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Effects of surrounding vegetation and soil moisture on establishment of *Artemisia tridentata* ssp. *vaseyana* seedlings following burning of sagebrush steppe

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ABSTRACT

Factors affecting establishment of *Artemisia tridentata* ssp. *vaseyana* (mountain big sagebrush) seedlings are important for a basic understanding of disturbance and succession in sagebrush-steppe, yet are not well known. We investigated how interactions with surrounding vegetation might affect the establishment of *A. t. vaseyana* seedlings after fire, by recording distances to surrounding vegetation for nearly 300 seedlings of *A. t. vaseyana* in sites that had burned 1, 4, 5, or 8 years prior to sampling. Biomass and distances of *A. t. vaseyana* seedlings to neighboring vegetation were also evaluated in watered treatment plots and unwatered control plots to determine the potential role of water in interactions of seedlings and surrounding vegetation. *A. t. vaseyana* seedlings were found at greater distances from surrounding vegetation in the site most recently burned, compared to in sites that burned 4, 5, or 8 years earlier. Distances of *A. t. vaseyana* seedlings were greater to forbs than to shrubs or grasses. Root:shoot biomass ratios decreased with increasing distance from surrounding vegetation for emergent seedlings that received supplemental water in the 2002 burn. Biomass and root:shoot ratios of *A. t. vaseyana* seedlings were less responsive to surrounding vegetation in unwatered plots, indicating that the intensity of competitive responses may be diminished by limited growth occurring under dry conditions. No emergent seedlings of *A. t. vaseyana* were detected in sites burned before 2002, and age distributions in each burn site indicated that seedling emergence occurs primarily in the year following fire. These data indicate that fire in mountain big sagebrush communities

may increase the availability of microsites for successful establishment of *A. t. vaseyana* seedlings, but only in the first growth season or so following fire. In subsequent years, new seedling establishment is likely inhibited by greater abundances of neighboring vegetation, though competitive effects do not appear equivalent for all plant types. Management activities or exotic plant invasions that affect the relative and absolute abundances of re-colonizing species could have important, long-term impacts on reestablishment of sagebrush populations following fire.

Introduction

Intense management of fire regimes, including prescribed burning and fire suppression, is common in sagebrush steppe ecosystems. Fire is applied in sagebrush steppe to promote forage production, reduce fuel loads, or restore disturbance for wildlife habitat (West *et al.* 1984; Wambolt *et al.*, 2001; Wrobleski & Kauffman 2003). Whether, and to what extent fire application achieves ecological goals is currently debated, due to uncertainties in ecosystem responses to fire (Welch & Criddle 2003). These uncertainties indicate the need for an understanding of succession in sagebrush steppe that is more resolute and mechanistic than possible from community-level assessments of changes in the relative cover of constituent populations (Harniss & Murray 1973; Young and Evans 1978; Humphrey 1984; West & Hassan 1985; Wambolt *et al.* 2001). Direct observations of how individual, establishing shrubs in aridlands relate to colonizing, neighboring plants should yield a more resolute understanding of how and why species change in a community, yet such observations are rare in the literature (Owens & Norton 1989; Tyler & D'Antonio 1995). Moreover, whether the diverse types of plants that occur after fire in sagebrush steppe have similar effects on young *A. tridentata* is not known. Seed dispersal and germination have been studied for *A. tridentata* and other aridland shrubs (Hassan & West 1986; Young *et al.*1990; Tyler 1995, Chambers 2000), but less is known about factors affecting seedling success. High mortality rates in young seedlings (Owens & Norton 1989) indicate the importance of the seedling life history stage for population dynamics (Harper 1977).

The intensity of plant competition varies with water availability in desert communities (Goldberg & Novoplansky 1997), and affects of surrounding vegetation on

A. t. vaseyana seedlings might also be dependent on water availability. Sagebrush steppe and other arid environments experience relatively high variability in precipitation and water availability within and between years (Frank & Inouye 1994). Therefore, understanding the role of water in plant interactions is key for predicting *A. t. vaseyana* seedling responses to surrounding vegetation.

The objective of this study was to determine how surrounding vegetation affects *A. t. vaseyana* seedlings. We also wished to determine whether the effects of neighboring plants on sagebrush seedlings were influenced by above- or belowground interactions, such as with sunlight or water availability. Specifically, we measured the effects of the following factors on *A. t. vaseyana* seedling establishment: 1) identity and proximity of surrounding vegetation, 2) time since burning, which affects the identity and density of surrounding vegetation, and 3) water availability. A better understanding of factors affecting *A. t. vaseyana* recruitment as it relates to plant interactions in succession following disturbance could help guide management decisions, such as prescribed burning, grazing after fire, seeding, and herbicide application - all of which can affect the species composition of communities (Seefeldt & McCoy 2003; West & Yorks 2002; Williams *et al.* 2002; Wambolt *et al.* 2001, Schuman *et al.* 1998).

Methods

We observed relationships of naturally established seedlings and surrounding vegetation in sites with different times since burning. To elucidate the importance of soil water to interactions of *A. t. vaseyana* seedlings and surrounding vegetation, we examined the responses of newly emerged seedlings in the 2002 burn site to experimental

manipulations of surrounding vegetation and soil water. All data were collected May-September 2003.

Site and Species

Research was conducted at the U.S. Sheep Experiment Station (USSES; 44°14'44" N Latitude, 112°12'47" W. Longitude; 1650 m a.s.l.) near Dubois, Idaho. Vegetation at the sites is a mixed sagebrush and perennial grass 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 is *Artemisia tridentata* ssp. *vaseyana* Nutt. Other less abundant shrubs are *Chrysothamnus* sp. Nutt., *Tetradymia canescens* DC. and *Purshia tridentata* (Pursh) DC. Perennial bunchgrasses such as *Agropyron dastychium* (Hook.) Scribn., *Festuca idahoensis* Elmer and *Poa sandbergii* Vasey are common. Numerous short-lived perennials such as *Achillea millefolium* L., *Antennaria* sp. Gaertn., *Erigeron* sp. L. and *Phlox* sp. L. are abundant. Soils are fine, loamy, mixed, frigid Calcic Argixerolls derived from wind blown loess or residuum (Natural Resources Conservation Service 1995). Total annual precipitation averaged 297 mm over the last 78 years, with 131 mm accumulating from May through August (Western Regional Climate Center, Desert Research Institute, Reno NV). 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 aum, 8.9 aum, 13.0 aum, and 21.3 aum, respectively. Grazing prior to the application of prescribed burns and in the year following fire did not occur on the 1995 and 1999 sites,

however it did occur in minor, short-term and low-intensity applications in the 1998 and 2002 sites.

