Natural Resources and Environmental Issues

Volume 16 Shrublands: Wildlands and Wildlife Habitats

Article 20

2011

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Effects of Spring Prescribed Fire in Expanding Pinyon-Juniper Woodlands on Seedling Establishment of Sagebrush Species

David I. Board¹, Jeanne C. Chambers¹, and Joan G. Wright²

ABSTRACT

Pinyon and juniper trees are expanding into mountain sagebrush communities throughout their ranges. Fire is used to restore these sagebrush communities, but limited information is available on seedling establishment of native shrubs and herbs. We examined effects of spring prescribed fire in the Great Basin on emergence and survival of five species (Artemisia tridentata vaseyana, Festuca idahoensis, Poa secunda, Eriogonum umbellatum and Lupinus argenteus) common to these communities. Data were collected in three microsites (undertree, undershrub and interspace) on a burned and unburned site following a prescribed fire and on the unburned site the year prior to the fire. Soil temperature and moisture were collected on both sites and years. Emergence and survival of A. tridentata was low. Grasses had higher emergence and survival under trees in 2003 in the unburned site, reflecting the pre-burn distribution of these species. E. umbellatum had high emergence and survival regardless of site or microsite. L. argenteus had moderate emergence that was lowest on the burned site under trees and highest on the unburned site in interspaces. Burned soils were warmer than unburned soils. Undertree microsites on the unburned site were cooler than other microsites on both sites due to shading and insulation by needle mats. Soil moisture was generally higher on the burn site due to fewer shrubs and trees. Pinyon appeared to have a facilitative role for grass seedling establishment on both sites. Spring prescribed fire did not have a negative impact on emergence or survival in these mountain sagebrush communities. Low establishment of some species indicate higher seeding rates or repeated seeding may be required. Keywords: Great Basin, sagebrush ecosystems, restoration, revegetation, seedling emergence and survival, microenvironmental conditions

INTRODUCTION

Sagebrush communities are among the most imperiled in North America (Noss and Peters 1995; Wisdom and others 2005) and researchers and managers are actively pursuing restoration strategies to increase their sustainability. Sagebrush communities once occupied 63 million ha in western North America (West 1996; Knick and others 2003), but as much as half of this land type has been lost in the Great Basin (Noss and others 1995; Hann and others 1997) due to agricultural clearing and land development (Wisdom and others 2005), overgrazing by livestock (Knapp 1996), cheatgrass invasion and the cheatgrass-

In: Wambolt, C.L. et al. comps. 2011. Proceedings – Shrublands: wildlands and wildlife habitats; 2008 June 17-19; Bozeman, MT. NREI, volume XVI. S.J. and Jessie E. Quinney Natural Resources Research Library, Logan, Utah, USA.

fire cycle (D'Antonio and Vitousek 1992; Knapp 1996) and expansion of pinyon and juniper woodlands (Miller and Wigand 1994; Miller and Tausch 2002). These communities provide critical habitat for numerous sagebrush obligate species, and the loss and degradation of sagebrush communities have been linked to the decline of several species of concern including sage grouse and pygmy rabbits (Knick and others 2003).

Expansion of pinyon-juniper woodland is the major threat in moister, higher elevation areas where sagebrush communities are dominated largely by Artemisia tridentata ssp. vasevana (Rydb.) beetle (Mountain sagebrush) (Suring and others 2005). As expanding woodlands age and canopy cover increases, the highly competitive trees can effectively eliminate the sagebrush semi-desert species in the understory. Over time the community may cross a biological threshold precluding the recovery of sagebrush communities without active restoration involving both tree removal and revegetation with sagebrush semi-desert species (Chambers 2005; Miller and others 2005). To avoid this situation managers and researchers are implementing prescribed fire projects to return landscapes to more sustainable sagebrush communities before a biological threshold is crossed (Miller and others 2005). Effective use of prescribed fire to restore and maintain sagebrush communities requires understanding fire effects on establishment of the plant species that occur in sagebrush communities, but few mechanistic studies have been conducted to date (but see Chambers and Linnerooth 2001; Wrobelski and Kauffman 2003; Wirth and Pyke 2003).

It is often assumed that prescribed burning will promote species associated with mountain sagebursh communities, but the responses of particular species can be quite varies. Fire kills most species of sagebursh (Tisdale and Hironaks 1981), but mature tussock grasses are often resistant to burning (Wright and Klemmedson 1965). Prescribed fire has been shown to reduce competition, and increase nutrient availability (Knapp and Seastedt 1986; Dudley and Lajtha 1993). However, fire also has been shown to result in harsher environmental conditions resulting from the removal of protective trees and shrubs and higher temperatures from solar heating of blackened soil (Chambers and Linnerooth 2001). How these changes affect seedling emergence and establishment is not clear. The response is likely to differ by species and with small scale environmental variations (microsites), such as being under a tree or shrub or in the interspace.

