Spatial and Temporal Patterns of Sagebrush (*Artemisia tridentata ssp. vaseyana*) Establishment Following Fire

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ABSTRACT

Long-term recovery of sagebrush populations following natural and prescribed fires has been inconsistent among sites in the Great Basin. Explanations for this variability are precluded in part by an incomplete understanding of factors affecting sagebrush establishment. Our objective was to determine how establishment of *Artemisia tridentata* ssp. *vaseyana* (mountain big sagebrush) varies in time and space, relative to climate fluctuations and neighboring plant species. We measured year of *A. t. vaseyana* establishment, distances of *A. t. vaseyana* seedlings to surrounding vegetation and community cover in four sites that were burned at different times, 1-8 years prior to sampling. Age distributions in each burn site indicated that seedling establishment occurred only in the first 1-3 years following each fire, irrespective of variations in climate that occurred among burn years. Distances of *A. t. vaseyana* seedlings to herbs became progressively smaller and moreover similar to distances of random locations to herbs, in sites having greater times since burning and correspondingly more herb cover. No spatial relationships were detected between *A. t. vaseyana* seedlings and older shrubs. Temporal patterns of *A. t. vaseyana* establishment reported here differ from relatively gradual and weather-dependent establishment patterns reported for other subspecies of big sagebrush, at lower elevations. Post-fire establishment of *A. t. vaseyana* appeared to be driven by more than episodes of optimal weather, and may be affected by changes in herb cover and seed availability that result from fire.

Keywords: rangeland, fire, sagebrush.

INTRODUCTION

Fire is an important component of disturbance-succession regimes in sagebrush steppe that is managed through suppression and prescribed application. Fire is applied in sagebrush steppe to promote forage production, reduce fuel loads, or restore disturbance for wildlife habitat. Whether, and to what extent application of fire achieves these ecological goals is currently debated, as indicated by much lower levels and higher variability of big sagebrush cover (*Artemisia tridentata*) up to 30 years following fire (Wambolt *et al.*, 2001) compared to studies conducted in earlier decades (Harniss and Murrary**,** 1973). Lack of *A. tridentata* recovery following fire is a major concern for sustaining sage grouse (*Centrocercus urophasianus*) and other wildlife (Leonard *et al*., 2000). Altered rates of *A. tridentata* reestablishment correspond in many cases with invasions by exotic herbs, which sagebrush steppe appears unusually vulnerable to (Brooks and Pyke, 2001). A better understanding of how native herb communities affect reestablishment patterns of key shrub species (e.g., Eliason and Allen, 1997) is needed to assess potential impacts of exotic herbs on ecological processes, such as disturbance-succession cycles.

Resprouting and rapidly colonizing herbs, as well as a few shrubs, tend to dominate burned sagebrush steppe in the decade or so following fire, while the slower-growing *A. tridentata* reestablishes (Harniss and Murray, 1973). Direct observations of interactions between sagebrush seedlings and other species are rare in the literature (e.g. Daubenmire, 1975; Owens and Norton, 1989; Berlow *et al*., 2002), especially for postfire conditions. Seed dispersal and germination have been studied for *A. tridentata* and other aridland shrubs in undisturbed and post-fire situations (e.g. Hassan and West, 1986; Young *et al.*, 1990; Tyler, 1996; Chambers, 2000), but less is known about factors affecting seedling success. High mortality rates during initial seedling establishment indicate the importance of this life history stage for dynamics of *A. tridentata* populations (Daubenmire, 1975; Owens and Norton, 1989).

The objective of this study was to determine spatial and temporal patterns of *A. t. vaseyana* establishment following fire, relative to climate variations and changes in abundance of other native plant species. Temporal patterns of establishment were estimated by determining seedling ages in sites burned 1-8 years prior to sampling. Spatial patterns of establishment relative to neighboring plants were determined by measuring the percent cover, identity and proximity of surrounding vegetation to *A. t. vaseyana* seedlings. We also examined interactions of azimuth orientations and distance of *A. t. vaseyana* seedlings to neighboring vegetation to determine if establishment near or away from neighboring plants might be affected by aboveground interactions, such as shading. Spatiotemporal patterns and correlates of *A. tridentata* establishment could yield important insight on disturbance-succession cycles in semiarid shrublands.

