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The influence of *Artemsia tridentata* ssp. *wyomingensis* on microsite and herbaceous vegetation heterogeneity☆

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Abstract

The spatial distribution of *Artemisia tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh within plant communities creates two distinct zones; underneath (subcanopy) and between shrub canopies (interspace). The purpose the study was to determine the influence of subcanopy and interspace zones on microsite characteristics and herbaceous vegetation. Study sites were located at the Northern Great Basin Experimental Range (NGBER) (56 km west of Burns, OR) and Baker Pass (80 km southeast of Burns, OR). At the NGBER, microsite and vegetation differences existed between subcanopy and interspace zones. Compared to the interspace, subcanopy zones were characterized by lower fluctuations in soil temperature, higher levels of soil organic matter, nitrogen, carbon, and water, and greater herbaceous biomass, cover, and density. *A. tridentata* ssp. *wyomingensis* appears to strongly influence the spatial arrangement of herbaceous vegetation at the NGBER. Zonal vegetation differences measured at the NGBER were not found at Baker Pass, a location with a more north-facing aspect than the NBGER. Our results suggest that the influence of *A. tridentata* ssp. *wyomingensis* on herbaceous spatial heterogeneity may be greater as sites become warmer and drier. Our study demonstrated the potential of *A. tridentata* ssp. *wyomingensis* to

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create herbaceous spatial heterogeneity, elucidated that the relationships between *A. tridentata* ssp. *wyomingensis* and herbaceous species are complex, and can be site specific.
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Keywords: Wyoming big sagebrush; Micro-environment; Subcanopy; Interspace; Plant interactions

1. Introduction

Underneath (subcanopy) *Artemisia tridentata* Nutt. (big sagebrush) canopies may provide a more conducive environment for herbaceous vegetation establishment and growth than between shrub canopies (interspace) (Charley and West, 1977; Doescher et al., 1984; Burke et al., 1987; Wight et al., 1992; Chambers, 2001). However, the influence of *A. tridentata* on the spatial arrangement of herbaceous vegetation is not well explained. Therefore, examining the influence of *A. tridentata* on both microsites and herbaceous vegetation characteristics in subcanopy and interspace zones is needed to advance the understanding of the functional and structural relationships within *A. tridentata* plant communities.

Differences in the influence of *A. tridentata* on associated vegetation between subcanopy and interspace zones have been best characterized with several tree species. The establishment and early growth and development of *Pinus monophylla* Torr. & Frém (singleleaf pinyon) (Callaway et al., 1996; Chambers, 2001), *Cercocarpus ledifolius* Nutt. (mountain mahogany) (Schultz et al., 1996), *Pinus contorta* Dougl. ex Loud. (lodgepole pine), and *Juniperus occidentalis* Hook. (western juniper) (Miller and Rose, 1995) were enhanced when situated underneath *A. tridentata* canopies. Factors that may contribute to this facilitation are an increased availability of soil nutrients and water, and a moderated micro-environment underneath *A. tridentata* canopies. Soil nutrient concentrations and availability, particularly nitrogen (N) and phosphorus (P) (Charley and West, 1977; Doescher et al., 1984; Burke et al., 1987), and soil water content (Wight et al., 1992; Chambers, 2001) have been reported to be greater under than between *A. tridentata* canopies. Moderated soil temperature regimes under *A. tridentata* (Pierson and Wight, 1991; Chambers, 2001) likely contribute to increased seedling establishment.

However, evidence for zonal differences in the influence of *A. tridentata* on herbaceous species is limited. *A. tridentata* is highly competitive for P relative to associated bunchgrasses (Caldwell et al., 1985, 1987, 1991), but may increase the availability of water to plants growing in the subcanopy via hydraulic lift (Caldwell and Richards, 1989). Herbage production tends to increase two to threefold following *A. tridentata* removal (Blaisdell, 1953; Harniss and Murray, 1973; Hedrick et al., 1966; Sneva, 1972) suggesting a strong competitive interaction between *A. tridentata* and herbaceous vegetation. However, Blaisdell (1953) and Peek et al. (1979) also reported no significant changes in herbage production after burning *A. tridentata* communities. Kranitz and Caldwell (1995) reported no difference in perennial grass root development for plants grown under and in the interspace of *A. tridentata* spp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush) canopies. However, in two different studies in North Dakota (Hazlett and Hoffman, 1975) and Nevada (Eckert et al., 1986) establishment of herbaceous plants was enhanced under *A. tridentata* canopies relative to interspaces. The conflicting conclusions from these studies may be a product of difference in sites, year effects, and the overstory and understory species/subspecies evaluated. Consequently, the spatial arrangement of herbaceous vegetation structural and microsite characteristics in relation to under and between *A. tridentata* canopies is not well explained.

Late seral *A. tridentata* ssp. *wyomingensis* (Beetle & A. Young) S.L. Welsh (Wyoming big sagebrush) communities were chosen for evaluation because this alliance is the largest, most arid, least resilient to disturbance, and most endangered of the three common subspecies of *A. tridentata* (Beetle and Young, 1965; Morris et al., 1976; McArthur and Plummer, 1978; West et al., 1978; Miller and Eddleman, 2000). With increasing site aridity, the spatial organization of vegetation and resources tends to become more concentrated into discrete patches (Schlesinger et al., 1990). Thus, by characterizing *A. tridentata* ssp. *wyomingensis* communities we expected that measurable spatial differences would be discovered for zonal micro-environments and resource distribution that would assist in explaining subcanopy and interspace herbaceous vegetation cover, biomass, and composition.