Observational study:

Artemisia tridentata spp. *vaseyana* seedling heights and surrounding vegetation were quantified in four prescribed burns that occurred in September of different years (1995, 1998, 1999, and 2002). The 1995 burn was 280 ha; the 1998 burn was 207 ha; the 1999 burn was 221 ha; and the 2002 burn was 105 ha. The four burns were all prescribed and occurred in fall of their respective years. Using differentially-corrected GPS points of all sampling locations, GIS, 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 on sloped terrain were on slopes ranging from 1° and 6°.

Artemisia t. vaseyana seedlings (seedlings were under 30 cm in height and lacking reproductive structures) were located at stratified-random sampling points in burn areas. These locations occurred at 200 m intervals along the perimeter of burn areas, and at random distances from the perimeter towards the center of the burn area. At each location, the nearest *A. t. vaseyana* seedling was identified. Three additional seedlings for measurement were located within approximately 15 m distances in three cardinal orientations from the initial seedling subject. Measurements for both actual seedlings and random points were necessary to characterize both the realized and available space for

seedlings. Therefore, the sampling scheme used to locate seedlings was repeated to generate random (hereafter referred to as 'reference') points for the characterization of space available to *A. t. vaseyana* seedlings. Reference points did not have sagebrush seedlings, by chance.

Distances from the base of each *A. t. vaseyana* seedling or reference 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 reference 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. Heights of all *A. t. vaseyana* above soil were measured. Ground cover was assessed in 0.5 m^2 plots at each reference point using the point intercept method (Floyd & Anderson 1987), to detect differences in the identity and abundance of vegetation in each burn site. In each 0.5 m^2 plot, ground cover under each of 16 points was recorded. Cover classes included shrub, herb, forb, litter, rock, and bare soil. The number of replicate sampling units in each burn for seedling and random points, respectively, were 56 and 16 in the 1995 burn, 75 and 23 in the 1998 burn, 52 and 10 in the 1999 burn, and 90 and 32 in the 2002 burn.

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 to determine the mean and variance of ages of *A. t. vaseyana* seedlings in each burn year. We measured seedling heights from the soil surface to tallest part of the plant. Establishment dates and ages of seedlings were determined from thin cross-sections of the stem, taken near 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 and 100x magnification (Remote Capture 2.2, Canon USA) and counted annual growth rings. Only first year, emergent seedlings were present in the 2002 burn, and cross-section analyses were not needed to determine their establishment dates.

Experimental study

To determine how water availability might affect interactions of *A. t. vaseyana* seedlings and their surrounding vegetation, we experimentally manipulated the surrounding vegetation and available water for seedlings that had germinated a few months earlier on the site burned in 2002. Five areas that each had between 20 and 30 first year *A. t. vaseyana* seedlings in about 6 m^2 areas were identified. Within each area four levels of vegetation treatment were identified or applied to randomly selected seedlings: 1) all vegetation except forbs removed, 2) all vegetation except grasses removed 3) all surrounding vegetation removed, 4) *A. t. vaseyana* that naturally emerged with no surrounding vegetation within a 5 cm radius. The purpose of the removed forb and grass treatments was to distinguish between effects of aboveground and belowground interactions of surrounding vegetation and *A. t. vaseyana* seedlings. *A. t. vaseyana* seedlings were considered to be "near" grasses or forbs if the neighboring vegetation was within 5 cm of the seedling. *A. t. vaseyana* seedlings were at least 10 cm from the nearest surrounding plant after treatment application if they were in the 'naturally surrounded by bare ground' or 'surrounding vegetation removed' treatments. Removal of surrounding vegetation was accomplished by clipping their aboveground structures and was repeated

at each visit. All plots were visited at least once every two weeks from July 25 through October.

The second treatment, water availability, had two levels: supplemental water and no supplemental water. We assigned supplemental water application to one half of each vegetation treatment. Water stored in 113-liter cisterns was fed into the root zones of seedlings using electric timers (Model 3020, Melnor USA) and drip irrigation. Plots with supplemental water received about 300 ml water in early morning and late evening every day from late July to October. Supplemental water treatments were only applied during the driest part of the growing season (30 July- 5 September) to alleviate drying of soil. Volumetric water content (VWC) of soils under all seedlings was measured using a handheld time domain reflectometer unit (Model CS616, Campbell Scientific Logan, UT) with 12 cm probes, in order to determine the effect of water treatments. Soil texture and bulk density were similar among the sites (Germino & Seefeldt, in prep). VWC was measured four times throughout the watering treatments: August 1 and 13, September 3, and October 3. After September, all experimental seedlings were harvested, rinsed in de-ionized water, separated into their root and shoot components, and dried in an oven at 21°C for 24 hours. The root and shoot lengths were measured to 0.1 mm and weighed separately to the nearest 0.01g.

Statistical analysis

One-way analysis of variance (ANOVA) followed by Tukey tests ($\alpha < 0.05$) for multiple comparisons were used to determine mean differences in distances from seedlings or reference points to the nearest plant (grass, forb, shrub) in each burn year. The same

statistical procedure was used to find the significance of within and among year differences for distances of *A. t. vaseyana* seedlings to surrounding vegetation for all cardinal directions. Heights of all *A. t. vaseyana* seedlings that were measured were tallied and put into binned categories. The proportion of seedlings in each height category was calculated for each burn year. Least-squares regression analyses were used to determine the correlations between *A. t. vaseyana* height and age, and age and burn year. Cover type data gathered with point frames were converted to percent cover for each category (grass, forb, shrub, litter, bare, and rock). Burn year and seedling age in addition to seedling age and seedling height were analyzed using ANOVAs and Tukey tests ($\alpha < 0.05$).

Individual and interactive effects of water and vegetation treatments on biomass and root:shoot of emergent seedlings in the 2002 burn site were evaluated using a split-split plot block experimental design and analyzed using a two-way ANOVA. Least-squares regression was used to determine correlations between biomass and root:shoot ratios to distance to nearest herb based on herb type (forb or grass) and water treatment (supplemental water application or no supplemental water application). All data (both observational and experimental studies) were not normally distributed and therefore transformed using the natural log. All analyses were conducted using JMP version 3.2.2 (SAS Institute, Cary NC).

