light interception reflected differences in temperature fluctuations among treatments in burned steppe, with NL and DL plots having the highest amount of light reaching the soil surface, whereas ML had the least.

Total KCl extractable soil inorganic N differed among sampling times ($F_{2,47} = 226.2$, $P < 0.0001$; Fig. 4d). Values were greatest in late March and then decreased in mid-June before increasing slightly in mid-August. The treatment with the most N varied over the growing season (treatment × time; $F_{10,94} = 1.9$, $P = 0.049$). In late March, LL plots had significantly more extractable N than ML or NL plots. In contrast, in June, FLT and LLT plots had more than NL and ML plots. By August, FLT plots had the most extractable N. At our sites, wind is an important factor influencing redistribution of nutrients post-fire. Eroded topsoil tended to accumulate in these plots, likely resulting in concentration of N-rich soil in this treatment by the end of the growing season. NH_4^+–N was the dominant form of N at the start of the growing season, but over time proportional amounts of NH_4^+–N and NO_3^-–N evened out (Fig. 4d). Potential net N mineralization and C:N of burned soil were unaffected by treatment (data not shown).

As in the prior year, by the April sampling, more than 80% of the seedlings that emerged during the growing

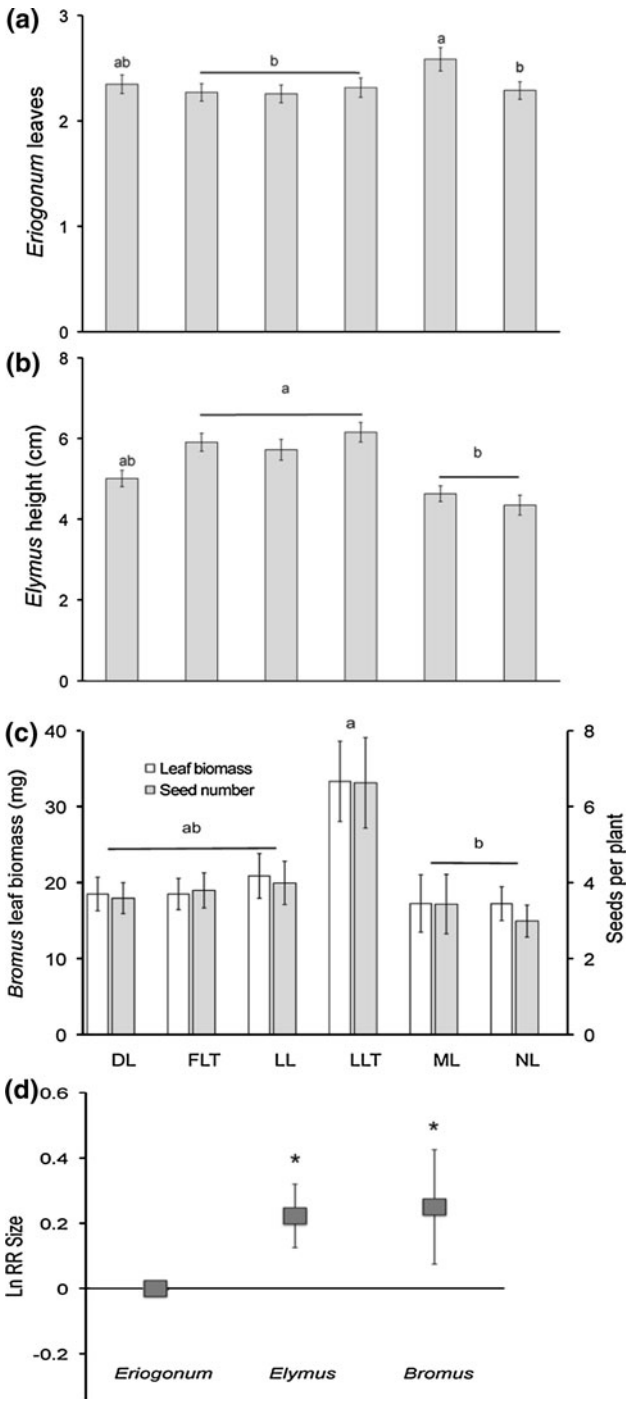

Fig. 3 Treatment effect on **a** mean number of *Eriogonum* leaves, **b** *Elymus* height (cm), and **c** *Bromus* biomass (mg) and seed production in unburned sagebrush steppe. Net effect of *L. argenteus* **d** on seedling size (leaf number, height, or biomass) expressed as Ln RR. *Negative values* indicate inhibition and positive values facilitation. Values are mean ± SE, $n = 15$. *Different letters* indicate significant differences among treatments ($P < 0.05$). *Asterisks* indicate values significantly different from zero (net positive or negative effect) at $P < 0.05$. Treatment abbreviations as in Fig. 1