MATERIALS AND METHODS

Site and species.—Research was conducted in sagebrush steppe at the US Sheep Experimental Station (USSES) near Dubois, Idaho (44°14’44” N Latitude, 112°12’47” W. Longitude; 1650 m a.s.l.) where fire and grazing records were available since about 1935. Vegetation in the particular region of the USSES that we examined (<50 km^2) is a diverse sagebrush and perennial herb community that is rare in having almost no invasive or exotic plants. The absence of exotic plants provided an opportunity to examine responses of sagebrush to its native community. The dominant shrub in this community, mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana* Nutt, shares the drought-deciduous foliage and dimorphic root traits of other subspecies of big sagebrush that occur in warmer and drier sites (*A. t. wyomingensis* and *A. t. tridentata*). Other, less abundant shrubs are *Chrysothamnus viscidiflorus* Nutt., *Tetradymia canescens* DC. and *Purshia tridentata* (Pursh) DC. Perennial bunchgrasses such as *Agropyron dastychium* (Hook.) Scribn., *Festuca idahoensis* Elmer and *Poa sandbergii* Vasey, and short-lived perennials such as

Achillea millefolium L., *Antennaria rosea* Rydb. Gaertn., *Erigeron corymbosus* L., *Phlox longifolia* L. and *Crepis* sp., are common herbs. Soils are fine, loamy, mixed, frigid Calcic Argixerolls derived from wind blown loess or residuum (Natural Resources Conservation Service). Total annual precipitation averaged 297 mm over the last 78 years, with most precipitation occurring as spring snow and early summer rain (Western Regional Climate Center, 'WWRC', Desert Research Institute, Reno NV).

All data were collected from June to July 2003, when herb abundances were at seasonal maxima. Seedlings of *A. t. vaseyana* were individuals less than 30 cm in height above ground and lacking reproductive structures. Adult *A. t. vaseyana* are frequently 1 to 1.5 m in height or taller.

Prescribed burns.—Burns were located within a few km of each other, and areal extents of each burn were 280 ha for the 1995 burn, 207 ha for the 1998 burn, 221 ha for the 1999 burn and 105 ha for the 2002 burn. The four burns were all prescribed, and occurred in fall of their respective years, prior to seed production by the sagebrush community. Grazing has occurred on all sites. Mean animal unit months (aum) from 1968-2003 for the 1995, 1998, 1999 and 2002 burns were 21.3, 8.9, 13.0 and 21.3, respectively. Grazing did not occur in the year prior to or during application of prescribed burns in 1995 and 1999. Short-term and low-intensity grazing (few animals) did occur following the 1998 and 2002 burns.

No seeding of any species occurred during or prior to the study and all sagebrush seedlings emerged from seed that dispersed and germinated naturally. Seed production in *Artemisia tridentata ssp. vaseyana* appears to be fairly consistent from year to year (Young *et al.*, 1989; Harniss and McDonough, 1976). Big sagebrush seedling densities near $2/m^2$ or frequently more were detected following fires on or near the USSES, even several km from unburned plants in large burn areas (Mueggler, 1956). Seeds of *A. t. vaseyana* can remain viable for at least several years in soil, and seedlings in Mueggler's study (1956) apparently germinated primarily from residual seed that endured fire (see also Hassan & West 1996), though seed transported by wind from unburned plants also appeared significant in some cases. Other studies reported narrow dispersal ranges for other species of sagebrush or subspecies of big sagebrush, with seeds most commonly dispersing and germinating within about 1 m from reproductive plants (e.g. Young et al. 1989; Berlow et al. 2002).

Seedling age distributions.—We used a stratified-random method to collect 10 seedlings from each of the 1995, 1998 and 1999 burns, and 30 emergent seedlings from the 2002 burn, for determination of establishment dates of *A. t. vaseyana* seedlings. Seedlings were collected from a 1-m wide, 20-40 m long belt transect in each burn. Only one seedling was collected from clusters of seedlings (eg, several seedlings within a few cm), when clusters were encountered, to ensure spatial dispersion of samples. Establishment dates and ages of seedlings were determined from thin cross sections of the stem, taken within a mm of the stem-root interface, that were stained with 1% basic fuchsin and 0.1% toluene blue. We captured images of each section with a microscope under 40-100x magnification (Remote Capture 2.2, Canon USA) and counted annual growth rings. Interannual (ie. false) or complete absence of rings is supposedly rare in big sagebrush (Maier *et al.*, 2001; Ferguson, 1964). Patterns of establishment among years were compared to precipitation and temperature records for the USSES, obtained from the WWRC. Cumulative precipitation from January to September was determined by summing total precipitation for each month. Average monthly maximum and mean temperatures from May to September were determined by averaging the maximum or mean values reported for each month, respectively.