Results

Relationships of Artemisia seedlings to surrounding vegetation

Mean sum distances from seedlings to shrubs were about 15% greater in the 1999 burn site than in the 1998 site, but distances in 1995 burn site were not statistically different from distances in other years ($F_{2,180} = 3.18$, $P = 0.04$, Fig. 1). Shrubs were absent in the 2002 burn. There were no differences in sum distances from seedling and reference points to shrubs in the 1995, 1998, and 1999 sites. *A. t. vaseyana* seedlings in the 2002 burn had almost 3-fold greater sum distances to herbs than in sites burned before 2002 ($F_{3,94} = 15.10$, $P < 0.0001$, Fig. 1), and compared to reference points in the 2002 burn ($F_{1,22} = 8.72$, $P < 0.01$, Fig. 1). Distances to neighboring forbs were similar between seedlings and reference points in the 1998 burn site. There were too few distance measurements for statistical tests from reference points to forbs in the 1995 and 1999 burn sites, due to higher percent cover of grasses than forbs. Seedling distances to grasses were up to 2.5 times greater in the 2002 burn compared to older burns ($F_{3,157} = 20.29$, $P<0.0001$). Seedlings were somewhat closer than reference points to surrounding grasses in the 1995 burn site ($F_{1,50} = 4.83$, $P = 0.03$), similar to reference points in 1998, and were considerably further than reference points in the 1999 ($F_{1,43} = 6.46$, $P = 0.01$) and 2002 sites ($F_{1,67} = 13.35$, $P < 0.01$, Fig. 1). The percent cover of forbs, rock and litter was similar among all burn years, but there was more bare ground ($F_{3,145} = 2.44$, $P < 0.001$) and less grass ($F_{3,176} = 3.24$, $P = 0.02$) in the 2002 burn than the 1998 burn. *A. t. vaseyana* cover was 7% of ground area in the 1995 site, 3% in the 1998 site and 2% in 1999 site (Fig. 2). Mean distances of *A. t. vaseyana* seedlings to shrubs and herbs were similar in all cardinal directions (Fig. 3).

Effects of supplemental water and surrounding vegetation on biomass

Volumetric water contents (VWC) in plots with supplemental water were 8-48% greater than in unwatered plots, on all dates measured ($F_{1,335} = 92.43$, $P < 0.0001$). Mean VWC of unwatered plots for monthly sampling dates from June to September were11.0 ± 1.0, 9.8 ± 0.3, 10.3 ± 0.6 and 13.9 ± 0.4; whereas mean VWC of watered plots were 17.9 ± 1.0, 16.2 ± 1.4, 20.0 ± 1.3, and 15.1 ± 0.5, respectively. There were ~13 mm of precipitation during the month of September, compared to a mean of 6.3 mm for each of the previous three months, which probably accounts for the increased VWC of unwatered plots on our last sampling date.

Total mean biomass of experimental seedlings increased with greater distances to neighboring vegetation with supplemental watering ($F_{1,21} = 4.32$, $P = 0.05$, Fig. 4), but not in unwatered control plots. Although the vegetation treatments alone did not have an effect on total biomass of *A. t. vaseyana* seedlings, they responded to an interactive effect of water and vegetation treatments ($F_{2,56} = 5.49$, $P < 0.01$). Root biomass was 67% higher in the watered compared to unwatered treatments ($F_{1,57} = 6.54$, $P = 0.01$). *A. t. vaseyana* seedlings also grew about 22% more in height with supplemental water than in unwatered treatments ($F_{1,55} = 6.56$, $P = 0.01$). Root:shoot ratios decreased as distances between seedlings and surrounding vegetation increased, but only in plots that received supplemental water ($r^2 = 0.28$, $P = 0.02$).

Frequency distributions of seedling height among burn years

Heights of seedlings in the 1995, 1998 and 1999 burns were similar, and collectively greater than seedling heights in the 2002 burn ($F_{3,59} = 233.37$, $P < 0.0001$, Fig. 5). Approximately 90% of seedlings in the 2002 burn were under 5 cm in height, and mean heights of seedlings increased consistently and positively among the sites with time since burning. One seedling in the 1995 and two in the 1998 burn were under 5 cm. The mean age of seedlings increased with time since burn ($F_{3,59} = 1137.05$, $P < 0.0001$, Fig. 6).

Discussion

The balance of competitive and facilitative interactions among plants can strongly influence species compositions of plant communities and can affect successional pathways (Connell & Slatyer 1977, Morris & Wood 1989). Humphrey (1984) suggested that sagebrush might be facilitated by species that initially colonize a site after a disturbance. His suggestion was based on changes in the relative cover of sagebrush and herbs across a chronosequence of burns in sites that were warmer and drier than our sites. In contrast, Humphrey (1984) categorized most other species in sagebrush steppe into the 'tolerance' model of Connell & Slatyer (1977); where individual species are present in both early and late stages of succession. Our measurements of spatial relationships between individual sagebrush and surrounding plants led to considerably different findings than Humphrey (1984). In cases where neighboring vegetation appeared to affect *A. t. vaseyana* seedlings, the effects appeared negative. Evidence for this was 1) similar or larger distances between *A. t. vaseyana* seedlings and surrounding vegetation than is likely to occur randomly (Fig. 1), and 2) greater allocation of carbon to roots than

shoots for *A. t. vaseyana* seedlings in microsites closer to surrounding vegetation (Fig. 4). Surrounding vegetation also had a negative effect on the shrub *Adenostoma fasciculatum* following fire in chaparral (Tyler & D'Antonio 1995), and *A. tridentata* ssp. *tridentata* seedlings had higher chances of surviving when they had greater distances to surrounding plants (Owens & Norton 1989).

The balance of competitive or facilitative effects in plant interactions may depend on the developmental stages, ecophysiological properties, and densities of the interacting species, a well as environmental stress levels (Callaway & Walker 1997). We found that spacing between *A. t. vaseyana* seedlings and neighboring plants depended on the type of neighboring vegetation, with much greater distances observed from seedlings to forbs than to grasses and especially shrubs (Fig. 1). The effects of neighboring plants on *A. t. vaseyana* seedlings also appeared dependent on soil water availability.