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Areas under trees and shrubs often have conditions quite distinct from interspace. Soils under trees and shrubs are often moister, cooler, and higher in nutrients than the surrounding interspaces (Blackburn 1975; Doescher and others 1984; Chambers 2001). The effect of fire on the relationship between overstory and seedlings is quite complex and depends on the relative levels of competition, facilitation and the mechanisms of these processes. Fire often kills the overstory plants thus eliminating competition between the overstory and understory but also eliminating the potential for facilitation. However, some of the effects of the overstory plants remain after fire. Increased nutrients associated with the overstory plants often remain and may even increase relative to the interspace (Blank and others 1994; 2003; Rau 2005). The trees are often left standing thus providing shading albeit to a lesser degree than living trees. Shrubs are typically completely removed and thus no longer provide shade, but nutrient effects may remain. Competition for soil moisture is reduced immediately after fire and, although soil moisture deeper in the soil may increase, soil moisture near the surface may be less than pre-burn levels (Chambers and Linnerooth 2001). The lack of shading combined with soil blackening may increase evapotranspiration and increase moisture stress for young seedlings. However, the increased temperatures could increase germination rates and promote early establishment as soils heat earlier in the spring (Chambers and others 2007). This could lengthen the germination establishment window between winter and summer.

This study examined the effects of a spring prescribed fire in a pinyon-juniper woodland on seedling establishment (emergence and survival) of one shrub (A. tridentata ssp. vaseyana), two grasses (Festuca idahoensis Elmer [Idaho fescue] and Poa secunda J. Presl. [Sandberg bluegrass]) and two forbs (Eriogonum umbellatum Torr. [Sulphur-flower buckwheat] and Lupinus argenteus Pursh. [Silvery lupine]) that occur in mountain sagebrush communities. Because of the effects of microsites in moderating environmental conditions in general, we also examined the effect of microsite (under tree, under shrub and interspace) and how it was modified after fire. Because of the importance of soil water availability in determining seedling establishment in these semi-arid ecosystems, we also examined the effects of the prescribed fire on soil temperature and soil water content on both control (not burned) and burned areas. We asked the following questions. (1) How does spring prescribed fire affect soil temperature and water content in under tree, under shrub and interspace microsites in pinyonjuniper woodlands? (2) How does spring prescribed fire affect seedling emergence and survival in under tree, undershrub and interspace microsites? We discuss the implications of the results for the restoration of sagebrush semi-desert following prescribed fire.

METHODS

Study Area

The study is located in Underdown Canyon, a Joint Fire Sciences Program demonstration area, in the Shoshone Mountain Range in Central Nevada on the Humboldt-Toiyabe National Forest (Austin Ranger District). Underdown Canyon (39° 15' 11" N, 117° 35' 83" W) is oriented east to west and contains infrequent springs and an ephemeral stream near the top of the drainage. Annual precipitation usually occurs as winter snow and spring rains averaging 23 cm at the lower elevations and 50 cm at the upper elevations. A standing rain gage located in the study area recorded 27 and 34 cm for the water years (October to October) of the two year study. The climate is characterized by cold winters and warm summers with temperatures ranging from -7.2°C in January to 29.4°C in August in Austin, NV (48 km northeast of Underdown Canyon at an elevation of 1911 m). Soils are classified as coarse loamy mixed frigid typic haploxerolls (Rau 2005).

The demonstration area is typical of an area experiencing pinyon-juniper expansion into mountain sagebrush communities in the Intermountain West (Miller and Tausch 2002). The vegetation is dominated by mountain sagebrush, Artemisia tridentata ssp. vaseyana and Pinus monophylla Torr. and Flem. (Single leaf pinyon) with a small component of Juniperus osteosperma (Torr,) Little (Utah juniper). The understory includes the grasses *Poa secunda*, Elymus elymoides Sweezey (Squirreltail), Hesperostipa comata (Trin. and Rupr.) Barkworth (Needle and thread grass, Achnatherum thurberianum (Piper) Barkworth (Thurber's idahoensis needlegrass), Festuca Pseudoroegneria spicata (Pursh) A. Love (Bluebunch wheatgrass), and forbs such as Eriogonum (Buckwheats), Crepis acuminata Nutt. (Tartip hawksbeard), Phlox spp., Lupinus argenteus and Penstemon spp. (Beardtongues) Bromus tectorum L. (Cheatgrass), an invasive annual grass, is not prevalent on the site.