Neighborhood relationships of seedlings and community cover.—A second stratified-random sampling regime was used to locate *A. t. vaseyana* seedlings for assessment of seedling heights, distances to neighboring plants, and community cover. These locations occurred at random distances of 1 to 100 m from the perimeter towards the center of each burn area. Distances originated at 200 m intervals along the perimeter of burns. Measurements for both actual seedlings and random points were necessary to characterize both the realized and available space for seedlings, respectively. Therefore, we measured distances from random points to neighboring plants, using the same protocol used for assessing neighboring plants for *A. t. vaseyana* seedlings. In all cases, random points did not have sagebrush seedlings, by chance.

Using differentially-corrected global positioning system points of all sampling locations, geographic information systems, and digital elevation models (GeoExplorer, Trimble Inc, CA; ArcGIS version 8, ESRI Inc, Redlands CA; 10 m pixel elevation data from United States Geological Survey), we determined that about 40% of 192 sample points ($N = 46$-51) that were recorded for all years combined were on flat ground with 0° slopes. The maximum slope was 9.26°, and 95% of sample points that were not on level ground were on <6°slopes.

Distances from the base of each *A. t. vaseyana* seedling, or random point, to the base of the nearest herb (forb or grass) and nearest shrub in each of four cardinal directions (NW, NE, SE, SW) were measured, for a total of eight distances per seedling or random point. The four measured distances were added together and considered the ‘sum distance’ of each *A. t. vaseyana* seedling or reference point to the surrounding vegetation. This sampling approach allowed us to generate more replicates than possible with techniques similar to Theissen polygons (e.g. Owens and Norton, 1989), but was more robust than simply measuring distance to only the nearest neighboring plant. Heights of all *A. t. vaseyana* seedlings above soil were measured. Ground cover was assessed in 0.5 m^2 plots at the random points using the point intercept method (Floyd and Anderson, 1987), to assess overall differences in the identity and abundance of vegetation in each burn site. Cover classes included shrub, herb, forb, litter, rock and bare soil. The number of seedlings and random points sampled, respectively, were 56 and 16 in the 1995 burn, 75 and 23 in the 1998 burn, 52 and 10 in the 1999 burn, and 89 and 32 in the 2002 burn. We initially did not make measurements of distances and abundances of neighboring plants for random points, leading to less sampling than for seedlings.

Vegetative and other ground cover were also measured in 87, 0.56-m^2 plots at midsummer before and the year after applying the 2002 fire (39 of the 87 plots burned), to further assess how herb cover changes as a result of fire. In each 0.56-m^2 plot, the amount of shrub, grass, forb, bare soil, litter, and rock cover was estimated without the use of point frames to the nearest 5%, except for 1% resolution for classes covering less than 5% of plots.

Statistical analysis.—Our analysis focused on determining whether heights or ages of seedlings, and distances of seedlings or random points to neighbors, varied among sites burned in different years. The 1995, 1998 and 1999 fires occurred as one large patch, and there was no basis for identifying spatial replicates of burns or separate seedling populations within each burn. We therefore caution that although we examined a substantial number of seedlings, our experimental design replicated seedlings but not sites within each burn year. The statistics reported herein are therefore a better measure of the population or community in each burn site, rather than how year of burn affects sagebrush populations.

The significance of mean differences in heights or ages of seedlings in sites with different times since burning was determined using one-way analysis of variance (ANOVA; $\alpha < 0.05$). Three-way ANOVA was used to determine the significance of mean differences in sum distances to neighboring vegetation among sampling type (seedlings or reference points), type of neighbor (grass, forb and shrub), and burn site (1995, 1998, 1999 and 2002 burn). We tested for differences in each cover class (shrub, grass, forb, bare soil, litter and rock) among each burn site (1995-2002 burn sites) using two-way ANOVA. The significance of changes in each cover class (shrub, grass, forb, bare soil, litter, rock) from before to after the 2002 fire (measurements in 2002 and 2003) was determined for burned and unburned plots using three-way ANOVA, with (1) cover class, (2) burn year, and (3) treatment (burned or unburned) as factors. Two-way ANOVA was also used to determine if distances of *A. t. vaseyana* seedlings to surrounding vegetation were affected by the cardinal orientation of seedling and neighboring plant (NE, SE, NW and SW), and whether distances in each cardinal orientation were similar among each burn site (1995-2002). Distances to neighboring vegetation and cover data were ln or arcsine transformed to satisfy ANOVA requirements for normal distribution. Analyses were conducted using SAS version 8 and JMP version 3.2.2 (SAS Institute, Cary NC).