The objective of the study was to (1) describe the influence of *A. tridentata* ssp. *wyomingensis* on micro-environments and the spatial distribution of soil resources, and (2) evaluate the influence of subcanopy and interspace zones on herbaceous composition and productivity. We hypothesized that: (1) microsite (temperatures, relative humidity, photosynthetic active radiation, and soil texture, water, and nutrients) differences exist between *A. tridentata* ssp. *wyomingensis* subcanopies and interspaces, and (2) subcanopies and interspaces result in zonal differences in resource availability to herbaceous vegetation, which (3) influences zonal variation in herbaceous vegetation composition and production.

2. Methods

2.1. Study sites

Study sites were determined to be late seral *A. tridentata* ssp. *wyomingensis* dominated plant communities that had limited livestock use based on criteria in Davies et al. (2006). The tall tussock, perennial bunchgrasses dominated the understory and exotic annual grasses were only a minor component ($<0.1\%$ cover) of the communities at the study sites. Regional climate is typical of the northern Great Basin with hot, dry summers and cool, wet winters.

2.1.1. Northern Great Basin Experimental Range (NGBER)

Six blocks were located at the NGBER, which is located in southeastern Oregon (lat 43°47′N, long 119°69′E) about 56 km west of Burns, OR. The study site at the NGBER receives on average 300 mm of precipitation annually. Elevation is ~1400 m above sea level, and topography is flat (slopes $<2°$). Soil surface texture is sandy loam to loamy sand. Incident radiation averages $0.93\,MJ\,cm^{-2}\,yr^{-1}$. *A. tridentata* ssp. *wyomingensis* is the dominant shrub and *Achnatherum thurberianum* (Piper) Barkworth (Thurber's needlegrass), *Festuca idahoensis* Elmer (Idaho fescue), *Koeleria macrantha* (Ledeb.) J.A. Schultes (prairie junegrass), *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass), and *Elymus elymoides* (Raf.) Swezey (squirreltail) are common perennial bunchgrasses on the study site.

2.1.2. Baker pass

Four blocks were located at Baker Pass, which is in southeastern Oregon (lat 43°05′N, long 118°19′E) about 80 km south of Burns, OR. Average precipitation at Baker Pass was estimated to range between 300 and 360 mm annually (Natural Resource Conservation Service, 1998). Elevation ranges from 1350 to 1450 m above sea level. Slopes average 13° and aspect is north-facing. Soil surface texture is loamy. Incident radiation averages 0.83 $MJ\,cm^{-2}\,yr^{-1}$. *A. tridentata* ssp. *wyomingensis* is the dominant shrub, and on three blocks *P. spicata* and on one block *F. idahoensis* is the dominant perennial bunchgrass.

2.2. Measurements

2.2.1. Micro-environment

Micro-environmental variables in subcanopy and interspace zones were measured at the NGBER site. Soil and air temperature, relative humidity, and photosynthetically active radiation (PAR) measurements were recorded every 3 h starting at midnight of each day from April though early November. Soil temperature (°C) was measured and logged with Hobo 4-Channel temperature units at a depth of 4 cm below the soil surface. Two Hobo 4-Channel temperature units were placed in each block. Two channels from each unit recorded temperature for each zone. Air temperature (°C) and relative humidity (%) were measured and logged at 30 cm above the soil surface with Hobo RH and TEMP units. Six Hobo RH and TEMP units were placed in each zone per block. PAR ($\mu mol\,m^{-2}\,s^{-1}$) was measured and logged with Hobo Microstations with smart sensors placed 10 cm above the soil surface. Four smart sensors measured PAR in each zone. For analysis, minimum and maximum temperatures and relative humidity, and average PAR were determined for each day and then averaged for each month.

2.2.2. Soil characteristics

In both zones of each block, five soil cores from 0–15 cm and 15–30 cm depths were collected at 2-week intervals during the growing season to measure soil water content. Water content of the soil was determined gravimetrically. Soil pH, total nitrogen, total carbon, and organic matter in the upper 15 cm of the soil profile were determined from five soil samples, collected in July, from each zone per block. Total carbon and total nitrogen were determined using a LECO CN 2000. Soil samples were not calcareous, thus organic matter was estimated using an amended Rather method (Nelson and Sommers 1982). Soil nitrate (NO_3^-) and ammonium (NH_4^+) content were measured by collecting two samples from each zone in each block every month during the growing season. Each sample consisted of five compiled 0–15 cm soil cores. Nitrogen fractions were extracted using 2 N KCl solution. The extracted solution was analyzed for NO_3^- and NH_4^+ content by Oregon State University's Central Analytical Lab. Soil surface texture (0–15 cm) was determined from five samples from each zone in every block using the hydrometer method (Gee and Bauder, 1986).

2.2.3. Herbaceous

Vegetation parameters measured to compare potential differences between the subcanopy and interspace were cover, biomass, density, photosynthetic rate, carbon and nitrogen isotope ratios, and carbon and nitrogen content. Herbaceous cover by species, functional group biomass, and perennial species densities were measured in 30 subcanopy and interspace zones using two 0.2 m^2 frames placed side by side resulting in a 0.4 m^2 (80 × 50 cm) sampling frame (Fig. 1). Mature *A. tridentata* ssp. *wyomingensis* subcanopies and interspaces were randomly selected. Density, cover, and composition were measured in 2003 and 2004. Biomass was measured in June 2004. Herbaceous vegetation was clipped, oven-dried, separated into current year's and previous years' growth, and weighed to determine biomass production.