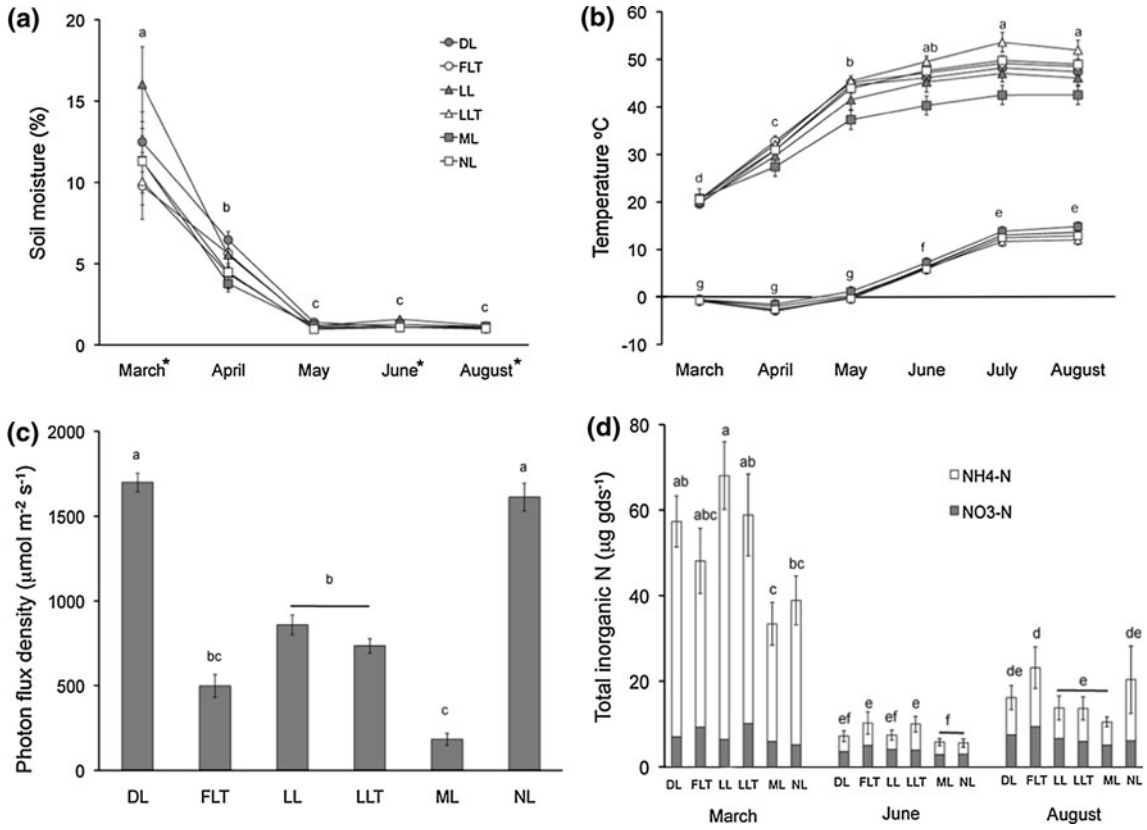

Fig. 4 Differences in **a** % soil moisture, **b** maximum and minimum soil temperature, **c** PFD, and **d** total soil inorganic N (NO_3–N + NH_4–N) among treatments in burned sagebrush steppe. Values are mean ± SE. $n = 9$ per treatment. *Different letters* indicate significant differences among sampling times (**a**, **b**) or among treatments (**c**) or treatment and time (**d**) ($P < 0.05$). *Asterisks* on *x axis* indicate significant differences between live and no *L. argenteus* treatments. Treatment abbreviations as in Fig. 1

season were already present (Fig. 5a–c). Emergence differed among the seeded species ($F_{2,404} = 51.9$, $P < 0.0001$), with *Bromus* having higher overall seedling emergence than either of the native species. The presence of *L. argenteus* did not influence emergence in the native species, but *Bromus* emergence was significantly reduced, with 17% lower emergence in LL compared to NL plots (Fig. 5d). Reduced emergence was correlated with cooler spring temperatures ($\rho = 0.79$, $P = 0.034$) under adult *L. argenteus*. There was no consistent effect of treatment on emergence across species, leading to a species by treatment interaction ($F_{10,404} = 17.4$, $P < 0.0001$). In DL and LL plots, emergence was similar among all species, but *Bromus* had greater emergence than either native species in the NL plots. Cumulative emergence in both *Bromus* and *Elymus* was greatest in LLT plots. In contrast, emergence of *Eriogonum* was reduced in LLT and FLT plots (Fig. 5a).