RESULTS

Frequency distributions of seedling height and age.—Heights of seedlings in sites burned in 1995, 1998 or 1999 were similar, and collectively greater than seedling heights in the 2002 burn ($F_{3,59} = 233.37$, $P < 0.0001$, Fig. 1), where 90% of seedlings were under 5 cm in height. Only one seedling in the 1995 burn, and two seedlings in the 1998 burn were under 5 cm. Correspondingly, seedlings aged in 2004 were considerably younger in sites burned more recently (Fig. 2). All seedlings in the site burned in 2002 established in 2003. In the sites burned in 1999 and 1998, 70% and 50% of seedlings established in the year following fire, respectively, and no establishments were detected after the 3rd year following fire. Similarly, no establishments were detected after the 3rd post-fire year in the site burned in 1995, but seedling establishments were more evenly distributed over the three years following the 1995 fire than observed in the 1999 and 1998 burns (Fig. 2). Mean ± SE ages of seedlings in 2004 were (in years) 1.0 ± 0.0 in the 2002 burn, 3.5 ± 0.3 in the 1999 burn, 4.3 ± 0.3 in the 1998 burn and 7.0 ± 0.3 in the 1995 burn ($F_{3,59} = 1137.05$, $P < 0.0001$). The range of seedlings ages (max. – min. age) within each burn was only 2 years.

No consistent relationships emerged between temperature or precipitation of years that came before, during, or after each fire, and age or height distributions of *A. t. vaseyana* in each burn site (Fig. 3 compared to Fig. 2). The 1995 burn occurred in a relatively wet and cool year and was followed by average conditions, and the 1998 and 1999 burns occurred during relatively wet years and were followed by relatively wet or average conditions. In contrast, weather before, during, and after the 2002 burn was among the warmest and driest in the past century (Fig. 3). Despite these climate variations among burn years, there was a consistent tendency for establishment within the first 3 years following each fire.

Relationships to surrounding vegetation.—Cover of *A. t. vaseyana* and other shrub species (*Chrysothamnus, Tetradymia*) was as much as 10% of ground area in sites burned from 1995-1999 (Fig. 4). Grass cover was about twofold greater in sites burned from 1995-1999 compared to in the 2002 burn ($F_{1,1265} = 5.4$, $P = 0.02$), and there was marginal statistical support for about 50% less soil exposure in sites burned in 1995-1999 compared to in 2002 ($F_{1,1265} = 1.9$, $P = 0.16$, Fig. 4). In the 2002 burn site, herbaceous cover was at least 50% lower and soil exposure threefold greater than before fire in 2002, when grass cover was 30.4 ± 2.1%, forb cover was 24.5 ± 1.8%, and bare soil was 13.4 ± 1.5% ($F_{1,1089} > 10.0$ and $P < 0.002$ for changes in each cover type from 2002-2003; data not shown). No changes in soil exposure were detected in neighboring, unburned plots from 2002 to 2003, however, forb cover decreased 22% ($F_{1,1089}$ = 4.6, P = 0.03) whereas there was marginal statistical support for a 16% increase in grass cover from 2002-2003 in these control plots ($F_{1,1089}$ = 2.03, P = 0.14).

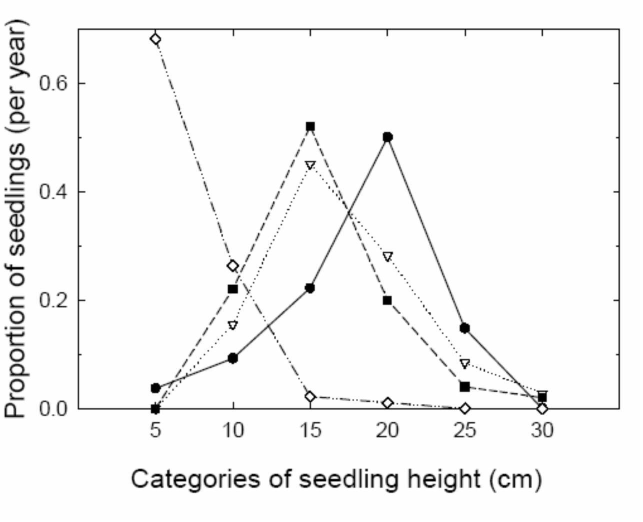

Figure 1. Frequency distribution of heights of A. t. vaseyana seedlings found on sites with different time since fire. The upper value of each 5-cm height category is shown on the x-axis. Seedlings are represented by round symbols in the 1995 burn; triangles in the 1998 burn; squares in the 1999 burn, and diamonds in the 2002 burn. N=52-89 seedlings per burn year.

