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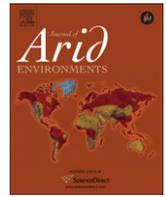
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Differential seedling performance and environmental correlates in shrub canopy vs. interspace microsites[☆]

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ABSTRACT

Shrubs in semi-arid ecosystems promote micro-environmental variation in a variety of soil properties and site characteristics. However, little is known regarding post-fire seedling performance and its association with environmental variation in former shrub canopy and interspace microsites. We compared post-fire seeding success and various soil properties important for seedling establishment between shrub canopy and interspace microsites in Wyoming big sagebrush (*Artemisia tridentata*) plant communities in southeast Oregon, U.S.A. We burned 5, 20 × 20 m sites and established paired canopy and interspace micro-transsects seeded with bluebunch wheatgrass (*Pseudoroegneria spicata*, 193 seeds/m) or crested wheatgrass (*Agropyron cristatum*, 177 seeds/m). At one year post-fire, seedling density was 69% higher ($p = 0.012$) for crested wheatgrass (compared to bluebunch wheatgrass) and 75% higher ($p = 0.019$) for interspace microsites (compared to canopy). However, tiller and leaf area production were over twice as high ($p < 0.05$) in canopy microsites. Soil color and soil temperature, explained 19–32% of variation in seedling performance metrics. Shrub effects on seeding success are complex and interact with abiotic disturbances, but patterns of increased seedling performance in canopy microsites and their relationships to soil variables may suggest tactics for increasing success of restoration practices.

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1. Introduction

Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Welsch) plant communities evolved under pyric influence (Mensing et al., 2006; Wright and Bailey, 1982), but are now at risk of fire-associated conversion to exotic annual grasses (Stewart and Hull, 1949; Young and Allen, 1997). Expansion of exotic annual grass populations threatens much of the western United States and represents one of the largest biological invasions ever recorded. Meinke et al. (2009) estimated a moderate to high probability of cheatgrass dominance on 28 million ha in the Intermountain West in Idaho, Oregon, Nevada, Utah, and Washington. Maintenance of native functional plant groups is seen as a key component of preventing continued expansion of invasive annuals. Multiple published efforts suggest that density of mature perennial

bunchgrasses is inversely correlated with that of invasive annual grasses (Chambers et al., 2007; Davies, 2008; Robertson et al., 1966). Additionally, some native perennial grasses may play important roles in facilitating recruitment of *Artemisia*, which can decrease in annual grass-dominated environments (Booth et al., 2003).

Because of post-fire exotic annual grass invasion (Chambers et al., 2007; Stewart and Hull, 1949), it is often critical to revegetate Wyoming big sagebrush plant communities after wildfire. However, post-fire restoration of perennial grasses in invaded Wyoming big sagebrush systems has proven difficult (Lysne and Pellant, 2004), particularly when using native species, and at lower elevations (Hull, 1974; Richards et al., 1998). Restoration difficulties can be associated, at least in part, with an extremely variable environment over space. Sources of large scale spatial variability may include slope, aspect, soil type, elevation, soil nutrient properties and macro meteorological variables (Boyd and Svejcar, 2009; Davies et al., 2007b; Norton et al., 2004). Another source of spatial variability in the restoration environment that has received less attention is the micro-environmental conditions associated with woody plants (Castro et al., 2002).

Shrubs have been shown to exert a strong influence on their immediate soil environment. For example, elevated localized

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concentrations of soil nutrients in otherwise low fertility soils can result from nutrient translocation by deep-rooted shrubs (Jackson and Caldwell, 1993a,b). Soil chemistry and hydrologic status may also be altered through litter deposition by shrubs (Huber-Sannwald and Pyke, 2005; Madsen et al., 2011; Rau et al., 2008). Compared to interspace microsites, micro-environments under shrub canopies (i.e., “canopy” microsites) are often characterized by increased soil water, more moderate soil temperature and increased soil nitrogen and carbon (Davies et al., 2007a; Esque et al., 2010a; Vetaas, 1992). Recent evidence suggests that elevated nutrient content in canopy microsites may persist for a short time following fire (Davies et al., 2009) or be accentuated by fire (Brooks, 2002; Stubbs and Pyke, 2005).

Previous research (Boyd and Davies, 2010) indicated differential success of seeded perennial grasses in association with interspace vs. canopy microsites within burned Wyoming big sagebrush communities. One year post-fire, undercanopy positions had up to 7× greater (depending on species) seedling density, higher incidence of reproductive tillers and increased seedling height relative to interspace positions. However, the specific environmental factors associated with this differential seedling performance have not been isolated. Identification of environmental correlates responsible for this relationship could have strong implications to post-burn management. Specifically, environmental data could be used to focus revegetation and restoration efforts on high probability sites (e.g., those sites with high pre-fire shrub abundance), or, alternatively, to help guide modifications to specific restoration practices to increase success.

Our objectives were to 1) identify differences in post-fire seedling performance in canopy vs. interspace microsites for native and non-native perennial bunchgrasses, 2) determine differences in soil-based environmental factors between burned canopy and burned interspace microsites, and 3) determine correlations between soil-based environmental factors and seedling performance across canopy and interspace microsites post-fire. We hypothesized that burned canopy microsites would have higher soil nutrient status, increased soil surface temperature, higher carbon and greater water content, and that these factors would correlate positively to seedling performance.