Survival differed among seeded species in burned steppe ($F_{2,404} = 294.9$, $P < 0.0001$; Fig. 5e–g). At the June harvest, *Bromus* had more plants surviving than either of the native species (*Bromus* 87%, *Elymus* 57%, and *Eriogonum* 36%). Only for *Elymus* was survival directly facilitated by *L. argenteus*. The presence of this perennial legume increased *Elymus* survival by 20% relative to NL plots (Fig. 5h) and was likely a result of increased moisture ($\rho = 0.63$, $P = 0.067$) and reduced temperature ($\rho = -0.69$, $P = 0.081$) in these plots. Each species responded differently to treatments resulting in a species by treatment effect ($F_{10,404} = 3.7$, $P < 0.0001$). *Elymus* had the greatest survival in the litter plots. In contrast, survival in *Eriogonum* was lowest in the litter plots. *Bromus* survival did not differ among treatments. By August, survival of *Elymus* decreased to 30% and *Eriogonum* to 21%.

Size of the seeded species was not directly influenced by *L. argenteus* in burned sagebrush steppe (Fig. 6d), and only *Elymus* height was significantly affected by treatments ($F_{5,63} = 0.19$, $P = 0.97$ for *Eriogonum*, $F_{5,68} = 6.1$, $P < 0.0001$ for *Elymus*, and $F_{5,66} = 1.3$, $P = 0.29$ and $F_{5,66} = 2.2$, $P = 0.06$ for *Bromus* biomass and seeds, respectively). *Elymus* seedlings were tallest in the FLT treatment (Fig. 6b).

Discussion

Our study indicates that *L. argenteus* can modify abiotic resources (soil moisture, N) and environmental