Surrounding vegetation had more negative effects on growth of shrub seedlings in the California chaparral in drier years (Tyler & D'Antonio 1995). However, in our study, supplemental watering appeared to increase the negative effects of neighboring vegetation on *A. t. vaseyana* seedlings (Fig. 4), which is more consistent with other cases of less competitive effects among plants under environmental stress (Callaway and Walker 1997). Moreover, previous studies suggested that belowground interactions tend to be more important than aboveground interactions between plants in arid environments (Fowler 1986). Our findings of 1) no differences in distance from seedlings to neighboring vegetation among cardinal directions (Fig. 3), 2) greater allocation to roots in emergent *A. t. vaseyana* seedlings nearer to surrounding vegetation (Fig. 4), and 3) dependency of neighbor effects on water availability (Fig. 4) indicated that interactions

between *A. t. vaseyana* seedlings and surrounding plants occurred mainly belowground. If aboveground interactions, such as shade from sun and corresponding microclimate played an important role in establishment, we would have expected variation in the abundance of *A. t. vaseyana* seedlings on north and south sides of adjacent vegetation.

Burning reduces viable seed (Hassan & West 1986), which leads to an expectation of more seedlings in unburned than burned areas. However, our findings of more than a six-fold greater abundance of first year seedlings in the most recent compared to previously burned sites (Fig. 5), combined with narrow age distributions of seedlings in each burn site with higher establishment in the year after fire (Fig. 6) indicate that post-fire conditions (e.g. possibly more bare ground) are necessary for new seedlings to establish. These findings contrast with previous suggestions that emergence of *A. t. tridentata* is limited to only occasional years with adequate moisture (Daubenmire 1975). Likewise, in California chaparral, significant establishment of shrub seedlings only occurs after fires (Tyler 1995). We observed widespread germination of *A. t. vaseyana* in all burn years under unusually wet conditions in 2004 ($n > 200$; personal observation, K. DiCristina), which may indicate that differences in the relative abundance of emergent seedlings among sites (Figs. 5 and 6) results from selective seedling survival in recently burned, less vegetated sites. These findings indicate that *A. t. vaseyana* appear more likely to fit the tolerance model of succession that previously appeared in Humphrey (1984) to be more relevant to species other than *A. tridentata* in sagebrush steppe. Differences between the studies may reflect methodological biases of inferring mechanisms of succession from relative population abundances, compared to more direct observations of relationships among individuals of different species. Another possibility

is that sagebrush responses to other species in its community are not consistent among sites that vary in temperature, precipitation, and subspecies of *A. tridentata*.

Summary and Implications

Our findings of limited shrub establishment except in the first year or so after fires, when herbaceous canopies are still recovering to pre-fire abundances, contrasts with the previous, long-held assumptions that 1) *A. tridentata* germinate and emerge into the herbaceous cover that usually dominates burned sites for decades (Harniss & Murray 1973) and 2) that emergence of sagebrush is driven mainly or only by years with suitably wet conditions (Daubenmire 1975). Although recovery of sagebrush canopy cover to pre-fire levels requires many years, individual sagebrush may establish much earlier following fire than previously assumed. Post-fire invasions of new exotic forbs into the sagebrush steppe, which is currently a widespread occurrence (Brooks & Pyke 2001), are likely to have a different and potentially more negative effect on subsequent establishment of seedlings than native species that re-colonize burned sites. Shifts in the relative and absolute abundances of grasses and forbs that result from management practices such as grazing (Seefeldt & McCoy 2003) or seeding are likely to have significant effects on reestablishment of *A. t. vaseyana* populations after fire.

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References

Brooks M.L. and Pyke D.A. 2001. Invasive plants and fire in the deserts of North America. In:. Galley K.E.M and Wilson T.P. (eds.), Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication NO. 11, Tall Timbers Research Station, Tallahassee, FL. pp. 1-14.

Callaway R.M. and Walker L.R. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78: 1958-1965.

Chambers J. 2000. Seed Movements and Seedling fates in disturbed Sagebrush steppe ecosystems: implications for restoration. Ecological Applications 10: 1400-1413.

Chapin F.S. 1991. Integrated responses of plants to stress: a centralized system of physiological responses. BioScience 41:29-36.

Connell J.H. and Slatyer R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119-1144.

Daubenmire R.F. 1975. Ecology of *Artemisia tridentata* subsp. *tridentata* in the state of Washington. Northwest Science 49: 24-35.

Floyd D.A. and Anderson J.E. 1987. A comparison of three methods for estimating plant cover. Journal of Ecology. 75:221-228.

Fowler N.L. 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17: 89-110.

Frank D. A. and Inouye R. S. 1994. Temporal variation in actual evapotranspiration of terrestrial ecosystems: patterns and ecological implications. Journal of Biogeography 21: 401-411.

Goldberg D.E. and Novoplansky A. 1997. On the relative importance of competition in unproductive environments. Journal of Ecology 85: 409-418.

Harper J.L. 1977. Population Biology of Plants. Academic Press, London.

Harniss R.O. and Murray R.B. 1973. 30 years of vegetal change following burning of sagebrush-grass range. Journal of Range Management 26: 322-325.

Hassan M.A. and West N.E. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. Ecology 67: 269-272.

Humphrey D.L. 1984. Patterns and mechanisms of plant succession after fire on *Artemisia*-grass sites in southeastern Idaho. Vegetatio 57: 91-101.

Morris W.F. and Wood D.M. 1989. The role of lupine in succession on Mount St. Helens: facilitation or inhibition? Ecology 70: 697-703.

Natural Resources Conservation Service. 1995. Soil investigation of Agriculture Research Service, United states Sheep Experiment Station headquarters range. United States Department of Agriculture, Natural Resource Conservation Service,

Rexburg, Idaho.

Noble I.R. and Slatyer R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43: 5-21.

Owens M.K. and Norton B.E. 1989. The impact of available area on *A. t. vaseyana tridentata* seedling dynamics. Vegetatio 82: 155-162

Seefeldt S.S. and McCoy S.D. 2003. Measuring plant diversity in the tall threetip sagebrush steppe: influence of previous grazing management practices Environmental Management 32: 234-245.

Schuman G.E., Booth D.T. and Cockrell J.R. 1998. Cultural methods for establishing Wyoming big sagebrush on mined lands. Journal of Range Management 51: 223-230.