Study Design

The basic study design was a doubly blocked split plot design. The largest blocks were located on two adjacent alluvial fans. One of the fans, the higher elevation fan at 2,225m, was burned while the other fan, the lower elevation fan at 2,195m, was not burned. Nested within each of the two fans were 4 smaller blocks referred to as plots, located in areas of intermediate tree cover (~38 percent cover). Areas within these plots were designated as different microsite types: undertree, undershrub and interspace. The higher elevation fan was burned by the USDA Forest Service on 11-14 May 2002 under favorable weather conditions (air temperature < 32°C, relative humidity > 15 percent, wind speed < 9 m*s⁻¹, and gravimetric fuel moisture ≈ 40 percent). The burn was patchy because of the high fuel moisture and created a mosaic of burned and unburned vegetation across the fan.

Because this study was part of a large-scale "restoration experiment," cost and logistics prevented burning multiple fans with similar environmental conditions. Thus, statistical inference is limited to differences between fans, rather than between burned and unburned areas. However, given that the fans were closely matched prior to burning, differences between the two fans are presumed to be due to fire. The limitations of pseudoreplication in large scale experiments have been detailed elsewhere (Hurlbert 1984; Carpenter 1990), as has the value of these types of management-scale experiments to ecology and restoration (Carpenter 1990; Miao and Carstenn 2006)

Soil Temperature and Water Measurements

Soil temperature and gravimetric soil water on both the burned and unburned blocks were measured within three of the plots for undershrub, undertree and interspace microsites (2 blocks x 3 plots x 3 microsites = 18 locations). Soil water samples were collected every 2 to 4 weeks during the growing season in 2001 and 2002 from a soil core divided into three depths (0 to 3, 3 to 8 and 8 to 23 cm) that reflected the natural soil horizons that exist on both fans (Rau 2005). Gravimetric soil moisture was determined based on wet versus oven-dry weights. Soil temperature data were collected with networks of three interconnected thermocouples of equal length, spaced 50 cm apart and installed at depths of 2, 5 and 20 cm. Hourly averages were taken from measurements taken every 5 minutes for June through October of 2002 and April through August of 2003 using Campbell Scientific CR-10 and CR-10x microloggers and then averaged over each month.

Seedling Emergence and Survival Measurements

Commercial seed lots of five common sagebrush semidesert were used including one shrub (A. tridentata ssp. vasevana), two grasses (Festuca idahoensis and Poa secunda) and two forbs (Eriogonum umbellatum and Lupinus argenteus). A standard tetrazolium test (Moore 1972; Peters 2000) determined viability of seeds less than one month before seeding. Seeding grids (50 x 50 cm quadrats) were placed within each of the four plots in undertree, undershrub and interspace microsites (4 plots x 3 microsites x 5 species = 60 quadrats). Planting occurred on the unburned site in 2001 and on both the unburned site and burned site in 2002 (n = 180 quadrats). Undertree quadrats were placed 50 cm from the tree canopy edge towards the bole. The undershrub quadrats were located to maximize shrub canopy coverage. Interspace quadrats were placed in the forb grass matrix surrounding the trees and shrubs. Each seeding quadrat was prepared for planting by removing understory plants and surface litter and reserving the litter. One hundred filled seeds of each species were then seeded in each quadrat by planting one seed into each of 100 grid cells (5.0 x 5.0 cm). Seed of P. secunda and A. tridentata were planted at a depth of 0.5 cm because of their small

size; all others were planted at 1.0 cm. Following seeding, a one centimeter layer of the reserved litter was spread over the quadrat. Seedling emergence and survival were monitored every two weeks from April through June after planting and monthly from July though October in 2002 and 2003 on the unburned block and in 2003 on the burned block.

Statistical Analysis

Environmental data

Analysis was based on a multilocation trial experiment with locations (fans) viewed as fixed effects. Plots were treated as random samples within each fan. A separate analysis was done for each year for the soil moisture and soil temperature data. For both the soil temperature and soil moisture data, depth was treated as a split plot factor within microsite. For soil temperature, correlation between the three depths for each core was modeled as a random effect with a toeplitz covariance structure. The month of sampling for each temperature sensor was treated as a repeated measure with a toeplitz covariance structure. For soil moisture, correlation between depths for a core was assumed to be zero because of model convergence problems. Date of sampling for each core depth was modeled as a repeated measure with the covariance structure being a power function $(\sigma^2 \rho^d_{ii})$ of the days between sample dates. The best fit covariance structures were selected using AIC from those structures available in SAS Proc Mixed (SAS 2000).