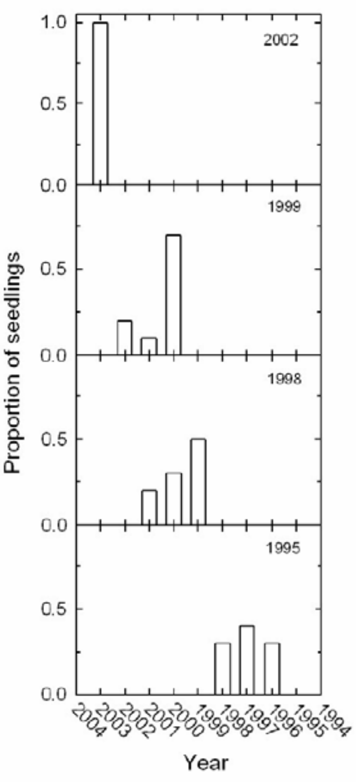

Figure 2. Frequency distribution of year of establishment for seedlings of *A. t. vaseyana* in each burn. N = 10 except in the 2002 burn, where N = 30.

Sum distances of *A. t. vaseyana* seedlings to shrubs did not vary appreciably among the sites burned from 1995-1999 (Fig. 5). Also, distances were similar from of *A. t. vaseyana* seedlings and random points to shrubs, in sites burned from 1995-1999 (Fig. 5). *Artemisia* seedlings in the 2002 burn had almost 3-fold greater sum distances to forbs than in sites burned before 2002 ($F_{1,483} = 83.5$, $P < 0.0001$), and compared to random points in the 2002 burn ($F_{1,483} = 8.4$, $P < 0.01$, Fig. 5). Distances of *Artemisia* seedlings to grasses were 1.4 to 2.5 times greater in the site burned in 2002 compared to sites burned prior to 2002 ($F_{1,483} = 62.2$, $P < 0.0001$), and compared to random points in the 2002 burn ($F_{1,483} = 12.9$, $P < 0.001$). Mean distances of *A. t. vaseyana* seedlings to shrubs and herbs were similar in all cardinal directions, for all burn years (not shown).

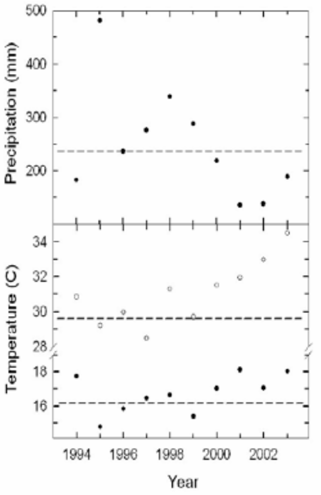

Figure 3. Cumulative precipitation from January-September (top panel) and average monthly maximum and mean temperatures from May-September (open and solid symbols, respectively, in lower panel). Dashed lines show mean values for the past 80 years.

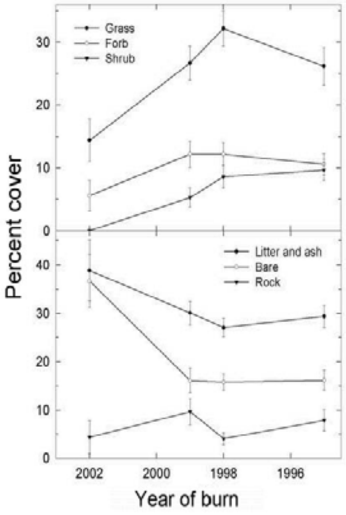

Figure 4. Mean (± 1 SE) percent cover of grass, forbs, shrubs (top panel) and litter, bare soil, and rock (bottom panel) in each burn year. N = 52-89.