Tyler C.M. 1995. Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. Journal of Ecology 83: 1009-1020.

Tyler C.M. and D'Antonio C.M. 1995. The effects of neighbors on the growth and survival of shrub seedlings following fire. Oecologia 102: 255-264.

Wambolt C.L. Walhof K.S. and Frisina M.R. 2001. Recovery of big sagebrush communities after burning in southwestern Montana. Journal of Environmental Management, 61: 243-252.

Welch B. and Criddle C. 2003. Countering misinformation concerning Big sagebrush.

Research paper RMRS-RP-40. Ogden, UT: US Department of Agriculture, Forest Service. Rocky Mountain Research Station. pp. 28.

West N.E., Provenza F. D., Johnson P. S. and Owens M. K. 1984. Vegetation change after 13 years of livestock grazing exclusion on sagebrush semidesert in west central Utah. Journal of Range Management 37: 262-264.

West N.E. and Hassan M.A. 1985. Recovery of sagebrush-grass vegetation following wildfire. Journal of Range Management 38: 131-134.

West N.E. and Yorks T.P. 2002. Vegetation responses following wildfire on grazed and ungrazed sagebrush semi-desert. Journal of Range Management 55: 171-81.

Williams M.I., Schuman G.E., Hild A.L. and Wicklund L.E. 2002. Wyoming big sagebrush density: effects of seedlings rates and grass competition. Restoration Ecology 10: 385-391.

Wrobleski D.W. and Kauffman J.B. 2003. Initial effects of prescribed fire on morphology, abundance, and phenology of forbs in big sagebrush communities in Southeastern Oregon. Restoration Ecology 11: 82-90.

Young J.A. and Allen F.L. 1997. Cheatgrass and range science: 1930-1950. Journal of Range Management 50: 530-535.

Young J.A. and Evans R.A. 1978. Population dynamics after wildfires in sagebrush grasslands. Journal of Range Management 31: 283-289.

Young J.A., Evans R.A. and Palmquist D. 1990. Soil surface characteristics and emergence of big sagebrush seedlings. Journal of Range Management 43: 358-367.

Figure 1. Mean sum distances of *Artemisia t. vaseyana* seedlings (solid bars) or random points (open) to shrubs, forbs, or grasses, in each burn year. There were no shrubs present in the 2002 burn. Missing bars are due to insufficient replication. Errors are 1 SE. N=10-89.

Figure 2. Mean percent cover of grass, forbs, shrubs (top panel) and litter, bare soil, and rock (bottom panel) in each burn year. Standard errors are plotted but are smaller than symbols. N=9-79.

Figure 3. Mean distances and standard errors from *A. t. vaseyana* seedlings to surrounding herbs (top panel) and shrubs (bottom panel) in each of four cardinal directions for seedlings in sites with different time since fire. Data for the 1995 are shown by open bars; for 1998 by left-hatched bars; for 1999 by cross-hatched bars, and for 2002 by right-hatched bars. Errors are 1 SE. N=51-97

Figure 4. Total biomass and root:shoot ratios of 1st year *A. t. vaseyana* seedlings, in relation to their distance to surrounding vegetation. Empty circles and dashed lines represent watered plots. Solid circles and lines represent unwatered plots. Data are from the 2002 burn area.

Figure 5. Frequency distribution of heights of *A. t. vaseyana* seedlings found on sites with different time since fire. Seedling height categories are binned groups of 5 cm increments; the upper values of each bin are 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=50-89.

Figure 6. Mean seedling age in each burn year. Errors are ± 1 SE. n=10 except in the 2002 burn, where n= 30. The line shows a 1:1 ratio of year of burn and seedling age.

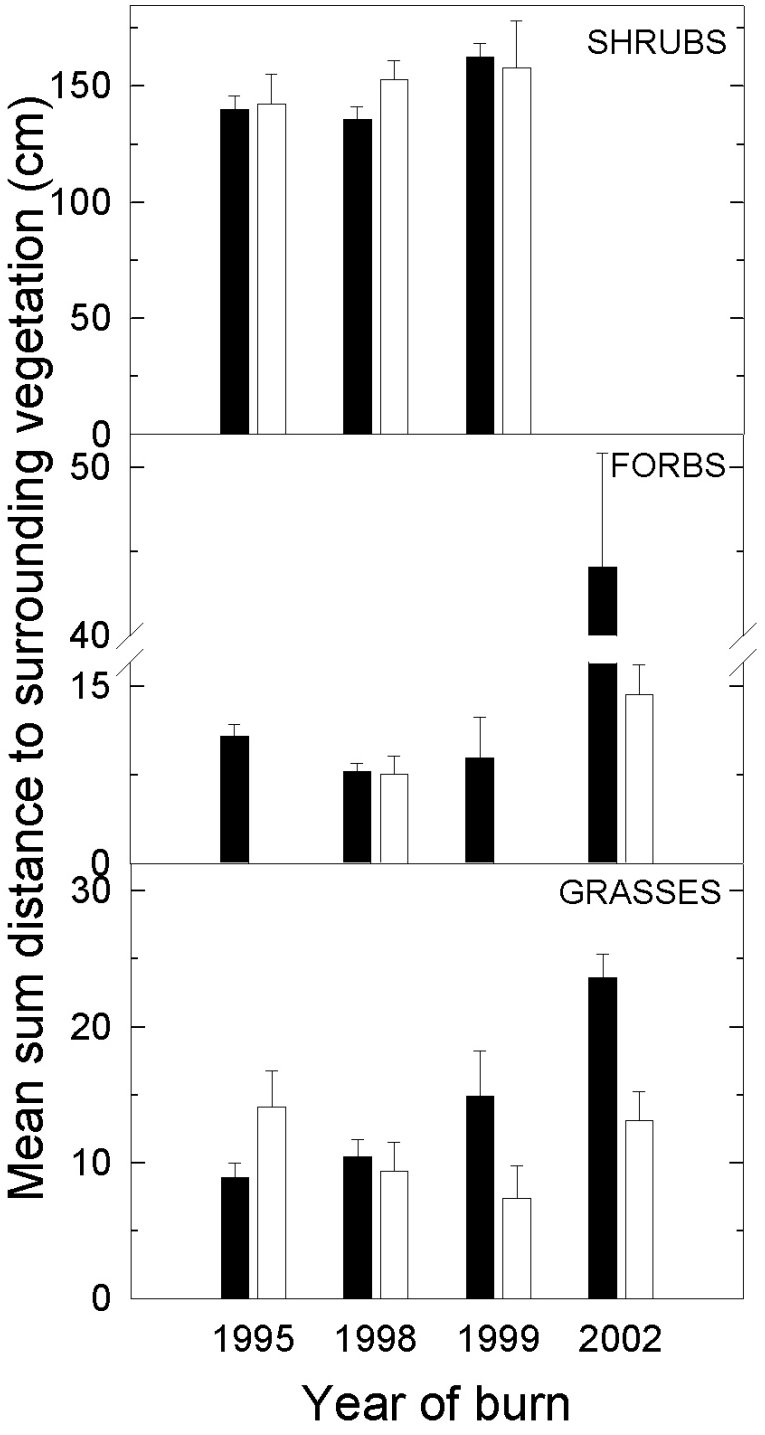
SHRUBS
FORBS
GRASSES
Mean sum distance to surrounding vegetation (cm)
150
100
50
0
50
40
15
0
30
20
10
0
1995
1998
1999
2002
Year of burn