Seedling Emergence and Establishment

The proportion of viable seeds that emerged from each quadrat and the proportion of those seedlings that survived until the final sampling period of the planting year (establishment) were arcsine square root transformed. The transformed emergence and establishment data also were analyzed based on a fixed multilocation trial study design. Each fan-year was treated as an independent location and requires the assumption of independence between fanyears. This allowed planned comparisons between 2002 and 2003 on the control and between the burned and unburned fan in 2003 as well as the related interaction with microsite by creating estimable functions for the particular hypothesis to be tested. Species were analyzed by functional group, (grass, forb or shrub) with species treated as a split factor within functional group. Each species was analyzed separately as well.

All statistical models were fit using SAS Proc mixed (SAS 2000). Standard checks of model assumptions were conducted and all were acceptable given the robustness of the model fitting procedures.

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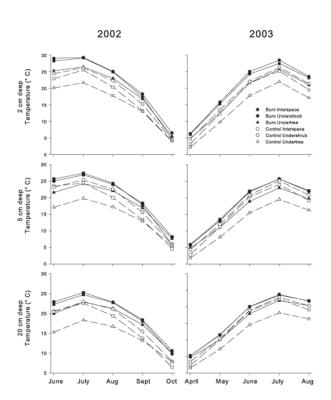


Figure 1—Average monthly temperature (°C) in the unburned and burned site for interspace, undershrub and undertree microsites at three depths, 2cm, 5cm and 20cm.

RESULTS

Effect of Site (Burned and Unburned Fan) and Microsite on Soil Moisture and Temperature

Soil temperature was highest in June, July and August with July being the warmest month in 2002 and 2003 (figure 1). The burned site soil temperatures were warmer than the unburned site in both years (table 1). The undertree microsite was cooler than the undershrub and interspace microsites on both sites and in both years. The differences between the microsites were most distinct during the warmest months sampled. The coolest locations were under trees on the unburned site in both years and all months. The undershrub and interspace microsites on the unburned site and the undertree microsites on the burned site were significantly cooler than the interspace and undershrub on the burned site in the warmest months. Soil temperature decreased with depth on both the unburned and burn sites for all microsites, but these differences were most apparent during the warmest months.

Soil moisture was highest in early spring dropping off quickly by mid-May. This pattern occurred at all depths, although the rate of decline decreased with depth and deeper soils remained wetter longer. In 2002, during the late spring the undertree microsite remained significantly wetter than other microsites on the unburned site (table 2;

figure 2). On the burned site the undertree microsites did not differ from the other microsites during this period except immediately after rain. In 2003, there were no significant differences between microsites on either site.

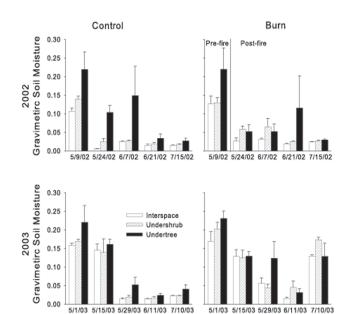


Figure 2—Average gravimetric soil moisture at the 0-3 cm depth from three samples taken on the control and burn sites in the interspace, undershrub or undertree microsites in May to Mid -July in 2002 and 2003. The burned site was burned on May 11 through the 14th 2002.

Effect of Site (Burned and Unburned Fan) and Microsite on Emergence and Survival

Emergence of the shrub *A. tridentata* was low, especially in 2003 (figure 3). The only significant difference was on the unburned site in 2002 versus 2003. Relatively high emergence occurred in the interspace in 2002 compared to the undershrub and undertree locations in 2003 (table 3; figure 3).

In 2002, none of the *A. tridentata* seedlings that emerged survived (figure 3). In 2003 A. tridentata seedlings that emerged on the unburned site under shrubs and on the burned site in the undertree locations did not survive. There were no significant differences among the remaining treatments.

The two grasses, P. secunda and F. idahoensis, had similar emergence patterns for year, site and microsite. In fact, if analyzed together there were no significant interactions with species, although F. idahoensis had significantly higher emergence (f1,9 = 6.38, p = 0.032; figure 3). Emergence did not differ among microsites for either F. idahoensis or P. secunda in 2002 on the unburned site. However, in 2003 the undertree microsite had higher emergence than the other two microsites for both species.