Photosynthetic rates and nutrient concentration in *A. thurberianum* from the two zones were used to determine differences in the availability of resources to herbaceous vegetation at the NGBER. *A. thurberianum* was selected for sampling because it was common at every block, while other perennial bunchgrass species, though common to the study area, were not common at every block. Photosynthetic rate was determined for three *A. thurberianum* plants from each zone per block every 2 weeks during the growing season using a LI 6200 Portable Photosynthesis Unit and a LI 2100 Leaf Area Meter (LI-COR, Inc., Lincoln, Nebraska, USA). Carbon isotope ratio, nitrogen isotope ratio, carbon concentration, and nitrogen concentration were measured from five *A. thurberianum* individuals from each zone in every block. Samples were collected in late June, oven-dried, and then ground to pass through a 40 mesh screen. Ground samples were sent to the University of Utah Stable Isotope Research Facility for Environmental Research for analysis. In a review of several studies, Evans (2001) showed that the heavier nitrogen-15 isotope discrimination increased with greater nitrogen availability. The nitrogen isotope ratio ($^{15}N/^{14}N$) was used to compare nitrogen availability between zones. ^{13}C is discriminated against in C_3 plants, allowing for a time-integrated estimate of water-use efficiency (Farquhar et al., 1989; Ehleringer et al., 1993), and discrimination has been reported to increase with greater

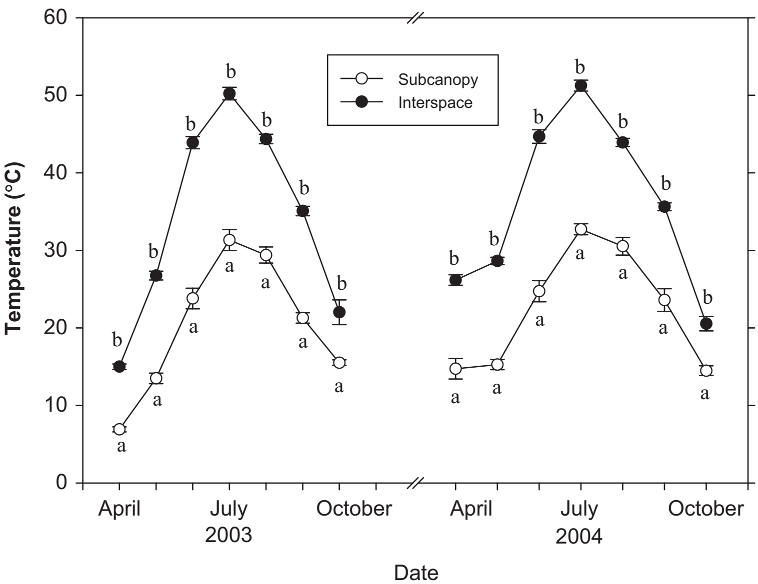

Fig. 1. Subcanopy and interspace zone maximum daily soil temperatures (mean ± SE) at 4 cm depth. Different lower case letters indicate when there is a difference between zones at that date ($P < 0.05$).

water availability (Toft et al., 1989). The carbon isotope ratio ($^{13}C/^{12}C$) was used to compare water availability between zones.

2.3. Experimental design and statistical analysis

A randomized block design was used to test the influence of *A. tridentata* ssp. *wyomingensis* on microsite characteristics and herbaceous vegetation. Six 80×50 m (0.4 ha) blocks were located across an *A. tridentata* ssp. *wyomingensis*-bunchgrass dominated landscape at the NGBER. Treatments were designated by zonal location: under (subcanopy) and between (interspace) *A. tridentata* ssp. *wyomingensis* canopies. Analysis of variance (ANOVA) was used to test for zonal differences in herbaceous vegetation and microsites variables that were not repeatedly sampled across the growing season. Repeated-measures ANOVA was used for variables that involved repeated sampling through the growing seasons (SAS Institute 2001). Between-subject effects were block and treatment. Within-subject effects were sampling date and the interactions of sampling date with between-subject effects.

To examine if zonal differences in vegetation cover and density were consistent among *A. tridentata* ssp. *wyomingensis* sites, four additional blocks with more northerly exposures were evaluated at Baker Pass. ANOVA tests were used to determine if zonal differences in vegetation cover and density existed at Baker Pass. Fisher LSD was used to test for differences in means. Means were considered to differ at $P<0.05$ ($\alpha = 0.05$). Both study sites were sampled in 2003 and 2004.

3. Results

3.1. Micro-environment

Maximum and minimum daily soil temperatures varied by sampling date and zone ($P<0.05$). The interaction of sampling date and zone was significant for both maximum and minimum daily soil temperatures ($P<0.05$). Subcanopy maximum daily soil temperature averaged 14.7 °C less than the interspace from April through October ($P<0.01$) (Fig. 1). Subcanopy minimum daily soil temperature averaged 2.2 °C warmer than the interspace ($P<0.01$).

Maximum and minimum daily air temperatures were not different between the zones ($P>0.05$), however, they varied by sampling date ($P<0.05$). Average daily PAR in the subcanopy was 297 $\mu mol\, m^{-2} s^{-1}$ less than the interspace from April through October ($P<0.0001$). Average daily PAR also varied by sampling date and the interaction between sampling date and zone was also significant ($P<0.01$). Maximum and minimum relative humidity varied by sampling date ($P<0.01$) but not by zone ($P>0.05$).

3.2. Soil characteristics

Percent clay, silt, and sand were not different between the subcanopy and interspace zones or years ($P>0.05$) (Table 1). Soil organic matter, pH, total C, and total N were greater in the subcanopy than the interspace zone ($P<0.05$) (Table 1), but did not differ among years ($P>0.05$). Though NO_3^- and NH_4^+ varied by sampling date ($P<0.01$) and

Table 1
Subcanopy and interspace soil characteristics (0–15 cm) at NGBER

Soil parameter	Subcanopy (mean)	Interspace (mean)	Significance for difference of means
Clay (%)	7.2	7.6	NS
Silt (%)	23.1	24.3	NS
Sand (%)	69.7	68.1	NS
PH	7.1	6.9	*
Organic matter (%)	1.4	1.2	*
Total carbon (%)	0.99	0.76	*
Total nitrogen (%)	0.08	0.07	*

Asterisk (*) and NS indicates significant difference ($P<0.05$) and non-significant difference in zonal means ($P>0.05$), respectively.