Figure 1

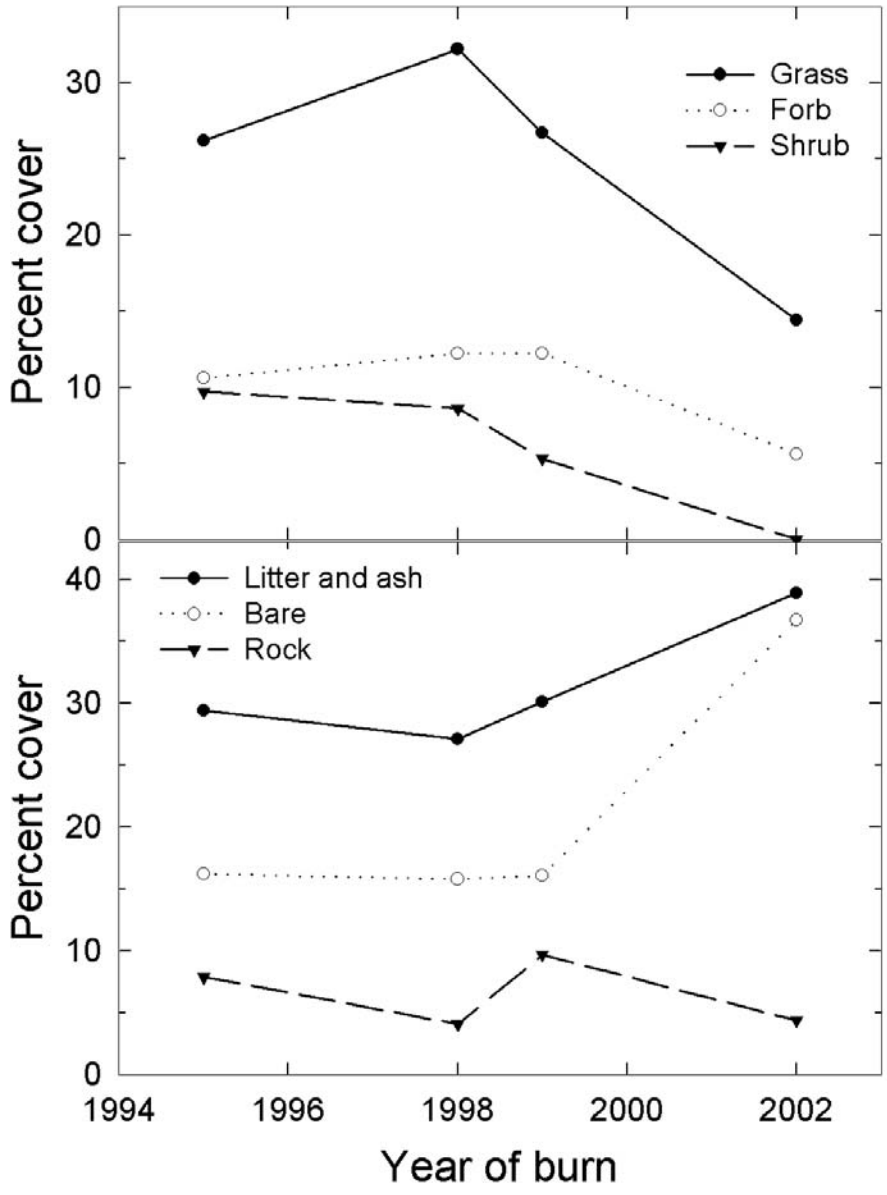
Grass
Forb
Shrub
Percent cover
0
10
20
30
Litter and ash
Bare
Rock
Percent cover
0
10
20
30
40
1994
1996
1998
2000
2002
Year of burn