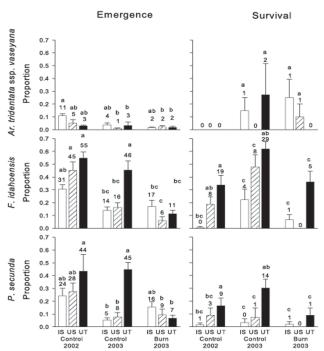


Figure 3—Proportional emergence and survival of *Ar. tridentata* spp. *vaseyana*, *F. idahoensis* and *P. secunda* in the control site in 2002 and 2003 and burn site in 2003 for interspace (IS), Undershrub (US) and Undertree (UT) microsites. Numbers above each bar indicate the average number of individuals emerging or surviving per quadrat out of 100 seeds planted. Bars that share the same letters in each graph are not significantly different than each other at an alpha of 0.05.

For P. secunda and F. idahoensis emergence within microsites did not differ between years although there was generally lower emergence in 2003. For P. secunda the difference between years was primarily due to decreased emergence in the interspace and undershrub locations. The difference between the years on the unburned fan for F. idahoensis was much greater for the undershrub locations and if taken individually this difference was significant (t1,26 = 4.04, ptukey = 0.017; figure 3; table 3).

The two grass species also had similar seedling survival patterns, with no significant interactions between species and microsite, year, or site. F. idahoensis had significantly greater survival overall than P. secunda (f1,45 = \neg 7.28, p = 0.010; figure 3). Both species had the highest survival rates under trees on the unburned site in both years, although for F. idahoensis survival under trees was not significantly greater than in the undershrub areas in 2002 (table 3). Survival in 2003 was higher than in 2002 for both species on the unburned site. For F. idahoensis survival in undershrub locations differed between years although survival in the other microsites did not. Survival did not differ among microsites on the burned site for either species, although survival in the undertree locations remained higher than other microsites. Neither species survived on the burned site in undershrub locations (figure 3).

Table 1—Repeated measures mixed effects ANOVA for average monthly soil temperatures (month and depth were treated as repeated measure with toeplitz covariance structure). P values ≤ 0.05 and > 0.01 are italicized, p values ≤ 0.01 and > 0.001 are bold faced and p values ≤ 0.001 are bold faced and italicized.

•		2002	2003			
Effect	df	F-Value	P	df	F-Value	P
Site	1,4	65.31	0.001	1,4	31.49	0.005
Microsite	2,8	16.26	0.002	2,8	44.66	<0.001
Microsite* Site	2,8	1.22	0.346	2,8	3.85	0.067
Depth	2,24	11.75	<0.001	2,24	60.75	<0.001
Depth*Site	2,24	1.37	0.273	2,24	1.90	0.172
Depth* Microsite	4,24	0.61	0.659	4,24	1.32	0.292
Depth* Site* Microsite	4,24	0.41	0.802	4,24	0.66	0.623
Month	4,144	2403	<0.001	4,144	2081	<0.001
Month* Site	4,144	19.25	<0.001	4,144	5.95	<0.001
Month* Microsite	8,144	10.93	<0.001	8,144	8.82	<0.001
Month* Microsite* Site	8,144	4.37	<0.001	8,144	1.29	0.254
Month* Depth	8,144	37.55	<0.001	8,144	17.55	<0.001
Month* Depth* Site	8,144	2.69	0.009	8,144	0.95	0.475
Month* Depth* Microsite	16,144	0.98	0.482	16,144	0.59	0.885
Month* Depth* Site* Microsite	16,144	0.54	0.924	16,144	0.12	1.000

Table 2—Repeated measures mixed effects ANOVA for gravimetric soil moisture (date was treated as repeated measure with a power covariance structure). P values ≤ 0.05 and > 0.01 are italicized, p values ≤ 0.01 and > 0.001 are bold faced and p values ≤ 0.001 are bold faced and italicized.

		2002		2003			
Effect	df	F-Value	P	df	F-Value	P	
Site (Burn vs. Unburned)	1,4	15.04	0.018	1,4	20.38	0.010	
Microsite	2,8	7.92	0.013	2,8	7.08	0.017	
Microsite* Site	2,8	0.40	0.686	2,8	0.93	0.433	
Depth	2,24	5.97	0.008	2,275	5.74	0.004	
Depth*Site	2,24	2.68	0.089	2,275	1.30	0.275	
Depth* Microsite	4,24	2.00	0.127	4,275	0.18	0.947	
Depth* Site* Microsite	4,24	0.55	0.701	4,275	0.49	0.742	
Date	9,324	262.60	<0.001	7,275	114.23	<0.001	
Date* Site	9,324	4.45	<0.001	7,275	6.66	<0.001	
Date* Microsite	18,324	3.41	<0.001	14,275	1.69	0.057	
Date* Microsite* Site	18,324	1.75	0.030	14,275	2.41	0.003	
Date* Depth	18,324	7.40	< 0.001	14,275	4.30	<0.001	
Date* Depth* Site	18,324	1.41	0.123	14,275	0.91	0.548	
Date* Depth* Microsite	36,324	1.21	0.197	28,275	0.68	0.886	
Date* Depth* Site* Microsite	36,324	0.73	0.870	28,275	0.30	0.999	