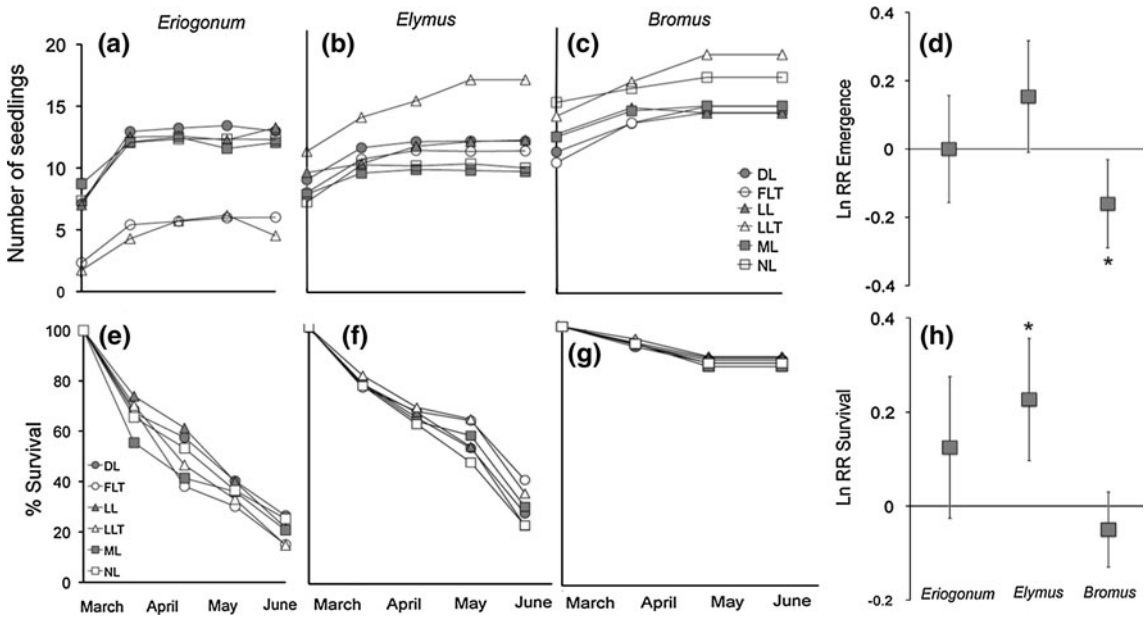

Fig. 5 Differences in **a–c** mean cumulative seedling emergence in unburned sagebrush steppe for *Eriogonum, Elymus*, and *Bromus* (out of 25 seeds) and **d** net interaction effect of *L. argenteus* on emergence expressed as Ln RR. Differences in **e–g** mean seedling survival and **h** net effect of *L. argenteus* on seedling survival expressed as Ln RR for *Eriogonum*, *Elymus*, and *Bromus*. $n = 15$ per species per treatment. For net effects, *asterisks* indicate values significantly different from zero at $P < 0.05$; negative values indicate inhibition and positive values facilitation. Treatment abbreviations as in Fig. 1

characteristics (light, temperature) that can influence seedling establishment within sagebrush steppe (Table 2). In both unburned and burned communities, there was higher spring soil moisture, increased shade and reduced maximum temperatures under *L. argenteus* canopies. Contrary to expectations, presence of adult *L. argenteus* resulted in greater amounts of soil N only in burned sagebrush steppe. However, addition of *L. argenteus* litter increased soil N under unburned and burned conditions in both years, indicating that the main mechanism responsible for legume associated N increase is decomposition of N rich tissue. Environmental modification by *L. argenteus* was similar in both years, but seasonal variability and fire resulted in different factors limiting seedling establishment. Thus, examining the interactions among a dominant sagebrush legume and seedling establishment under different environmental conditions can provide insights into how plant–plant interactions change with shifts in abiotic stress.

In unburned conditions during year 1, soil moisture decreased rapidly early in the growing season and, similar to other studies in sagebrush steppe, was likely a main factor limiting seedling establishment (Chambers and Linnerooth 2001; Huber-Sannwald and Pyke 2005). *Lupinus argenteus* presence increased soil moisture and decreased temperature and light, but had a net neutral effect on emergence of natives. Similar studies have found, on average, net neutral effects of neighbors on emergence, especially with herbaceous benefactors (Aguiar et al. 1992; Gomez-Aparicio 2009). In contrast, *L. argenteus* had a weak, non-significant inhibitory effect on *Bromus* emergence. Other field studies investigating the effects of mature herbaceous vegetation on *Bromus* emergence have found both positive and negative effects (Chambers et al. 2007; Griffith 2010). Emergence differed among species with *Bromus* having the highest overall percentage of seeds emerge (59%) followed by *Elymus* (54%) and *Eriogonum* (32%). Low dormancy and consistently high emergence of the annual grass *Bromus* has been observed elsewhere (Chambers et al. 2007; Griffith 2010), and undoubtedly contributes to its invasiveness.

In year 1, the presence of *L. argenteus* in unburned steppe facilitated plant size and survival of the native perennial grass, *Elymus*, but had no effect on the native forb, *Eriogonum*. Survival and seedling height of *Elymus* were high in live *L. argenteus* and *L. argenteus* litter plots, but were similarly high in fake *L. argenteus* litter plots indicating that modification of the soil surface and microclimate were the dominant facilitative mechanisms. Increased early season soil moisture, combined with greater shade and reduced soil temperature under *L. argenteus*, likely reduced evapotranspiration and water stress by reducing vapor pressure differences between leaves of the beneficiary and ambient air (e.g., Moro et al. 1997; Bullock 2009; Maestre et al. 2009). The net neutral interaction between *L. argenteus* and *Eriogonum* may be due to the similarity in life form between benefactor and beneficiary