Figure 2

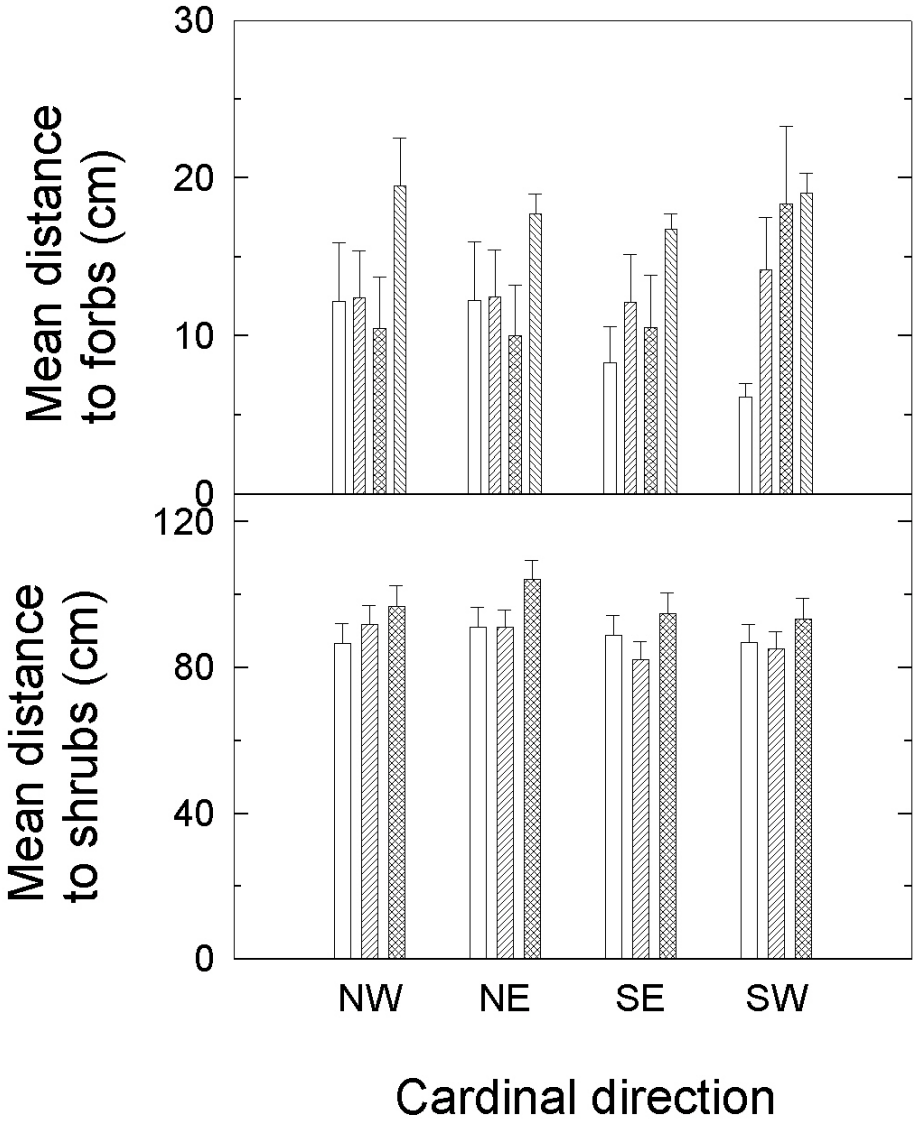
Mean distance to forbs (cm)
30
20
10
0
Mean distance to shrubs (cm)
120
80
40
0
NW
NE
SE
SW
Cardinal direction

Figure 3

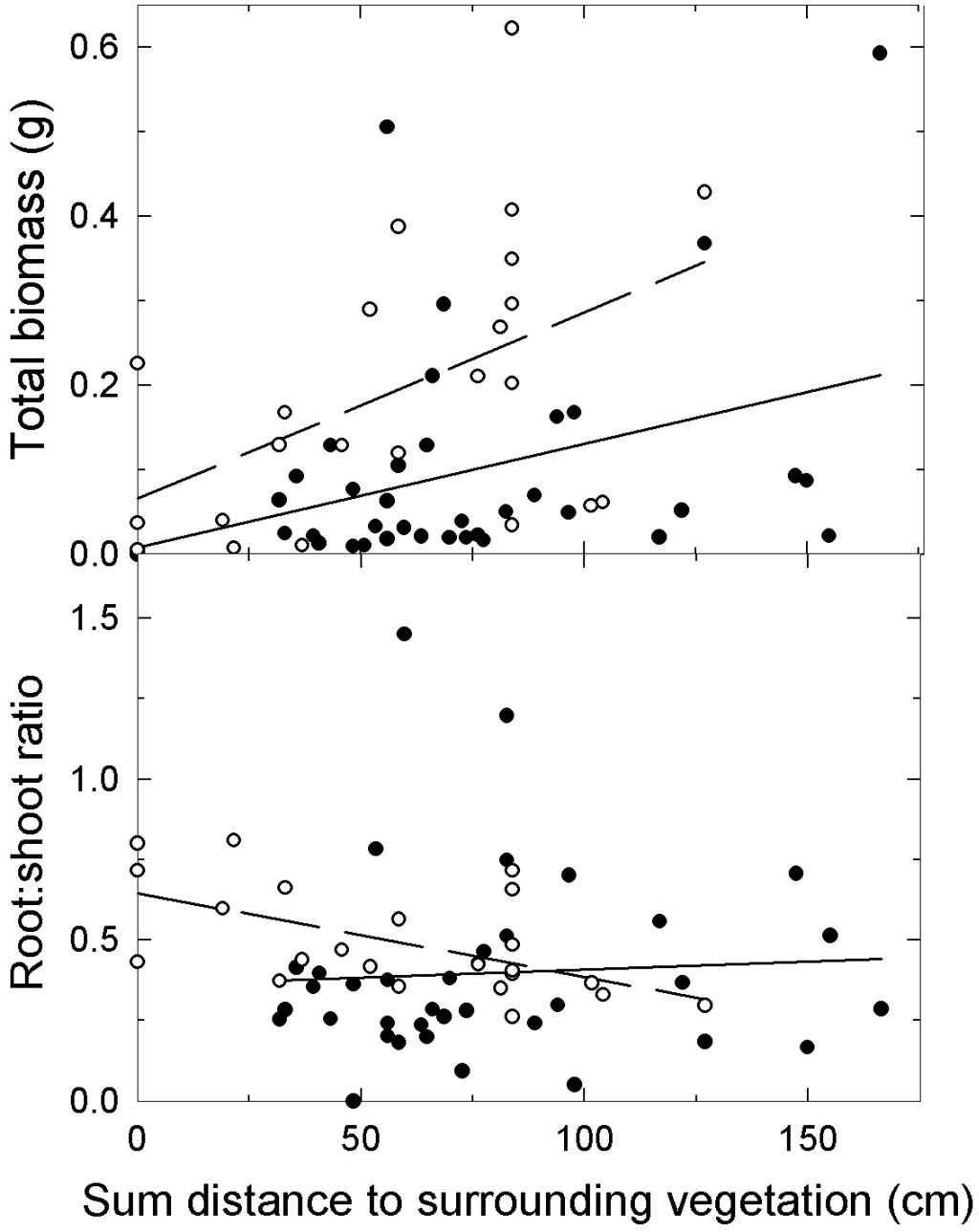
Total biomass (g)
0.0
0.2
0.4
0.6
Root:shoot ratio
0.0
0.5
1.0
1.5
0
50
100
150
Sum distance to surrounding vegetation (cm)