The two forbs had quite different emergence patterns compared to the grasses. If analyzed together they also did not show any significant interactions for species although there was a significant species effect: *E. umbellatum* had higher emergence than *L. argenteus. E. umbellatum* analyzed alone had no significant differences in emergence between years, sites or microsites (figure 4, table 3). *L. argenteus* had no significant difference among microsites on the unburned site in 2002, but in 2003 the interspace areas had significantly higher emergence than the undershrub areas. There was no difference in emergence among different microsites on the burned site. The undertree areas on the burned site had significantly less emergence than interspace areas on the unburned site.

The two forbs were similar in their survival patterns, showing no significant interactions between species or other factors when analyzed together. *E. umbellatum* did have significantly greater survival than *L. argenteus* (f1,48 = 26.21, p < 0.001). *E. umbellatum* had no significant differences in survival with microsite, year, site or their interactions (table 3). *L. argenteus* did not survive in the undershrub locations on the unburned site in 2003 or the undertree locations on the burned site (figure 4).

Overwinter and Second Year Survival on Unburned Site

Seedlings that emerged in 2002 on the unburned site were followed over winter and during the 2003 growing season. Overwinter survival was high for all species ranging from 33 to 100 percent and averaging 82 percent. Overwinter survival was not significantly different between microsites for any species. The second season survival was much more

variable ranging from 0 to 85 percent with a mean of 35 percent. The only significant difference was for the grasses where undertree and undershrub microsites had higher survival than interspaces (f2,8.3 = 7.11; p = 0.01). Demographic stochastisity probably played a large role in the survival estimates during this period, especially in those species that had low initial emergence and survival.

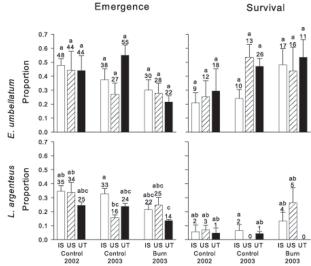


Figure 4—Proportional emergence and survival of *E. umbellatum* and *L. argenteus* in the control site in 2002 and 2003 and burn site in 2003 for interspace (IS), Undershrub (US) and Undertree (UT) microsites. Numbers above each bar indicate the average number of individuals emerging or surviving per quadrat out of 100 seeds planted. Bars that share the same letters in each graph are not significantly different than each other at an alpha of 0.05.

Table 3—ANOVA tables for arcsine square root transformed emergence and survival through the first growing season for A. tridentata, P. secunda, F. idahoensis, E. umbellatum and L. argenteus. Year effects were tested on the control sites and site effects (burn versus control site) were only tested in 2003. P value ≤ 0.05 and > 0.01 are italicized, p values ≤ 0.01 and > 0.001 are bold faced and p values ≤ 0.001 are bold faced and italicized.

Effect		A.tr	identata	P.secunda		F.idahoensis		E.umbellatum		L.argenteus	
Emergence	df	F	<i>p</i> -value	F	<i>p</i> -value	F	<i>p</i> -value	F	<i>p</i> -value	F	<i>p</i> -value
Microsite	2,9	7.16	0.058	6.16	0.009	10.66	0.001	0.95	0.406	5.49	0.014
Year (Control)	1,9	9.94	0.004	5.62	0.042	16.84	0.003	0.46	0.515	2.81	0.128
Site (2003)	1,9	0.06	0.814	1.91	0.200	13.48	0.005	2.16	0.175	1.20	0.302
Year*Microsite	2,18	0.73	0.493	2.78	0.088	2.30	0.129	2.15	0.146	4.27	0.030
Site*Microsite (2003)	2,18	0.41	0.666	9.36	0.002	7.88	0.004	3.23	0.063	6.54	0.007
Survival											
Microsite	2,9	0.52	0.601	7.61	0.005	10.29	0.001	0.33	0.725	6.12	0.009

DISCUSSION

The patterns of microsite environmental conditions and seedling establishment observed in this study are consistent with most studies of fire and microsite in the Great Basin. Higher soil temperatures on the burn site especially at the surface may be attributed to several factors including increased solar radiation reaching the soil and increased soil heating from soil blackening. Higher soil temperatures have been reported after harvesting in pinyon-juniper woodlands (Everett 1985) and in burned riparian corridors dominated by Artemisia tridentata var. tridentata (Chambers and Linnerooth 2001). The relatively lower temperatures in the undertree microsites compared to the interspace and undershrub microsites on the burned site was likely caused by partial shading from standing dead trees as well as the retention of needle mats after the fire that insulated the soil. The low temperatures on the undertree microsites on the unburned site were probably due not only to the needle mats but also the increased shading provided by live trees.