2. Methods

2.1. Study area

Our study area was located within the Wyoming big sagebrush alliance at the Northern Great Basin Experimental Range, approximately 56 km west of Burns, OR (43.48 N, 119.72 W). Elevation was approximately 1500 m. Annual precipitation is highly variable, but crop year inputs (September–June) average 25.7 cm with the majority falling as rain or snow during the October to March period (long term dataset, Eastern Oregon Agricultural Research Center, Burns, Oregon). Sites were flat to 3° with variable aspect. Prior to burning, Wyoming big sagebrush was the dominant shrub (about 98% of shrub canopy cover) with limited amounts of rabbitbrush (*Chrysothamnus nauseosus* (Pall.) and Britt.). Common perennial grasses at sites included bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love), needlegrass (*Achnatherum* sp. P. Beauv.), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.), Sandberg's bluegrass (*Poa secunda* J. Presl), and the non-native crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.). Prominent perennial forbs included milk vetch (*Astragalus curvicaupus*), tailcup lupine (*Lupinus caudatus* Kellogg), hawksbeard (*Crepis acuminata* Nutt.), and long-leaf phlox (*Phlox longifolia* Nutt.). Annual forbs included pale alyssum (*Alyssum alyssoides* Stapf), fireweed (*Epilobium*

paniculatum Nutt.) and maiden blue-eyed Mary (*Collinsia parviflora* Lindl.). The non-native cheatgrass (*Bromus tectorum* L.) was the only annual grass present at the sites. Sites have a history of moderate growing season grazing by cattle but were not grazed during the course of the study. Sites had not burned in the last 30 years.

2.2. Experimental design

We utilized a randomized block design with 5 blocks (sites), 2 plant species (native and non-native) and 2 microsites: 1) areas under sagebrush canopy (canopy) and 2) areas not influenced by shrub cover (interspace). Blocks (20 × 20 m) were within 1.5 km of each other, and contained an abundance of mature sagebrush. Within each block we randomly selected 5 mature Wyoming big sagebrush plants prior to burning, measured shrub height and crown diameter and marked the shrub with a metal tag. At each shrub we permanently marked the beginning and end of 2, parallel (25 cm apart) canopy transects and 2 interspace transects. Transects were run along a random azimuth and transect length was equal to the distance from the shrub base to a downward projection of the edge of the shrub canopy (i.e., dripline). Within microsite, we randomly assigned transects to be planted with either native (bluebunch wheatgrass) or non-native (crested wheatgrass) perennial grass seeds. Precipitation data were collected at an existing nearby (<1 km) weather station.

2.3. Fire and fuel characteristics

Plots were burned in September 2009 using a strip headfire technique and drip torches with a 50:50 mixture of unleaded gasoline and diesel. Temperature, humidity and wind speed were recorded and all plots were burned within a 3-h period. We characterized fire temperature at canopy and interspace microsites using temperature sensitive paints (TempilaqoG, Big Three Industries Inc., Tempilo Division, South Plainfield, NJ) adhered to galvanized metal strips (Graham and McCarthy, 2006; Iverson et al., 2004; Kennard et al., 2005). These paints are designed to change color at a minimum critical temperature. We used paints with 16 different minimum critical temperatures ranging from 79 to 538 °C for interspace microsites and from 135 to 760 °C for canopy microsites. Within a block we randomly selected two shrubs and, under each shrub, we placed one galvanized strip with small dots of each paint on bare soil and one strip within the basal crown of a perennial grass; this design was repeated for adjoining interspace microsites at each shrub. Herbaceous, shrub and total fuel loads averaged 46.6 ± 10.9 , 652 ± 204.0 , and 698 ± 205.9 g/m², respectively. Humidity at the time of burning varied from 15 to 29%, air temperature from 27.8 to 33.3 °C and wind speeds from 4.5 to 3.4 m/s⁻¹. Percent combustion of fuels (herbaceous and shrub combined) was $91.4 \pm 1.66\%$ among blocks. Fire temperature in canopy microsites averaged 223.9 ± 24.2 and 285.0 ± 25.0 °C for bare soil and bunchgrasses, respectively. Temperature for bunchgrasses in interspace microsites was 157.2 ± 21.0 °C. Fire temperature on bare soil within interspace microsites was lower than could be recorded by our temperature-sensitive paints at 4 of 5 locations; the fifth was 135 °C. Shrub combustion was nearly complete with only a few centimeters of the original stem present post-fire.

2.4. Seeding

Transects were hand-seeded in November, 2009, approximately 2 months post-fire. We seeded directly into a small furrow running the length of each transect and covered seeds with approximately

1 cm of soil. Seeding rate was 177 and 193 viable seeds/transect m for crested and bluebunch wheatgrass, respectively.