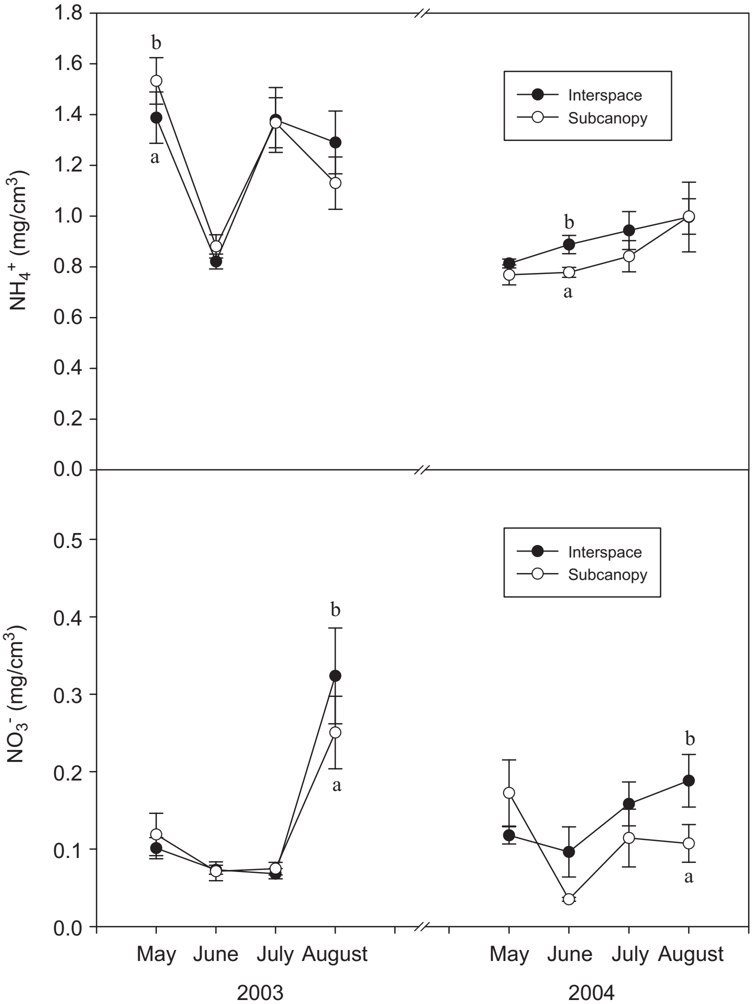

Fig. 2. Soil nitrate and ammonium content (mean ± SE) in the subcanopy and interspace zone. Different lower case letters indicate when there is a difference between zones at that date ($P<0.05$).

between zones on a few select dates (Fig. 2), they were not different between zones across the growing seasons ($P > 0.05$) (Table 1).

Soil water content (0–15 cm) varied by sampling date and zone ($P < 0.05$). The interaction between sampling date and zone was also significant ($P < 0.01$). The subcanopy had greater soil water content (0–15 cm) than the interspace during the growing season ($P < 0.01$). However, the subcanopy and interspace were not always different on individual sampling dates (Fig. 3(a)). Soil water content (15–30 cm) varied by sampling date and zone ($P < 0.05$). The interaction between sampling date and zone was also significant ($P = 0.04$). Soil water content (15–30 cm) was infrequently different between zones on individual sampling dates (Fig. 3(b)).

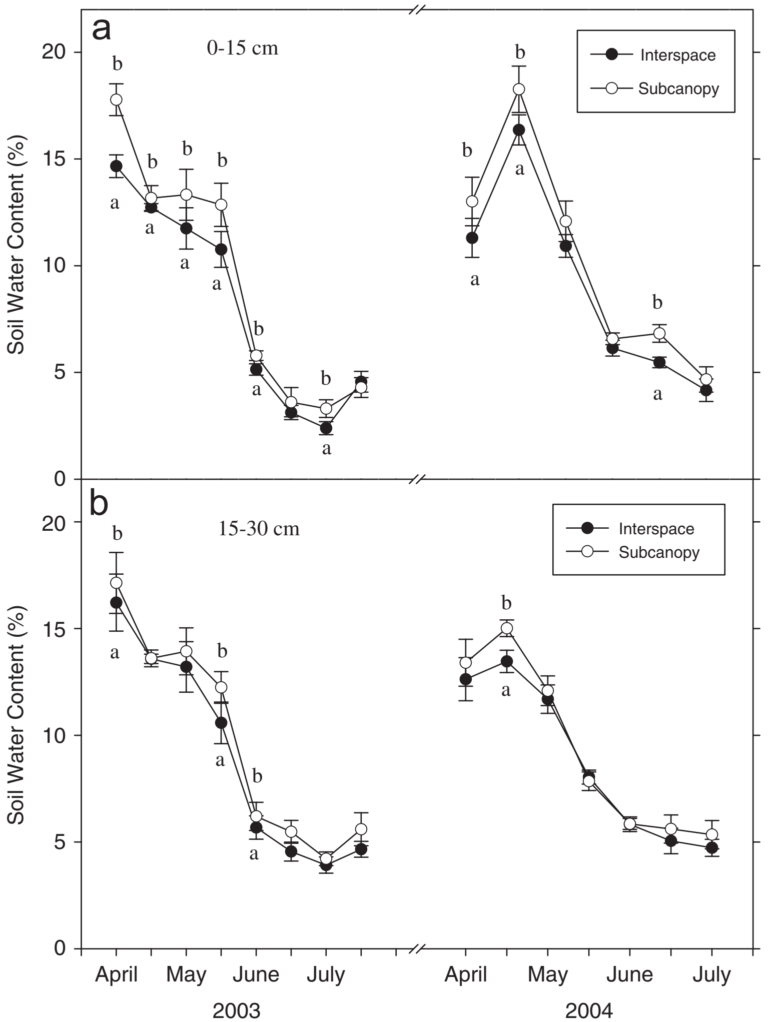

Fig. 3. Soil water content (mean ± SE) in the subcanopy and interspace zones at 0–15 cm and 15–30 cm depths. Different lower case letters indicate when there is a difference between zones at that date ($P < 0.05$).