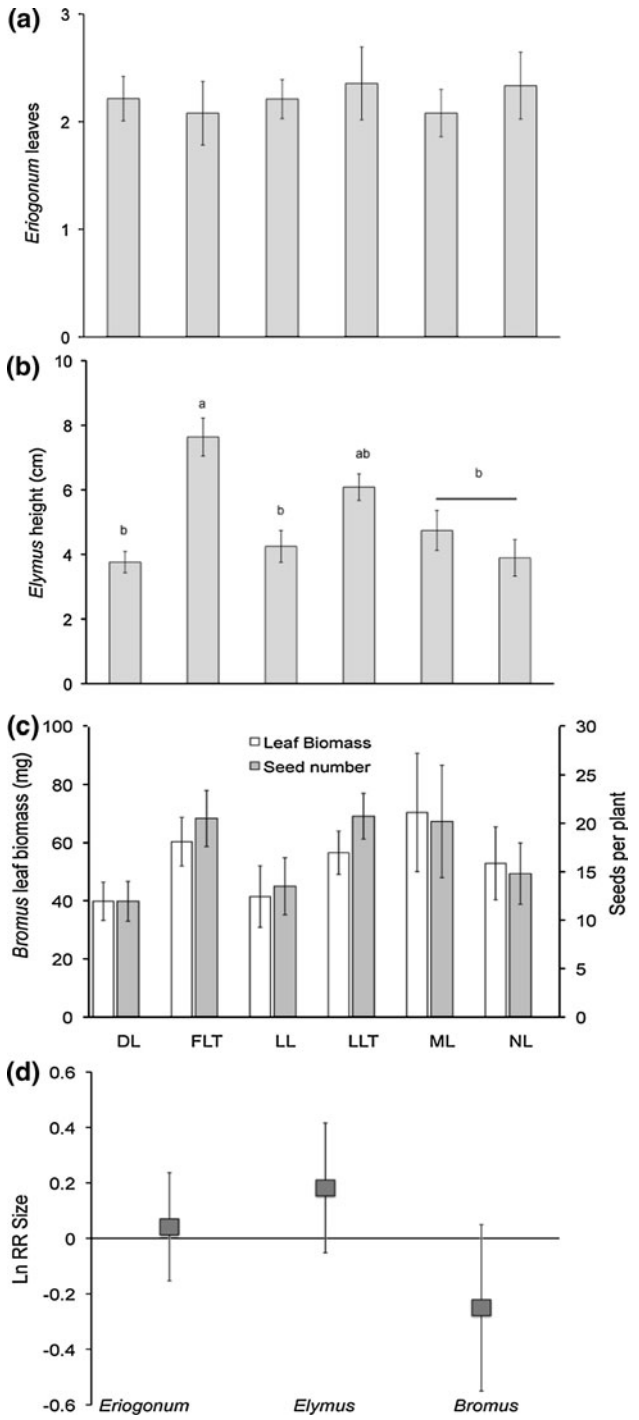

Fig. 6 Treatment effect on **a** mean number of *Eriogonum* leaves, **b** *Elymus* height (cm), and **c** *Bromus* biomass (mg) and seed production in burned sagebrush steppe. Net effect of *L. argenteus* **d** on seedling size (leaf number, height, or biomass) expressed as Ln RR. Negative values indicate inhibition and positive values indicate facilitation. Values are mean ± SE, $n = 15$ per species per treatment. *Different letters* indicate significant differences among treatments ($P < 0.05$) within year. Treatment abbreviations as in Fig. 1

(Gomez-Aparicio 2009). However, it could also be a function of life history and ecophysiology of *Eriogonum*, which tended to have the highest establishment in micro-environments with intermediate light levels.

The highest overall survival and size of *Bromus* occurred in *L. argenteus* litter plots. *Bromus* is a nitrophilic plant that can rapidly utilize increased resources (James 2008a, b), and this result likely reflects a response by *Bromus* to significantly higher levels of available soil N in litter plots. The presence of *L. argenteus* had a weak negative effect on survival of *Bromus* in unburned steppe. Interference by *L. argenteus* on *Bromus* survival in our study may have resulted from root competition for both nutrients and water (e.g., Huber-Sannwald and Pyke 2005) or colder spring soil temperatures delaying emergence and maturation. Despite fewer plants surviving under adult *L. argenteus* in unburned steppe, *Bromus* plants that did persist were larger and more fecund, producing 25% more seeds than plants in no *L. argenteus* plots without environmental modification. Conditions under established vegetation may be more amenable to growth of seedlings than to seed germination and seedling emergence (Chambers 1995), and may account for the observed pattern. A similar result was observed for *Anaphalis margaitacea* and *Epilobium angustifolium* plants recruiting under *Lupinus lepidus* on Mount St. Helens (Morris and Wood 1989).