2.5. Plant response

Emergent seedlings of seeded species were counted at approximately 2-week intervals from April 9 until June 23, 2010. The number of wind-exposed seeds along each transect was counted on April 9, 2010. Other seedling performance measures (including a final density count) were recorded on June 23, 2010. Tillers of all seedlings (seeded species) were counted along each transect. Leaf area was measured for seedlings with one tiller by measuring mid-point width and length of all leaves and then multiplying mid-point width by length to estimate area of each leaf. Leaf area was then summed across all leaves present on the tiller to determine tiller leaf area. For seedlings with > one tiller, a single tiller was randomly selected for measurement and the total number of tillers for that seedling multiplied by the leaf area of the measured tiller to estimate seedling leaf area. The number of reproductive (seed bearing) seedlings was recorded for each transect. Cover and density of non-seeded plant species were measured at interspace and canopy microsites in June 2010. One 40 × 50 cm quadrat was placed to overlap transects within microsite with the long axis of the quadrat running parallel to transect orientation. Percent cover of all non-seeded species plus bare ground and litter was ocularly estimated; density of non-seeded species was quantified by direct count within the quadrat.

2.6. Environmental variables

Environmental variables were sampled for each interspace and canopy microsite. Because soil moisture and temperature critical periods can vary across years for perennial grass seedlings (Hardegree et al., 2003), we measured soil moisture and temperature values at two-week intervals from April 9 to June 23, 2010. Soil surface temperature for each microsite was recorded using a handheld infrared thermometer (Ranger ST; Raytek, Santa Cruz, CA). Readings were taken at a point between the two transects (within microsite) and all data for a given date were collected between the hours of 1200 and 1300. Soil temperature data were only collected when clouds were not directly influencing incoming solar radiation. Soil samples for water content were collected at surface (0–5 cm) and sub-surface (5–10 cm) depths and a portion of each sample retained for subsequent nutrient analysis. Gravimetric soil water content was determined by the difference between field and oven dry weight. Total soil carbon and nitrogen were determined using a LECO CN-2000 (LECO Corp., St. Joseph, MI). Bulk density samples were collected using a 2.5-cm diameter soil core driven to 5-cm depth; scores were calculated by dividing sample volume by soil weight following drying. To determine soil surface color, images of the center of each microsite were captured with a handheld digital camera at 1 m elevation in May of 2010. We then hand-digitized a polygon (excluding all live plant matter) between the two transects (native and non-native) within each microsite using SigmaScan Pro software (Jandel Scientific, San Rafael, CA). Average gray scale value (0 = black, 255 = white) for pixels within each polygon was calculated using algorithms within the software.

2.7. Data analysis

Seedling performance measures were expressed both on a per plant basis as well as per meter of transect. We collated abundance data of non-seeded species by functional group including large perennial bunchgrasses, Sandberg's bluegrass, perennial forbs, annual forbs and shrubs. Data were examined for skewness and

kurtosis (Proc Univariate; SAS, 1999). When normality or homogeneity of variance assumptions were violated, data were weighted by the inverse of the treatment variance (James and Drenovsky, 2007; Neter et al., 1990). We used analysis of variance (Proc Mixed; SAS, 1999) to determine the influence of microsite on seedling performance measures, abundance of non-seeded species, and soil-associated environmental variables. Differences in density of emergent seedlings across sampling dates were determined using repeated measures ANOVA (Proc Mixed; SAS, 1999). Block and the block × treatment interaction were considered random effects in the models. Covariance structures were determined using the Akaike's Information Criterion (Littell et al., 1996). Comparisons of values for environmental variables by microsite were considered significant at $\alpha = 0.10$. All other main effects, interactions and treatment differences were considered to be significant at $\alpha = 0.05$. When significant main or interactive effects were found we assessed differences in treatment means using the LSMEANS (SAS, 1999) procedure ($\alpha = 0.05$). We used stepwise multiple linear regression (Proc Reg; SAS, 1999) to determine the relationship between seedling performance (within species) and all environmental variables that differed ($\alpha = 0.10$) between microsites. We allowed for a greater probability of type-1 error when comparing values for environmental variables between microsites, because the main purpose of this exercise was to narrow the pool of variables to be used in regression equations relating seedling performance to values of environmental variables. Regression analysis was conducted across microsites using forward selection with an alpha level of 0.15 for variable entry into the model. All mean values are reported with their associated standard error.

3. Results

Shrubs ranged from 62 to 117 cm in height and from 72 to 181 cm in diameter. Transects ranged in length from 25.5 to 62 cm. Precipitation for the calendar year 2009 was 244 mm (85.5% of long-term average) and in 2010 was 285.2 (101.2% of long-term average).

3.1. Plant response

The number of wind exposed seeds was 16.7 ± 5.6 and 6.3 ± 1.8 seeds/m for canopy and interspace microsites, respectively. Density of seeded species (no./m, Fig. 1a) was 75% higher ($p = 0.019$) in interspace microsites (compared to canopy) and 69% higher ($p = 0.012$) for non-native (compared to native). Microsite effects on reproductive seedlings (no./m) varied by species ($p < 0.001$) and occurrence was highest for non-native species in canopy microsites ($\bar{X} = 1.5 \pm 0.3$ /m, Fig. 1b). Reproductive seedlings were not found in interspace microsites and the average abundance for reproductive seedlings in native canopy transects ($\bar{X} = 0.09 \pm 0.09$ /m) did not differ ($p > 0.05$) from zero.