Table 2
Zonal carbon and nitrogen characteristics of *A. thurberianum* at the NGBER

Characteristic	Subcanopy (mean)	Interspace (mean)	Significance for difference of means
$^{13}C/^{12}C$ ratio (‰)	−26.6	−26.1	*
$^{15}N/^{14}N$ ratio (‰)	2.6	2.8	NS
Total carbon (%)	42.0	42.1	NS
Total nitrogen (%)	1.3	1.2	NS

Asterisk (*) and NS indicates significant difference ($P<0.05$) and non-significant difference in zonal means ($P>0.05$), respectively.

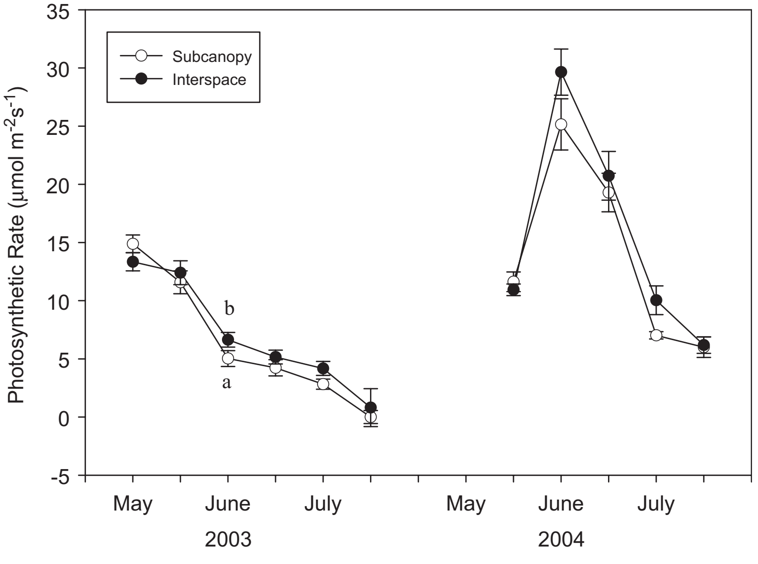

Fig. 4. Photosynthetic rates (mean ± SE) for *A. thurberianum* in subcanopy and interspace zones. Different lower case letters indicate a difference in photosynthetic rates between zones on that date ($P<0.05$).

3.3. Vegetation

3.3.1. Physiological response of A. thurberianum to zonal location

A. thurberianum carbon isotope ratio was more negative when grown in the subcanopy than interspace zone ($P<0.01$) (Table 2). Total percent carbon and nitrogen, and nitrogen isotope ratio of *A. thurberianum* were not different between zones ($P>0.05$) (Table 2). Total percent carbon and nitrogen isotope ratio varied by year ($P = 0.02$ and <0.01, respectively).

Photosynthetic rates of *A. thurberianum* did not differ between zones ($P = 0.06$). Photosynthetic rates varied by sampling date because it generally declined over the growing season ($P<0.01$) (Fig. 4). Photosynthetic rates rarely varied by zone on individual dates sampled.

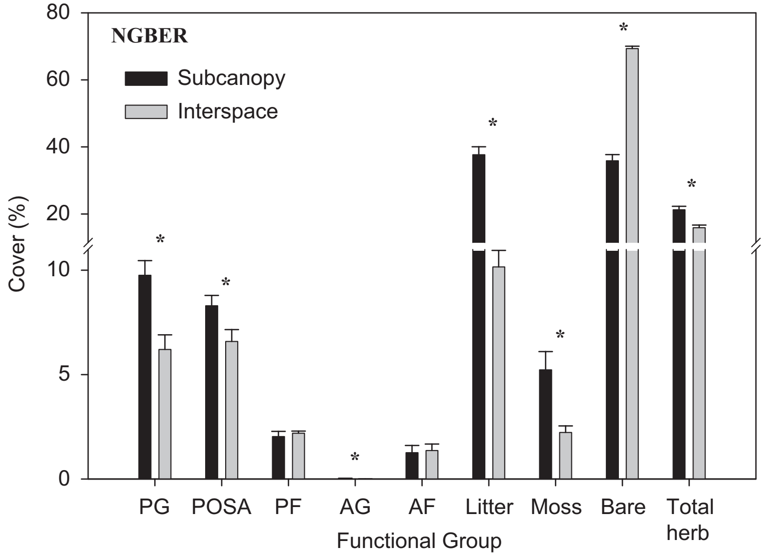

Fig. 5. Zonal functional group cover values at NGBER (mean ± SE). Asterisk (*) indicates significant differences in zonal means ($P<0.05$). PG = Tall tussock perennial grass, POSA = *P. sandbergii*, PF = Perennial forb, AG = Annual grass, AF = Annual forb, Bare = Bare ground, and Total herb = Total herbaceous.