DISCUSSION

New establishment of *A. t. vaseyana* in the initial 1-3 years after each fire, followed by no new establishments in the next 4-8 years (Figs. 1, 2), differ considerably from the general perception that sagebrush establishment occurs progressively over decades following fire (Harniss and Murray, 1973; Meyer, 1994). Mueggler (1956) reported substantial seedling establishment (frequently >2 seedlings per m^2) in the first growth season following 4 of 5 burns years at the USSES. Mueggler (1956) also speculated that most seedlings established in the initial postfire year, on a site burned 4 years prior to his sampling. Similarly, in another study at the USSES, juveniles (<15 cm) were about 10 times as abundant as 'seedlings' (presumably new emergents, with low densities near 0.03 individuals/m^2) in a site burned 11 years prior to sampling, reflecting a previous pulse of establishment (Harniss and Murray, 1973).

New establishments of *A. t. vaseyana* as well as *A. t. tridentata* can apparently occur in later stages of succession, decades following fire (Harniss and Murray, 1973; Daubenmire 1975; Young and Evans, 1978, 1989; Wambolt *et al*., 2001). For example, individuals of *A. t. vaseyana* in the youngest seedling size classes were 10-fold more abundant (0.3-0.5 seedlings/ m^2) on unburned sites than on sites burned about 10 years prior to sampling (Harniss and Murray, 1973). Thus, our study combines with Mueggler (1956) and Harniss and Murray (1973) to indicate that new establishment of *A. t. vaseyana* may be most common in sites burned in the previous three years, least evident in sites at intermediate stages of succession, but apparent again in sites having some mature *A. t. vaseyana* after decades of recovery since burning.

Temporal patterns of sagebrush establishment described above are nearly opposite of typical changes in herbaceous cover during disturbance-succession cycles in sagebrush steppe. Herb cover is usually least abundant immediately following and in the first growth seasons after fire, but most abundant thereafter for about a decade, in a variety of *A. t. vaseyana* and other *A. tridentata* communities (Fig. 4; Young and Evans, 1978; West and Hassan, 1985; Akinsoji, 1988; Cook *et al*., 1994, Ratzlaff and Anderson, 1995; Perryman *et al*., 2002, West and Yorks, 2002). Decreases in herb cover in later stages of succession correspond to progressive recovery of mature shrub canopies (Sneva, 1972). Based on these relationships, we propose two possible explanations for the cessation of new establishments of *A. t. vaseyana* in sites burned four or more years before our sampling: 1) negative effects of recolonizing herbs on *A. t. vaseyana* seedlings and 2) depletion of residual seed banks.

Big sagebrush seeds are apparently relatively short-lived in storage and could be similarly so in the field (reviewed in Meyer, 1994). Depletion of big sagebrush seed banks reportedly occurred several years following fires, as a possible result of germination (Young and Evans, 1989). Depletion of seed banks is unlikely to occur near burn edges that are within the dispersal range of unburned shrubs. We found no new establishments after the third post-fire year in the few sampling locations that happened to be near unburned shrubs, similar to in sampling areas that were distant from shrubs (for data in Fig. 2).

Previous reports of neighborhood relationships, seeding trials, and root-exclusion experiments indicated that seedlings of the other species of big sagebrush are negatively affected by neighboring herbs (e.g. Blaisdell 1949, Richenberger and Pyke, 1990; Schuman *et al.*, 1998; Owens and Norton, 1989; Williams *et al.*, 2002). Greater distances of *A. t. vaseyana* seedlings than random points to neighboring herbs, and greater distances of both seedlings and random points to neighboring herbs (Figs. 2, 5) could reflect negative effects of herbs on *A. t. vaseyana* seedlings. Moreover, growth and carbon assimilation were significantly lower in *A. t. vaseyana* seedlings that had smaller distances to neighboring herbs, compared to seedlings located further from herbs following fire (DiCristina and Germino, in review). Decreased spacing between *A. t. vaseyana* and neighboring herbs in less recently burned areas may have been made possible by deeper rooting in older seedlings compared to shallower root systems that were likely in younger seedlings of more recent burns. Shallower roots of younger *A. t. vaseyana* would be more likely to match shallower rooting patterns typical of herbs.