Tillers per seedling were 4.5-fold higher ($p < 0.001$) for canopy microsites (Fig. 1c). Tillers per transect (no./m) were 2.6-fold and 2.2-fold higher for canopy microsites ($p = 0.010$) and non-native species ($p = 0.025$), respectively (Fig. 1d). Leaf area per seedling was 7.7-fold higher ($p = 0.008$) for canopy microsites (Fig. 1e) and leaf area per transect was 10.1-fold higher ($p = 0.023$) for canopy microsites (Fig. 1f).

Density of seedlings varied by date × microsite ($p < 0.001$, Fig. 2). Seedling density under canopies was 50% higher ($p < 0.05$) than interspaces on the initial collection date (April 9), but decreased through time such that by the final collection date (June 23) seedling density was 69% higher ($p < 0.05$) in interspaces than canopies. Canopy cover of non-seeded perennial grasses was 2.9-fold higher ($p = 0.017$) for interspace microsites and cover of

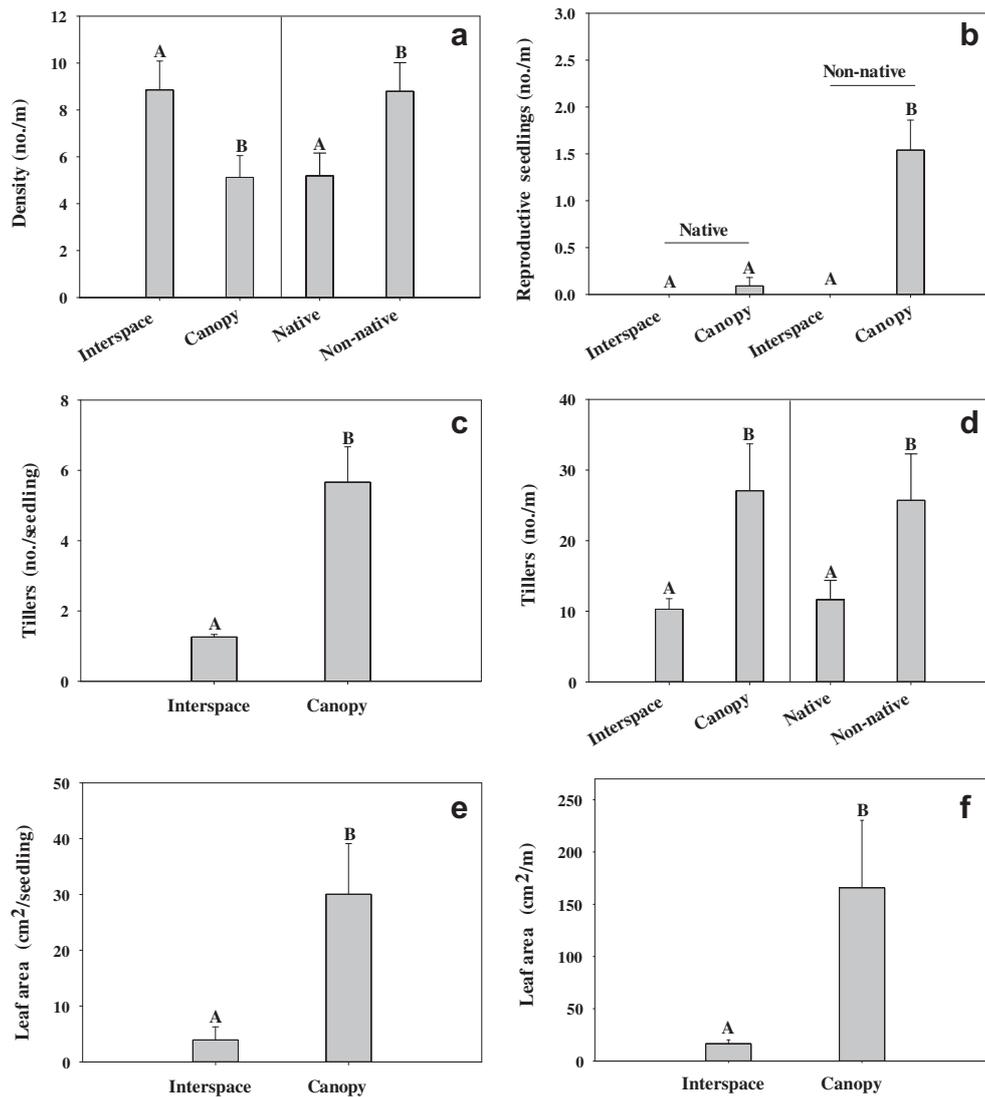


Fig. 1. Post-burn (2010) measures of seedling performance by species (native = bluebunch wheatgrass, non-native = crested wheatgrass) and microsite for fall-seeded (2009) plots in Wyoming big sagebrush plant communities in southeastern Oregon as a function of seedlings per transect (a), reproductive seedlings per transect (b), number of tillers per seedling (c), tillers per transect (d), leaf area per seedling (e), and leaf area per transect (f). Bars with different letters within a panel or graph are statistically different ($\alpha = 0.05$).