3.3.2. Cover

NGBER site: Zonal location influenced herbaceous cover values (Fig. 5). The subcanopy zone had greater tall tussock perennial grass, *Poa sandbergii* Vasey (Sandberg bluegrass), annual grass, total herbaceous, litter, and moss cover and less bare ground than the interspace ($P<0.05$). Moss, tall tussock perennial grass, *P. sandbergii*, and total herbaceous cover values differed between years ($P<0.05$). Tall tussock perennial grass, *P. sandbergii*, moss, and total herbaceous cover were greater in 2003 than 2004 ($P<0.05$), but the interaction of treatment and year was not significant ($P>0.05$). All other functional groups did not differ between years ($P>0.05$). *F. idahoensis*, *K. macrantha*, and *E. elymoides* cover values were greater in the subcanopy than the interspace ($P<0.05$) (Fig. 6). *P. spicata*, *Hesperostipa comata* (Trin. & Rupr.) Barkworth (needle-and-thread), and *A. thurberianum* cover values did not differ between zones ($P>0.05$) (Fig. 6).

Baker Pass sites: Few zonal differences in cover were measured at Baker Pass (Fig. 7). Litter and moss cover were greater and bare ground was less in the subcanopy compared to the interspace zone ($P<0.05$). Perennial forb cover was greater and tall tussock perennial grass cover was lower in 2004 compared to 2003 ($P<0.05$), but the interaction of treatment and year was not significant ($P>0.05$). Except for *E. elymoides* ($P = 0.04$), tall tussock perennial grass species cover values did not vary by zone ($P>0.05$) (Fig. 8). *E. elymoides* cover averaged 1.21% and 0.67% in the subcanopy and interspace, respectively. None of the tall tussock perennial grass species cover values varied by year ($P>0.05$).

3.3.3. Density

NGBER plots: The subcanopy had greater density of *P. sandbergii*, tall tussock perennial grass, and total perennial species than the interspace ($P<0.05$) (Table 3). Tall tussock

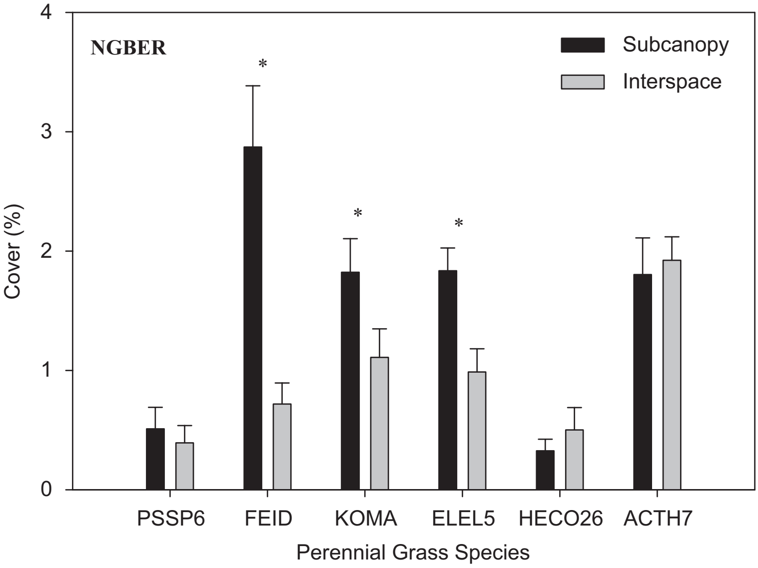

Fig. 6. Zonal tall tussock perennial grass species cover values at NGBER (mean ± SE). Asterisk (*) indicates significant differences in zonal means ($P<0.05$). PSSP6 = *P. spicata*, FEID = *F. idahoensis*, KOMA = *K. macrantha*, ELEL5 = *E. elymoides*, HECO26 = *H. comata*, and ACTH7 = *A. thurberianum*.

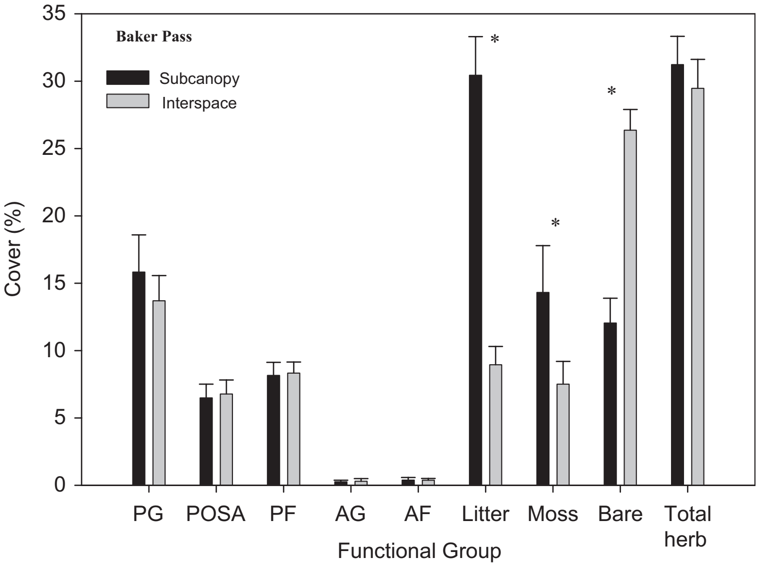

Fig. 7. Subcanopy and interspace cover values at Baker Pass (mean ± SE). Asterisk (*) indicates significant differences in zonal means ($P<0.05$). PG = Tall Tussock perennial grass, POSA = Sandberg bluegrass, PF = Perennial forb, AG = Annual grass, AF = Annual forb, Bare = Bare ground, and Total herb = Total herbaceous.