Figure 4

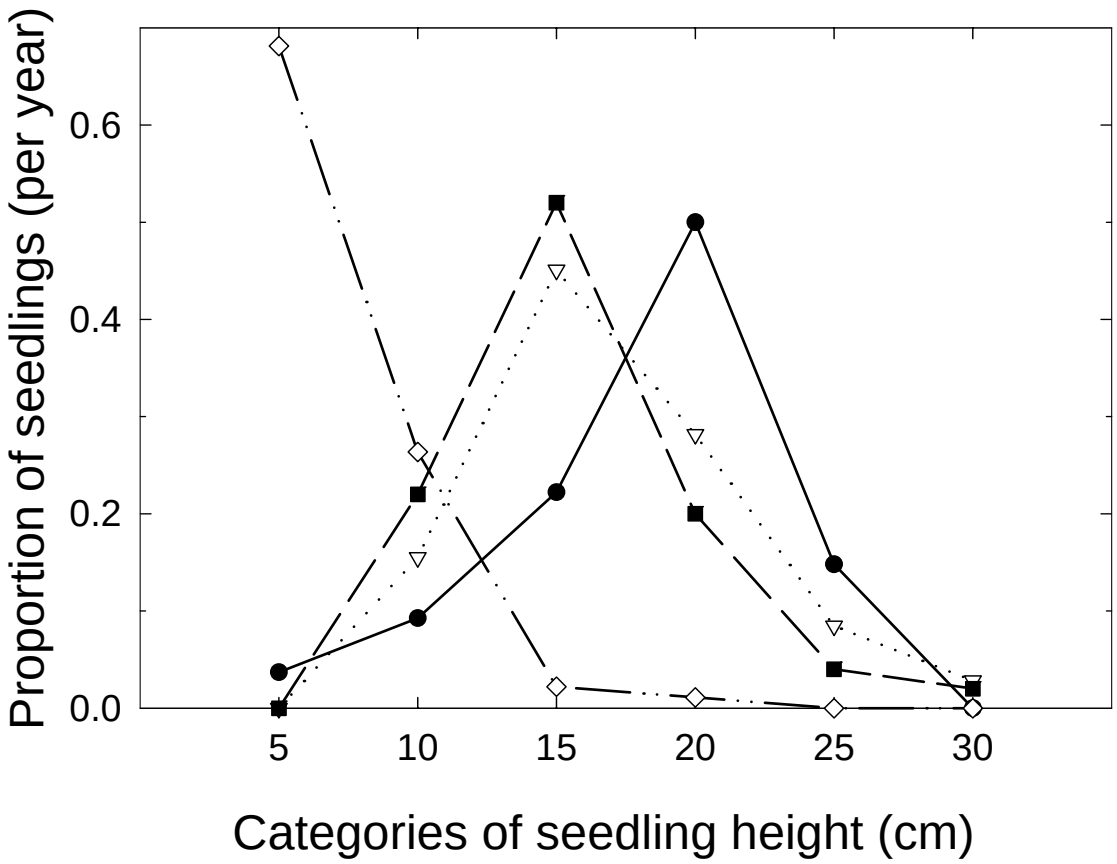
Proportion of seedlings (per year)
0.0
0.2
0.4
0.6
5
10
15
20
25
30
Categories of seedling height (cm)

Figure 5

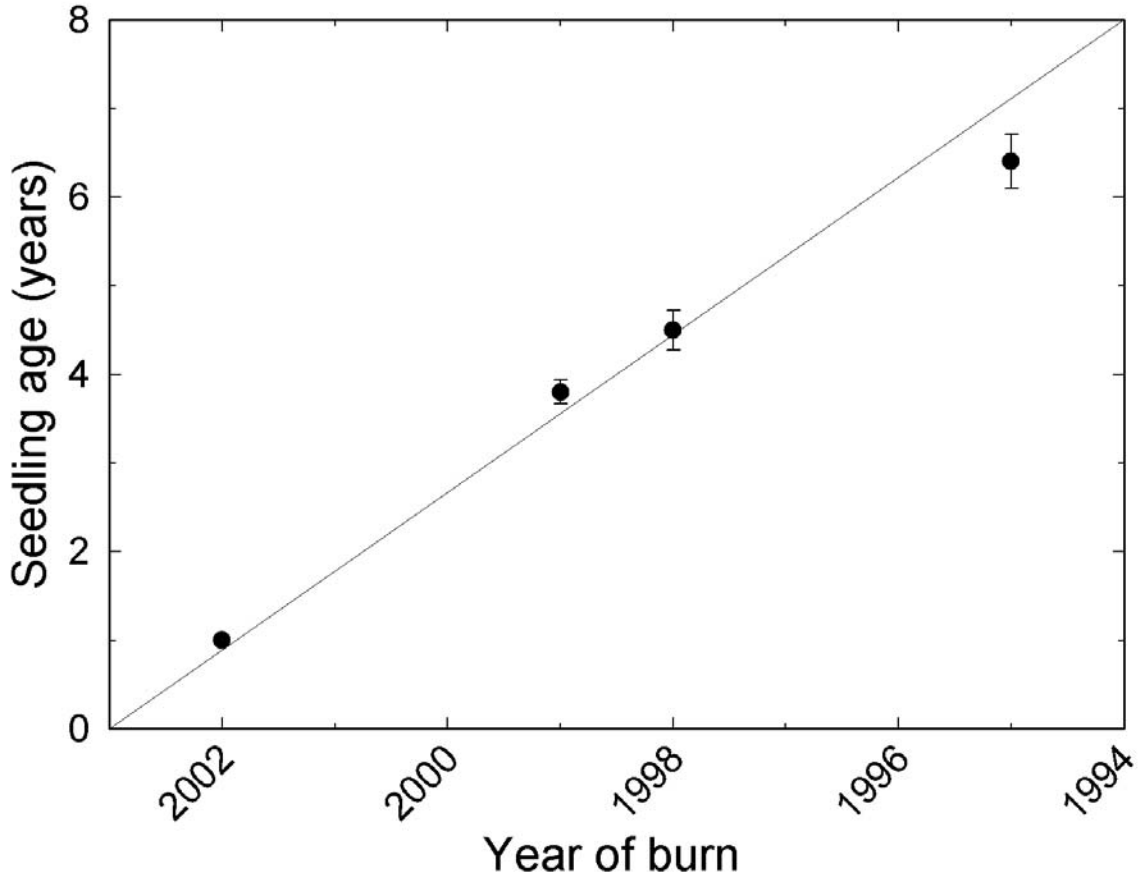
Seedling age (years)
0
2
4
6
8
2002
2000
1998
1996
1994
Year of burn

Figure 6