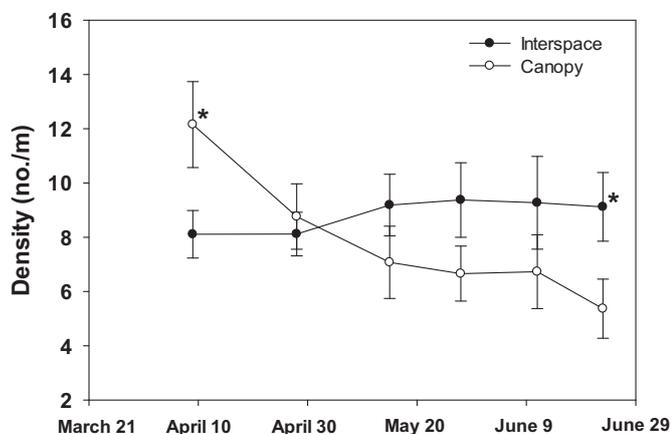


Fig. 2. Post-burn (2010) seedling density for fall-seeded (2009) perennial grasses in interspace and canopy microsites in Wyoming big sagebrush plant communities in southeastern Oregon. Within a date, an asterisks denotes a statistical difference ($\alpha = 0.05$) between microsite means.

Sandberg's bluegrass was 7-fold higher ($p = 0.017$). Density of non-seeded perennial grasses, Sandberg's bluegrass and annual forbs (Fig. 3b) was 2.5 ($p = 0.056$), 8.4 ($p = 0.032$) and 2.4-fold ($p = 0.007$) higher in interspace microsites, respectively.

3.2. Environmental variables and seedling performance

Of the 24 environmental variables tested, 6 differed ($p < 0.10$) between canopy and interspace microsites (Table 1). Using these 6 variables to model seedling performance produced significant ($p \leq 0.05$) models for 10 of 12 seedling performance regressions (Table 2). Model R^2 values ranged from 0.19 to 0.32. Seven of the 10 models included soil color and dark colors (lower gray scale values) were associated with increased seedling performance. Five of the 10 models included soil surface temperature, with higher temperature generally associated with increased seedling performance; density of non-native seedlings was inversely related to temperature.

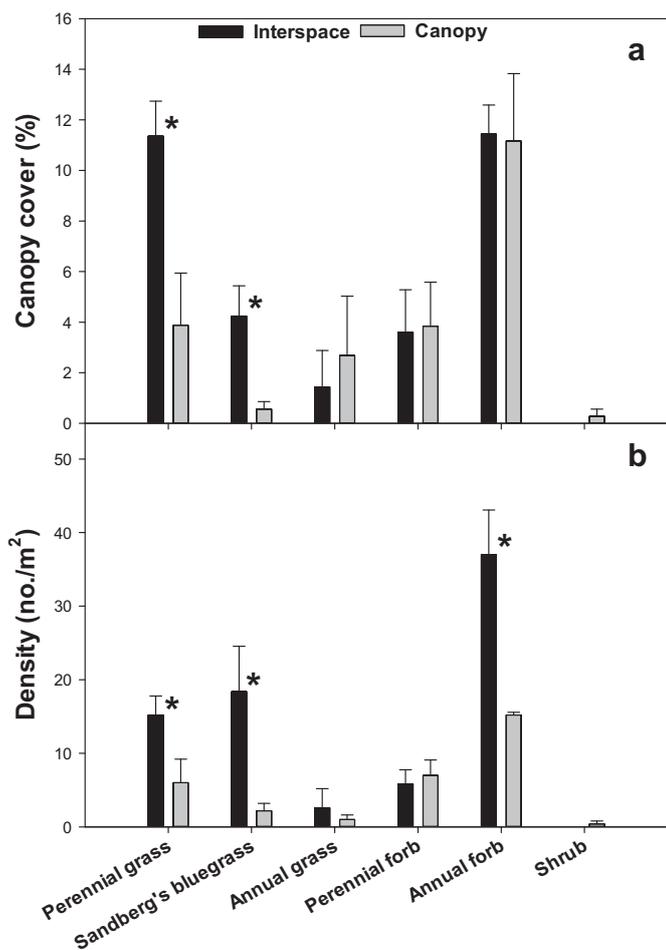


Fig. 3. Post-burn (2010) canopy cover (a) and density (b) for non-seeded species, by functional group, in interspace and canopy plots in Wyoming big sagebrush plant communities in southeastern Oregon. Within a graph and functional group, an asterisks denotes a statistical difference ($\alpha = 0.05$) between microsite means.