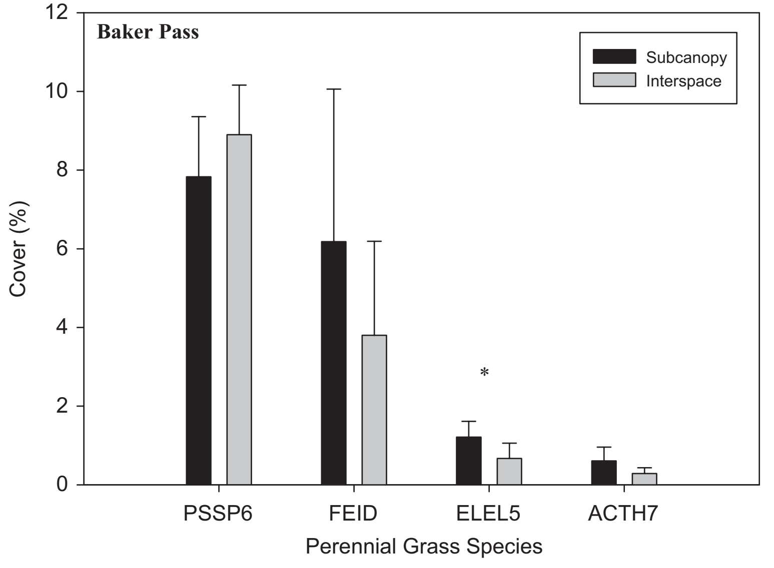

Fig. 8. Zonal tall tussock perennial grass species cover values at Baker Pass (mean ± SE). Asterisk (*) indicates significant differences in zonal means ($P<0.05$). PSSP6 = *P. spicata*, FEID = *F. idahoensis*, ELEL5 = *E. elymoides*, and ACTH7 = *A. thurberianum*.

Table 3
Zonal vegetation densities at the NGBER and Baker Pass study sites

Study site	Vegetation	Subcanopy mean density (#/m^2)	Interspace mean density (#/m^2)	Significance for difference of means
NGBER	PG	11.8	8.9	*
	POSA	20.2	17.0	*
	PF	4.7	5.9	NS
	Total P.S.	36.7	31.7	*
	PSSP6	0.6	0.4	NS
	FEID	1.6	0.6	*
	KOMA	3.7	2.4	*
	ELEL5	2.5	1.1	*
	HECO26	0.2	0.4	NS
	ACTH7	1.8	2.0	NS
Baker Pass	PG	11.2	10.5	NS
	POSA	22.8	28.9	*
	PF	18.3	18.6	NS
	Total P.S.	56.3	65.7	NS
	PSSP6	4.1	7.7	*
	FEID	2.1	2.3	NS
	ELEL5	0.7	0.5	NS
	ACTH7	2.4	2.4	NS

Asterisk (*) and NS indicates significant difference ($P<0.05$) and non-significant difference in zonal means ($P>0.05$), respectively. PG = Perennial grass, POSA = *P. sandbergii*, PF = Perennial forb, Total P.S. = Total perennial species, PSSP6 = *P. spicata*, FEID = *F. idahoensis*, KOMA = *K. macrantha*, ELEL5 = *E. elymoides*, HECO26 = *H. comata*, and ACTH7 = *A. thurberianum*.

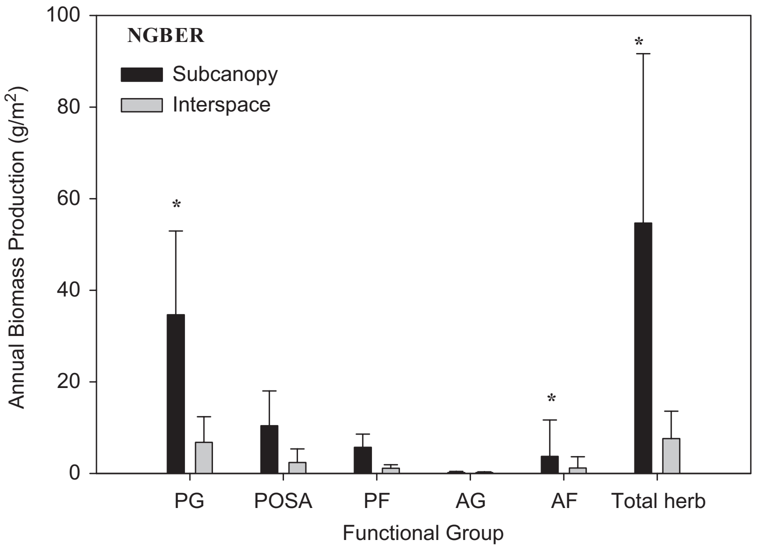

Fig. 9. Subcanopy and interspace functional group annual biomass production at the NGBER in 2004 (mean ± SE). Asterisk (*) indicates significant differences in zonal means ($P<0.05$). PG = Tall tussock perennial grass, POSA = *P. sandbergii*, PF = Perennial forb, AG = Annual grass, AF = Annual forb, and Total herb = Total herbaceous.

perennial grass, *P. sandbergii*, and total perennial species densities were greater in 2003 than 2004 ($P<0.05$), but the interaction of year and treatment was not significant ($P>0.05$). *F. idahoensis*, *K. macrantha*, and *E. elymoides* densities were greater in the subcanopy than interspace ($P<0.05$), but did not vary by year ($P>0.05$). Perennial forb, *P. spicata, H. comata*, and *A. thurberianum* densities did not differ among zones or years ($P>0.05$).

Baker Pass plots: *P. sandbergii* and *P. spicata* densities differed between zones at Baker Pass. *P. sandbergii* averaged 23 and 29 plants/m^2 in the subcanopy and interspace, respectively ($P<0.01$) (Table 3). *P. spicata* density was 4.1 and 7.5 plants/m^2 in the subcanopy and interspace, respectively ($P = 0.04$). None of the other perennial functional groups or tall tussock perennial grass species densities varied between zones ($P>0.05$). Perennial forb density was greater in 2004 than 2003 ($P<0.01$), while tall tussock perennial grass density was greater in 2003 than 2004 ($P = 0.04$). The interaction of year and treatment were not significant for perennial forb or tall tussock perennial grass densities ($P>0.05$).