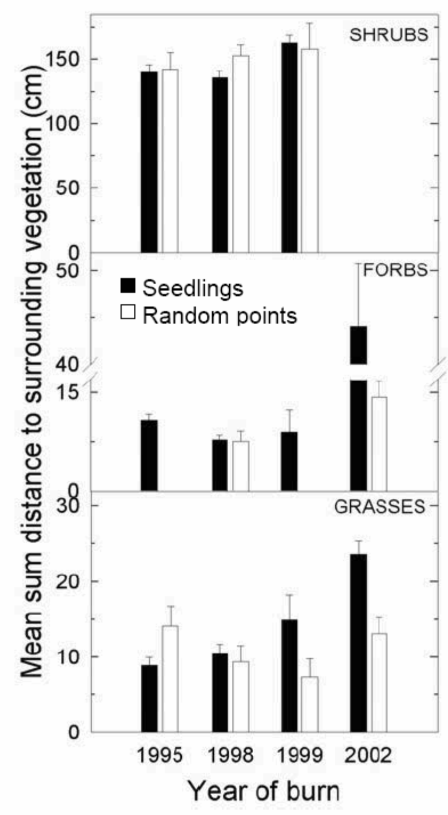

Figure 5. Mean sum distances (+ 1 SE) of Artemisia t. vaseyana seedlings (solid bars) or random points (open bars) to shrubs, forbs, or grasses, in each burn year. N=10-89.

Initially, we anticipated detecting positive or facilitative associations of *A. t. vaseyana* seedlings and adult shrubs, based on speculations by Daubenmire (1975) and findings of Owens and Norton (1989) for other subspecies of *A. tridentata*. Mature shrubs can favorably alter soils, soil water, sunlight and evaporative demand for seedlings in semiarid lands, and thereby could potentially ameliorate the drought conditions which we previously found to limit *A. t. vaseyana* seedling growth (DiCristina and Germino, in review). However, we detected no evidence for direct positive associations of *A. t. vaseyana* seedlings and neighboring plants, and moreover observed no evidence of preferential establishment of *A. t. vaseyana* on north or south aspects of neighboring plants to indicate potential shading effects. Although there was no evidence for direct facilitation, mature shrubs could indirectly facilitate *A. t. vaseyana* establishment by having negative effects on abundances of herbs (Anderson and Inouye, 2001).

Establishment of sagebrush is commonly thought to occur mainly in response to favorable climate conditions that occur sporadically across decades (Daubenmire, 1975; Maier *et al.*, 2001), but the patterns of establishment reported here are closely linked to the fire-induced changes in herb cover (Figs. 1-5). Consistent establishment in years 1-3 following each fire, irrespective of climate variations (Figs. 2, 3), is some indication that precipitation is commonly abundant enough for *A. t. vaseyana* to germinate and establish in most years. However, survival of newly germinated seedlings may be less likely during intermediate stages of succession (Fig. 2) when herbs are most abundant (Figs. 4) or when emergence could become limited by seed availability. Shrub establishment in communities that have relatively greater plant cover than sites dominated by *A. t. vaseyana* appeared reliant on disturbances that reduce vegetative cover; such as small mammal disturbances that allow *A. rothrocki* to invade montane meadows (Berlow *et al*., 2002) or pulses of shrub establishment following fire in chapparal (Tyler, 1996).

Summary and implications.—Recovery of *Artemisia tridentata* canopies to prefire levels may require decades (Harniss and Murray, 1973; Wambolt *et al.*, 2001), however, initial establishment of *A. t. vaseyana* in the first growth seasons following fire may be more important than previously assumed. Temporal patterns of *A. t. vaseyana* establishment may be attributable to negative relationships of seedlings with neighboring herbs or depletion of seed banks, though further experimental verification of these effects are needed. Competitive displacement of seedlings of other *Artemisia* shrub species by an exotic grass appears contributes to site conversion to grassland (eg. Eliason and Allen 1997), and long-term displacement of *A. t. tridentata* or *wyomingensis* through accelerated of fire frequency by *Bromus tectorum* are well known (reviewed in Brooks and Pyke 2001). Dense and persistant invasions of new exotic forbs (eg. *Centaurea* sp. and thistles) into *A. t. vaseyana* communities are becoming increasingly common, particularly following fires. *Artemisia t. vaseyana* seedlings appeared to require greater distances from forbs than grasses during initial postfire establishment (Fig. 3), indicating that *A. t. vaseyana* may interact differently with herb communities as they become enriched in exotic forbs.

ACKNOWLEDGEMENTS

This study was made possible by a grant from the National Aeronautics and Space Administration Goddard Space Flight Center. ISU would also like to acknowledge the Idaho Delegation for their assistance in obtaining this grant. Richard Inouye provided helpful comments.

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