4. Discussion

Sagebrush and other woody species have been shown to alter microsite characteristics to facilitate establishment and growth of other plant species (Abella et al., 2009; Chambers, 2001; Griffith, 2010; Huber-Sannwald and Pyke, 2005; Pueyo et al., 2009). We found strong evidence to support the hypothesis that canopy microsites had higher seedling performance. In particular, seeded perennial grass leaf area and tiller density per transect meter were between 2 and 10 orders of magnitude higher for canopy microsites compared to interspace microsites. Reproductive tillers on seeded perennial grasses were completely absent in interspace microsites but were present in canopy microsites. These relationships are consistent with our previous work (Boyd and Davies, 2010) indicating increased plant size and reproductive performance in canopy microsites within a large-scale post-fire restoration project. Contrary to both our previous work and current hypothesis, the present study found higher seedling density in interspace microsites. Based on the otherwise strong seedling performance, we suspect that reduced seedling density for canopy microsites was at least partially a reflection of wind erosion of seeds; about 9% of canopy and 3.5% of interspace seeds. Additionally, many of the seedlings in canopy microsites (but not interspace) had exposed near-surface roots (likely due to wind erosion) which may have impaired post-emergence survival. Other authors (Sankey et al.,

2010; Whicker et al., 2002) have noted increased wind-erosion of under-shrub microsites following fire and the high organic matter content of canopy microsites (Davies et al., 2007a) may pre-dispose them to aeolian-based soil loss following fire or other disturbances that remove shrubs.

4.1. Microsite characteristics

We found differences in soil physical properties, the soil abiotic environment and soil nutrient status in association with microsite (Table 1). Previous research suggests decreased soil bulk density in sagebrush canopy (vs. interspace) microsites (Chambers, 2001). A lack of microsite effect on bulk density in the current study was surprising but may be related to post-fire wind erosion of surface organics as described above. Soil moisture has been reported to be higher in canopy vs. interspace microsites in unburned sagebrush (Davies et al., 2007a) and other woody plant communities (Chambers, 2001). In unburned plant communities, increased soil moisture in undercanopy microsites has been associated with elevated humidity and decreased irradiance (Castro et al., 2002). However, we found no relationship between microsite and soil water content following burning, perhaps because shrubs were completely combusted (or nearly so) during the fire.

Darker soil color associated with canopy microsites was likely due to burned organic materials on the soil surface. Higher soil surface temperatures in canopy microsites were associated with soil color, with darker colors absorbing more heat than lighter-colored interspace microsites. Our field observations suggest that altered soil color is not long lasting, particularly in sandy soils, and differences may dissipate within a year of burning. In unburned woody plant communities soil temperatures are typically cooler in canopy locations (Breshears et al., 1998; Suzan et al., 1996; Vetaas, 1992). Our results agree with those of Davies et al. (2009) who reported higher soil temperatures for burned canopy microsites but also found that unburned canopy microsites had lower soil temperatures than burned, indicating that fire and microsite interact to influence soil temperature dynamics.

Consistent with the present study, others authors have reported elevated nutrient concentrations (including total carbon and nitrogen) in both burned (e.g., Davies et al., 2009; Rau et al., 2007, 2008) and unburned (Chambers, 2001; Davies et al., 2007a; Doescher et al., 1984) canopy microsites in sagebrush plant communities and Stubbs and Pyke (2005) noted that the magnitude of differences in soil nitrate and ammonium between canopy and interspace microsites increased following fire. Similarly, Esque et al. (2010a) found higher inorganic nitrogen pools in canopy microsites (relative to interspace) of creosote bush (*Larrea tridentata* (DC) Cov.)/white bursage (*Ambrosia dumosa* (A. Gray) Payne) communities following fire and that fire increased ammonium pools more in undercanopy microsites. Localized elevated nutrient concentration in association with woody plants has been widely reported in unburned shrub and tree ecosystems including the Mojave (Schlesinger et al., 1996) and Chihuahuan (Cross and Schlesinger, 1999) deserts, coastal shrub communities (Gutierrez et al., 1993), chenopod shrublands (Castro et al., 2002), conifer woodlands (Everet et al., 1984) and *Acacia* savanna (Dean et al., 1999).

4.2. Seedling performance in relation to microenvironment

In the present study, variable seedling performance associated with microsite was at least partially explained by differences in a limited subset of environmental variables. We found positive associations between increased soil surface temperature and/or darker soil color and most measures of seedling performance

Table 1

One-year post-burn (2010) values for environmental variables measured in interspace and canopy microsites in Wyoming big sagebrush plant communities in southeastern Oregon. Plots were seeded in fall of 2009. Asterisks denote variables that differed between microsites ($\alpha = 0.10$).