Under burned conditions in year 2, levels of extractable N were on average five times greater than the prior year. Soil moisture also decreased more slowly despite earlier increases in maximum temperature resulting in an average of 60% more soil moisture in the spring of 2008 than in the prior April and May, the time of maximum plant growth. These higher resource conditions likely decreased environmental stress experienced by seedlings relative to the prior year. Establishment in post-fire environments can be positively influenced by decreased competition and increased nutrient availability (Carrington 1999; Rau et al. 2008), but it can also be negatively affected by increased temperature and exposure (Bullock 2009). Our results indicate that rapid resprouting of *L. argenteus* post-fire provides important environmental modifications by further increasing soil N and moisture and decreasing light and temperature under its canopy. However, the presence of *L. argenteus* was neutral for native emergence and negative for *Bromus* emergence. These results parallel those for the relatively more stressful prior growing season. Treatments also differentially affected the seeded species. Emergence of *Elymus* and *Bromus* were increased by presence of litter, but unlike the prior year, litter decreased emergence of *Eriogonum*. Litter can improve conditions for seedling emergence (increased water and nutrients, reduced thermal amplitude), but can also have negative impacts on emergence by creating a physical barrier on the soil surface and

Table 2 Summary table of *L. argenteus* treatment effects on resource environment and seedling establishment

	DL	LL	ML	LLT	FLT
Year 1 unburned					
Soil moisture	0	0	0	0	0
Soil temperature	0	−	−	0	0
PAR	−	−	−	−	−
Inorganic N	0	0	−	+	0
Emergence					
Bromus	0	0	0	0	0
Elymus	0	0	0	0	0
Eriogonum	0	0	0	0	0
Survival					
Bromus	0	0	0	+	0
Elymus	0	+	o	+	+
Eriogonum	0	0	0	0	0
Growth					
Bromus	0	+	0	+	0
Elymus	0	+	0	+	+
Eriogonum	0	0	+	0	0
Year 2 burned					
Soil moisture	0	+	0	0	0
Soil temperature	0	−	−	0	0
PAR	0	−	−	−	−
Inorganic N	0	+	0	+	+
Emergence					
Bromus	0	−	0	+	0
Elymus	0	0	0	+	+
Eriogonum	0	0	0	−	−
Survival					
Bromus	0	0	0	0	0
Elymus	0	+	0	+	+
Eriogonum	0	0	0	−	−
Growth					
Bromus	0	0	0	0	0
Elymus	0	0	0	0	+
Eriogonum	0	0	0	0	0

+ A significant increase, − decrease, or 0 no difference relative to NL plots that had no modification of the physical or nutrient environment

DL dead *L. argenteus*, *LL* live *L. argenteus*, *ML* mock *L. argenteus*, *LLT L. argenteus* litter, *FLT* fake *L. argenteus* litter

via leaching of phytotoxic compounds (Facelli and Pickett 1991). Despite interference of *Bromus* emergence by *L. argenteus*, and neutral effects on the native species, *Bromus* still had greater overall emergence than either native species.

Survival of *Elymus* in burned sagebrush steppe was facilitated by *L. argenteus*, and was more than 20% greater in live *L. argenteus* than no *L. argenteus* plots. As in the prior year, this was likely due to modification of the microenvironment. In contrast, the presence of *L. argenteus* had no effect on survival or size of *Eriogonum* or *Bromus*. The difference between years for *Bromus* is likely due to a combination of increased resources and life history characteristics. The greater soil N, spring temperatures, and soil moisture associated with *L. argenteus* in burned steppe, may have minimized the negative effect of competition on survival. Compared to the prior year, *Bromus* plants were twice as large and produced on average three times as many seeds, regardless of treatment. Biomass and seed production in *Bromus* increase with addition of N (e.g., James 2008a, b; Vasquez et al. 2009), and decreased competition and elevated N associated with fire were likely the main factors influencing *Bromus* biomass and reproduction in burned steppe.

Our study indicates that *L. argenteus* can facilitate seedling establishment in semi-arid systems, but the net effects depend on the species examined, traits measured, and level of abiotic stress (Table 2). Because *L. argenteus* is a N_2-fixing legume associated with greater levels of soil N (Goergen and Chambers 2009), we expected it to

facilitate nitrophilous *Bromus*. *Lupinus argenteus* negatively affected emergence and survival of *Bromus*, and only increased biomass and reproduction in unburned plots. However, *L. argenteus* had positive facilitative effects on growth and survival of the native perennial grass, *Elymus*, in both unburned and burned plots. This is consistent with a companion study which found that perennial grass and forb cover exhibited a greater positive response than *B. tectorum* to the presence of *L. argenteus* in both burned and unburned sagebrush steppe (Goergen and Chambers 2009). Communities with well-established perennial herbaceous species appear to have a high resistance to invasion by *B. tectorum* (Booth et al. 2003; Chambers et al. 2007), and, contrary to expectations, *L. argenteus* may help increase stability within sagebrush steppe by facilitating functional groups that increase resistance to invasion.

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