The generally higher soil moisture in the burn site might be due to lower transpiration rate due to vegetation loss. Soil moisture during the growing season in burned riparian corridors dominated by big sagebrush was also higher on burned sites (Chambers and Linnerooth 2001). Soil moisture in pinyon-juniper woodlands has been reported to increase during the first 2 to 3 years after tree harvesting as well indicating that tree death or removal is driving the difference (Everett 1985). The higher soil moisture under trees during spring and early summer is probably due to lower evaporation due shading, the insulating effect of the litter mat and higher organic content of these soils compared to the undershrub and interspace locations.

Seeding success of *A. tridentata* is typically low (Young and Evans 1986; Meyer 1990; Booth and others 1999) and natural recruitment is believed to be episodic (Lommasson 1948; Cawker 1980; Perrymann and others 2000). Many of the reported reasons for poor seeding success might have affected this study as well. The planting depth of 0.5 cm

was similar to that recommended for this species (broadcast seeding to < 0.5cm; McArthur and Welch 1982; McArthur and others 1995), but in undertree and shrub microsites an additional 1 cm of litter was added that may have decreased emergence rates. Although the seeds provided by the commercial growers were from areas with similar environmental characteristics, the lack of locally-adapted populations may have resulted in mis-timed germination and caused increased mortality (Meyer and Monson 1990). We may have under estimated emergence because A. tridentata is expected to emerge in late winter to early spring often under snow (Meyer et al 1990; Meyer and Monson 1990) or coincident with snow melt (Monson 1999) before sampling began. Mortality can be high in the first few weeks of emergence (a period when the study site was inaccessible). This mortality has been associated with damping off (Meyer and Monson 1990) and early moisture stress (Boltz 1994). The low seedling survival of those that were detected as emerging was likely due to the combined effects of late spring frosts as observed by Meyer and Monson (1990) and low soil moisture as observed by Owens and Norton (1992). The two years sampled were dry to normal based on annual precipitation years (14.9 and 21.0 cm total for the water year 2002 and 2003 respectively compared to a 30 year mean of 20.1 cm from the Austin, NV weather station).

The emergence and survival patterns of the two grasses parallels their distribution on the landscape. Both grasses are more common under trees, especially at the edge of the litter layer (Everret and others 1983), and generally higher grass cover under trees has been reported in North American arid landscapes (Armentrout and Pieper 1988). Greater survival of grasses under shrubs has been reported for arid shrub communities (Garcia-Moya and McKell 1970; Huber-Sannwald and Pyke 2005) and, although this pattern of higher survival was seen in our data, the increase was not significant. The increase in emergence and survival under trees was not observed on the burned site. Also, neither *F. idahoensis* nor *P. secunda* survived in undershrub microsites on the burned site. Increased exposure and more

extreme soil temperatures can cause higher seedling mortality in undershrub and undertree microsites following burning (Chambers and Linnerooth 2001). However, resource availability, both nutrients (Blank and others 1994, 2003) and water (Chambers and Linnerooth 2001), typically increases following fire and can result in increased growth and reproduction of surviving seedlings (Chambers and others 2007). Growing season conditions appeared to modify both emergence and survival patterns. On the unburned fan, 2002 had better emergence than 2003. Near-surface soil temperatures averaged 10°C warmer in 2002 than in 2003 and this may have led to increased germination rates (for example, Chambers and others 2007). In contrast, survival on the unburned sites was higher in 2003, a wetter year compared to 2002.

The two forbs did not show any clear patterns in response to microsite or location (fan). E. umbellatum was not affected by microsite or burning and emergence and survival was high in all locations. E. umbellatum is common throughout both the burned and unburned site and natural seedlings were observed establishing in equal abundance on both sites (Dhaemers 2006). L. argenteus had fair to poor emergence and very poor survival. Emergence was higher in interspaces in 2003 than in undershrub microsites on the control site although this was not the case in 2002. The universally poor survival of L. argenteus observed here contrasted with an observed increase in cover and natural seedling establishment on the burned site three years later (E. Goergin University Nevada, Reno, NV, personal communication). This indicates that both locally adapted seed sources and site modification may be important for establishing L. argenteus following prescribed fire.