Variable	Canopy		Interspace		p value
	Mean	se	Mean	se	
<i>Soil physical properties</i>					
Bulk density (g/c ³)	0.97	0.05	1.09	0.05	0.148
*Soil surface color (grayscale)	127.58	3.31	151.79	5.33	0.005
<i>Soil abiotic environment</i>					
*Soil surface temperature °C 4.9.2010	37.26	1.10	29.81	0.93	<0.0001
*Soil surface temperature °C 4.28.2010	26.73	0.69	24.78	0.62	0.068
Soil surface temperature °C 5.15.2010	43.58	2.52	39.62	1.70	0.229
Soil surface temperature °C 5.28.2010	32.11	2.77	28.92	2.61	0.425
*Soil surface temperature °C 6.11.2010	33.72	1.25	29.21	0.81	0.017
Soil surface temperature °C 6.23.2010	52.03	2.55	47.29	2.04	0.184
% Soil water (0–5 cm) 4.9.2010	0.18	0.03	0.15	0.01	0.455
% Soil water (5–10 cm) 4.9.2010	0.17	0.03	0.18	0.02	0.870
% Soil water (5–5 cm) 4.28.2010	0.18	0.03	0.14	0.02	0.286
% Soil water (5–10 cm) 4.28.2010	0.19	0.02	0.18	0.02	0.888
% Soil water (0–5 cm) 5.15.2010	0.14	0.02	0.12	0.01	0.325
% Soil water (5–10 cm) 5.15.2010	0.15	0.02	0.16	0.02	0.778
% Soil water (0–5 cm) 5.28.2010	0.13	0.02	0.11	0.01	0.483
% Soil water (5–10 cm) 5.28.2010	0.15	0.02	0.15	0.02	0.986
% Soil water (0–5 cm) 6.11.2010	0.15	0.02	0.14	0.01	0.572
% Soil water (0–10 cm) 6.11.2010	0.16	0.02	0.15	0.02	0.784
% Soil water (0–5 cm) 6.23.2010	0.03	0.01	0.03	0.01	0.865
% Soil water (0–10 cm) 6.23.2010	0.07	0.01	0.51	0.43	0.335
<i>Soil nutrient status</i>					
*% Soil nitrogen (1–5 cm)	0.13	0.02	0.09	0.01	0.099
% Soil nitrogen (5–10 cm)	0.10	0.02	0.08	0.01	0.270
*% Carbon (1–5 cm)	1.58	0.15	1.01	0.14	0.025
% Carbon (5–10 cm)	1.15	0.16	0.86	0.09	0.158

(Table 2). We suspect that soil color acted mainly through its association with soil surface temperature; dark soils have been shown to increase heat absorption and temperature (Covington and Sackett, 1984; Davies et al., 2009; Wroblewski and Kauffman, 2003). Relationships between soil temperature and seedling performance have not previously been reported for post-fire microsites in sagebrush plant communities. Higher soil surface temperatures in early spring for burned canopy microsites (Table 1) may promote earlier emergence and accelerated development of emergent seedlings. Our data indicate that seedling density for canopy microsites was higher in the early growing season (Fig. 2), which is consistent with a temperature effect on emergence date. Additionally, higher soil temperatures may help decrease cold stress on developing seedlings at critical demographic stages. Cold tolerance of perennial grass seedlings has been reported to decrease with advancing pre-emergence development and

excessively cold temperatures may reduce or delay germination (Laude, 1956). In the study area, minimum daily temperatures at or below freezing are common through May and can occur during any month (Eastern Oregon Agricultural Research Center data file). In other systems, soil microbial activity has increased in association with elevated soil temperature following fire (Bissett and Parkinson, 1980). Soil temperature was inversely related to seeded plant density (non-native, Table 2). This finding is associated with increased density of seedlings in interspace microsites (which had cooler soil temperatures), and perhaps the disproportionate and negative influence of wind erosion on canopy seedling density.

An alternate hypothesis to explain our finding of increased tillering and leaf area of canopy seedlings would be that high fire temperatures under shrubs reduced soil seed pools to the extent that post-fire competition was limited. Our data do indicate higher

Table 2

Regression models used to predict seedling performance of seeded perennial grasses based on environmental variables.

Dependent variable	Independent variable	Coefficient	p value	Partial r ²	Model R ²	Model p value
Density/m (native)	None
Density/m (non-native)	Soil surface temperature 4.28	-1.263	0.128	0.132	0.213	0.056
	% Soil carbon (0–5 cm)	-0.702	0.057	0.082		
Tillers/plant (native)	Soil color	-0.081	0.025	0.186	0.186	0.025
Tillers/plant (non-native)	Soil surface temperature 6.11	0.559	0.004	0.288	0.288	0.004
Tillers/m (native)	Soil surface temperature 4.28	3.370	0.094	0.189	0.265	0.025
	Soil color	-0.313	0.129	0.076		
Tillers/m (non-native)	Soil color	-0.873	0.013	0.224	0.224	0.013
Leaf area/plant (native)	Soil color	-0.475	0.023	0.191	0.191	0.023
Leaf area/plant (non-native)	Soil surface temperature 6.11	6.369	0.010	0.237	0.237	0.010
Leaf area/m (native)	Soil color	-3.247	0.020	0.198	0.198	0.020
Leaf area/m (non-native)	Soil color	-5.783	0.105	0.195	0.268	0.024
	Soil surface temperature 6.11	33.298	0.134	0.074		
Reproductive seedlings/m (native)	None
Reproductive seedlings/m (non-native)	Soil color	-0.049	0.002	0.317	0.317	0.002

abundance of some non-seeded plant species in interspace microsites, which is consistent with fire-induced decreases in soil seed pools in canopy microsites (Brooks, 2002). Additionally, non-seeded perennial grasses were a mix of plants that survived the fire and post-fire seedlings. We suspect that increased fire temperature in canopy microsites (Korfmacher et al., 2003; Rau et al., 2007) acted to increase mortality of perennial grass clumps, and perhaps reduce soil seed pools as has been noted for shrub ecosystems in the Mojave Desert (Abella et al., 2009; Esque et al., 2010b), partially explaining differences in non-seeded perennial grass abundance between microsites. Brooks (2002) reported reduced undercanopy populations of annual grasses in association with higher fire temperatures in undercanopy microsites within creosote bush plant communities and speculated that elevated fire temperatures reduced soil seed pools. We recorded undercanopy temperatures of approximately 254 °C, which is almost double those recorded by Brooks (2002) and hot enough to kill seeds of most plants (Daubenmire, 1968; Wright and Bailey, 1982).