3.3.4. Biomass production

Tall tussock perennial grass and total herbaceous biomass production were greater in the subcanopy than the interspace at the NGBER ($P = 0.04$ and 0.03, respectively) (Fig. 9). Annual forb biomass production was greater in the interspace than the subcanopy ($P = 0.05$).

4. Discussion

We measured differences in *A. tridentata* ssp. *wyomingensis* subcanopy and interspace microsites at the NGBER, thus supporting our first hypothesis. Subcanopy zones have moderated soil temperatures, greater soil water content, lower average PAR, and higher soil C, N, pH, and OM than interspace zones. Our results agreed with other studies that reported moderated soil temperatures (Pierson and Wight, 1991), greater soil water content (Wight et al., 1992; Chambers, 2001), and higher C and N (Charley and West, 1977; Doescher et al., 1984; Burke et al., 1987) beneath *A. tridentata* canopies compared to interspaces. Though we accepted the first hypothesis, it should be noted that not all the environmental/soil factors we hypothesized would vary between zones did in fact differ between the subcanopy and interspace.

The microsite zonal differences appeared to explain the zonal differences measured for herbaceous vegetation at the NGBER site. Greater herbaceous cover, perennial grass densities, and total herbage production in the subcanopy suggested this zone provides a more favorable microsite for herbaceous growth than the interspace. Physiological response of *A. thurberianum* indicated that *A. tridentata* ssp. *wyomingensis* created zonal differences in the availability and use of resources. Greater discrimination by *A. thurberianum* against ^{13}C when growing in the subcanopy zone indicated that water was more available to *A. thurberianum* growing in the subcanopy than interspace. In agreement with our second hypothesis, the results indicated that there is a zonal difference in the availability of resources to herbaceous vegetation.

In contrast to the NGBER site, the Baker Pass site had fewer measurable differences in zonal vegetation characteristics. This suggests the influence of microsite on the spatial distribution of herbaceous vegetation in *A. tridentata* ssp. *wyomingensis* communities is site dependent. Doescher et al. (1984) found the spatial distribution of soil nutrients in *A. tridentata* communities to vary with dominant plant species/subspecies and also the proportion of perennial grasses to shrubs at a site. Microsite characteristics were not measured at Baker Pass, and it is possible that zonal differences for these variables were not as pronounced at this location compared to the NGBER site. However, the macro-environment at Baker Pass is less harsh for plant growth than the NGBER. At Baker Pass, aspect is north-facing and steep; thus, the site is less exposed (lower incident radiation) than the NGBER site. Lower incident radiation and/or other unmeasured site characteristics may also be responsible for the lack of zonal differences in herbaceous composition at Baker Pass. For example, at the NGBER site, *F. idahoensis* and *P. sandbergii* mainly occupied subcanopy zones, while at the Baker Pass site no zonal preference was measured for *F. idahoensis* and zonal preference was reversed for *P. sandbergii*. The strong zonal vegetation differences at the NGBER site resulted in acceptance of the third hypothesis for that particular site, but not for the Baker Pass site. Though not conclusive, the result suggest that zonal differences may be greater and play a more influential role as site conditions become warmer and drier.

As well as site dependency, measurements at the NGBER site suggest that zonal herbaceous distribution may also be species dependent. Cover and density of *F. idahoensis*, *K. macrantha*, and *E. elymoides* were greater under the sagebrush canopy than the interspace, while other grass species exhibited no zonal preference. Other authors have also found differing species response to zonal location. *P. monophylla* establish preferentially under *A. tridentata* canopies, while *Pinus ponderosa* P.& C. Lawson (ponderosa pine) establish best in interspaces (Callaway et al., 1996). In contrast to our study, Hazlett and Hoffman (1975) and Eckert et al. (1986) found that forbs preferentially established under *A. tridentata* canopies, while grass cover was greater in the interspaces. The lack of zonal differences in forbs in our study may be a reflection of year effect. Both study years were below average for precipitation and were characterized by dry springs (Eastern Oregon Agricultural Research Center data file). At the NGBER and elsewhere in the Great Basin, forb production is correlated to spring precipitation (Passey et al., 1982; Sneva, 1982; Bates, 2004). The study years for the Eckert et al. (1986) study coincided with above average precipitation. Though, we may have found differences in forb density and/or cover if our study had encompassed an above average precipitation year, *A. tridentata* ssp. *wyomingensis* influence on herbaceous vegetation clearly varied by zone at the NGBER even in below average precipitation years.

5. Conclusions

Relationships between *A. tridentata* ssp. *wyomingensis* and herbaceous species are complex, however, this study has advance the understanding of *A. tridentata* ssp. *wyomingensis* zonal influence within a plant community by investigating microsite and herbaceous zonal differences. *A. tridentata* ssp. *wyomingensis* appears to modify microsite and resource availability within stands. *A. tridentata* ssp. *wyomingensis* is an important component contributing to the heterogeneity of herbaceous vegetation within a community. However, by comparing zonal herbaceous characteristics from two different *A. tridentata* ssp. *wyomingensis* communities, we found the influence of *A. tridentata* ssp. *wyomingensis* on herbaceous spatial heterogeneity to be site dependent. Our result suggest the influence of *A. tridentata* ssp. *wyomingensis* on microsite differences and subsequently herbaceous spatial heterogeneity may be greater as sites become warmer and drier, but more research investigating the influence of site environmental characteristics on the expression of zonal differences is needed to verify this hypothesis. This also indicates that herbaceous response to *A. tridentata* ssp. *wyomingensis* removing disturbances may vary by site.

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