This study was conducted in plots with intermediate tree cover (38 percent) and the immediate effects of the spring prescribed burn appeared to be more negative for seedlings than adult plants. In a concurrent study on the same site there was an increase in cover of both the perennial grass and forb species on the burned site, including the species observed in this study (Dhaemers 2006). Adult plants that survived the fire were undoubtedly more tolerant of the harsh post-fire environment than seedlings, and the increase in cover came largely from pre-existing individuals. Survivors were released from competition from the shrubs and trees, and exhibited increased productivity because of an increase of available soil water and nutrients (Rau 2005). The effects of the prescribed fire on seedling emergence and survival appeared to moderate over time, and seedling establishment from reproducing adults occurred on the site within three years after the burn (Dhaemers 2006).

As expanding woodlands mature and canopy cover increase, perennial grass and forb cover typically decreases and the risk of high severity crown fire increases (Miller and Tausch 2002). On the study site areas dominated by

trees (78 percent canopy cover) had low cover and biomass of perennial herbaceous species and limited shrub establishment three years after the burn (Dhaemers 2006). Low abundance of perennial herbaceous species on these sites resulted in limited seed input (Allen and others submitted), and environmental conditions after prescribed fire were at least as harsh as those on areas with intermediate tree cover. This indicates that as tree cover increases the probability of unassisted recovery of these sites decreases and the importance of revegetation and seedling establishment increases. Sites with high tree cover may have crossed biological thresholds, and restoration to sagebrush semi-desert species following either prescribed fire or wildfire will likely require revegetation with native semi-desert species.

CONCLUSIONS

This study contributes to our basic understanding of the effects of fire on seedling establishment in semi-arid woodlands and shrublands and has important implications for their restoration. The spring prescribed fire in the study resulted in increases in soil resources, including both soil nutrients (Rau 2005) and soil water as has been observed after wildfires or fall prescribed burns in similar ecosystems (Blank and others 1994, 2003; Chambers and Linnerooth 2001). Increased exposure and blackened soils following the burn resulted in higher soil temperatures as observed elsewhere (Chambers and Linnerooth 2001), but environmental conditions differed among microsites. Shrubs and their litter usually were consumed completely by the fire resulting in a harsher microenvironment. In contrast, while trees were killed by the relatively cool spring burn, the litter mats remained intact and the standing trees coupled with the litter mats moderated the soil environment. Individual species responses to the burn differed, but seedling establishment was generally low. Grasses are often associated with trees in semi-arid ecosystems (Everett and others 1983; Armentrout and Pieper 1988), and emergence and survival of both F. idahoensis and P. secunda were lower on the burned than unburned site. In contrast, there were no detectable differences in emergence and survival on burned vs. unburned sites for A. tridentata, E. umbellatum, or L. argenteus. Differences in growing season conditions affected seedling emergence and survival on the unburned site and likely influenced seedling establishment on the burned site as well. An early and warm growing season in 2002 resulted in higher seedling emergence, but cooler and wetter conditions in 2003 resulted in greater seedling survival.

Several recommendations for the revegetation of sagebrush ecosystems that have crossed biological thresholds due to pinyon-juniper encroachment follow from the results of this research. Our data confirm the need for increasing the seed

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availability of adapted populations of native species. Seeds of some species, like E. umbellatum, exhibited relatively high establishment across sites and years and appear to be fairly broadly adapted. Other species, like L. argenteus and A. tridentata ssp. vaseyana, exhibited generally low emergence or survival from purchased seeds and may require locally adapted ecotypes for successful establishment (see Meyer and others 1990) As observed elsewhere. seedling establishment depended environmental conditions in these ecosystems and was highly variable among years (Chambers 2000; 2001). Seeding species at higher rates than is typical may be necessary to ensure establishment during more favorable years. Also, repeated seeding of A. tridentata species (which have short-lived seeds) in high priority areas may be required to promote establishment. Clearly, effective approaches for restoring mountain sagebrush ecosystems are needed to ensure their sustainability. A major focus should be on increasing the seed availability of locallyadapted species and developing methods for their establishment

ACKNOWLEDGEMENTS

This research was funded by the US Forest Service, Rocky Mountain Research Station, Great Basin Ecosystem Management Project, and Joint Fire Sciences Program Project # O1B-3-3-01. We thank the Humboldt-Toiyabe National Forest for facilitating this research, Dave Turner for assistance with the statistical design, and Monica Mazzola, Eugenie Mont Blanc, Ben Rau and Rich Redd for field assistance.

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