However, we did not find clear evidence that post-fire competition between seeded and non-seeded species was reduced in canopy microsites. For example, the ratio of canopy cover to density provides a measure of plant size. This ratio for non-seeded perennial grasses was 0.77 and 0.63, in interspace and canopy microsites, respectively, indicating that canopy plants were actually of smaller stature which is the opposite of what we would predict if competition were controlling plant abundance in the interspace. Additionally, the population of emergent seedlings was relatively constant over time for interspace microsites (but actually declined over time for canopy microsites as discussed previously) which is not what we would predict if competition were relatively higher in interspace microsites. Taken together, the preceding do not lend strong support to the idea of competition (either inter or intraspecific) as a limiting factor controlling seedling performance in the present study.

We found that seedling density, reproductive performance, and tillers per transect were higher for non-native vs. native seedlings. These findings are in line with a growing body of evidence indicating that “crested wheatgrass” (including *Agropyron cristatum*, *A. desertorum* (Fisch. Ex Link) Schult., and *A. fragile* (Roth) P. Candargy) establishment is superior to many native perennial bunchgrasses when establishing plants from seed (Davies et al., 2011). From a land management standpoint, the establishment qualities of crested wheatgrass make it an important tool for limiting encroachment of exotic annual species (Davies et al., 2010), given that large, established perennial bunchgrasses can be effective in limiting encroachment of annual grasses into sagebrush plant communities (Davies, 2008). In fact, some have proposed crested wheatgrass as an important intermediate step for eventual restoration of native perennial species in exotic annual grass-prone environments (Cox and Anderson, 2004). However, the use of crested wheatgrass in a restoration context should be balanced against the reality that, to date, the success of subsequent re-establishment of native perennial forbs and grasses within crested wheatgrass plant communities has been limited (Bakker et al., 2003; Fansler and Mangold, 2011; Hulet et al., 2010).

Seedling performance beyond first year establishment was not addressed in the present study. However, germination, emergence and survival to the end of the first growing season represents a major demographic milestone for perennial grasses. In our region, germination rates are fairly high and the most critical demographic stage during the life of a seedling is the transition from germinated seed to emergent seedling. Working at sites near the current study, and within the same vegetation type, James et al. (2011) reported germination rates for hand-seeded perennial grasses of greater than 70% and survival of post-emergent seedlings to adult was

equally high. However, emergence of germinated seeds was less than 10% (see also James and Svejcar, 2010). Emergence represents a major demographic bottleneck for establishing perennial grasses from seed, and we believe that the first year seedling performance results of the present study have strong application to plant community restoration.

5. Conclusions

We found strong evidence that perennial bunchgrasses in sagebrush canopy microsites had higher tiller and leaf area production and greater reproductive performance as compared to interspace microsites. These results underscore the importance of shrub conservation to post-fire revegetation or restoration efforts. Conversely, seedling density was less in the canopy. Differences in density were apparently tied to high post-emergence seedling mortality in canopy microsites. We associated this differential mortality with increased seed and seedling loss to wind erosion in canopy microsites as opposed to initially lower seedling density; which was actually higher for canopy microsites. Microsites also differed with respect to soil environmental properties including soil color, temperature, and nutrient content and these variables, in turn, explained a significant amount of the variation in most measures of seedling performance.

Our data support a growing body of work indicating that the influence of shrubs on plant community dynamics is variable based on interactions with abiotic disturbances. In comparing our results for burned sagebrush communities to the results of others for unburned communities, we found that the influence of shrubs on microenvironmental conditions was at least partially dependent on fire history. For example, fire can apparently ameliorate the positive effect of shrubs on soil moisture, reverse the influence of shrubs on soil surface temperature and accentuate elevated soil nutrients in canopy microsites. Additionally, fire can interact with other abiotic disturbances (in our case, wind erosion) to shape the influence of shrubs on successful reproduction from seed. In our study, the high rate of seed loss associated with wind erosion in canopy microsites is in contrast to the increased soil deposition noted by Whicker et al. (2002) for shrub microsites in unburned plant communities.

The associations between seedling performance and environmental variables described in this manuscript are based on correlative data and as such do not constitute definitive tests of ecological relationships. However, the magnitude of differences in some aspects of seedling performance relative to microsite is compelling, particularly given the critical nature of further progress in restoration effectiveness in the face of exotic annual grass invasion (Pellant et al., 2004). Our work provides a basis for linking differential seedling performance to micro-spatial variation in environmental properties and further manipulative research to test the role of specific environmental correlates, in particular soil color, in modulating seedling performance. Ultimately, this work could then serve as the basis for amending current restoration techniques to impart the benefits of canopy microsites in a more uniform manner over space, and in plant communities with, or without pre-fire shrub presence.

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