Correlation of Neighborhood Relationships, Carbon Assimilation, and Water Status of Sagebrush Seedlings Establishing After Fire

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ABSTRACT
Interactions of *Artemisia tridentata ssp. vaseyana* (mountain big sagebrush) and neighboring herbs may affect community development following fire in sagebrush steppe. Biomass, photosynthesis, and water relations were measured for seedlings of *A. t. vaseyana* occurring at different distances from neighboring herbs in the initial growing seasons following fire, when herbs dominate plant community cover. Biomass gain was nearly twice as great for *A. t. vaseyana* seedlings located furthest from neighboring herbs, compared to seedlings located adjacent to neighboring herbs. Similarly, carbon assimilation (Anet) was greater for *A. t. vaseyana* in microsites further from herbs, but only in early and not mid-late summer. Xylem pressure potentials (XPP) of seedlings were not correlated with their distances to neighboring herbs, on any sampling date. Moreover, supplemental watering had no effect on relationships between biomass of *A. t. vaseyana* seedlings and distances to neighboring herbs. In mid-late summer, when Anet, stomatal conductance, and XPP of seedlings decreased markedly as soils dried, Anet was no longer correlated with distances to neighboring herbs. Longer-term responses of *A. t. vaseyana* to neighboring herbs following fire may result largely from interactions between them in early summer, before the seasonal onset of water limitations. Although soil-plant water relations could explain much of the seasonal variability in Anet and growth of seedlings, correlations of Anet or biomass and proximity to neighboring herbs were not likely to result from water limitations in microsites near herbs.

Keywords: sagebrush; seedling establishment, photosynthesis, plant-soil water relations, fire, *Artemisia tridentata spp. Vaseyana*.

INTRODUCTION

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. 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 sagebrush cover (*Artemisia tridentata*) up to 30 years following fire (Wambolt et al. 2001) compared to expectations based on previous studies (Harniss and Murray 1973). Lack of sagebrush recovery following fire is a major concern for sustaining sage grouse (*Centrocercus urophasianus*) and other wildlife (Leonard et al. 2000). Altered rates of sagebrush reestablishment may result from changes in floristics of herb communities that are resulting from exotic plant invasions (Brooks and Pyke 2001).

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 shrub, Artemisia tridentata, reestablishes (Harniss and Murray 1973). Direct observations of interactions between sagebrush seedlings and other plant species are rare in the literature (e.g., Daubenmire 1975, Owens and Norton 1989; Berlow et al. 2002), especially for post-fire conditions. Seed dispersal and germination have been studied for *A. tridentata* and other aridland shrubs in undisturbed and post-fire situations (e.g., West & Hassan 1985; Young et al.1990; Tyler 1996, Chambers 2000), but less is known about factors affecting seedling success. New establishment of *A. t. vaseyana* seedlings was detected in sites burned 1-3 years prior to sampling and in sites in later stages of succession (i.e., having mature shrubs), but not in sites at intermediate stages of succession that had denser herb layers (DiCristina et al, in review, Harniss and Murray 1973, Young and Evans 1978). These temporal patterns of *A. t. vaseyana* establishment are nearly opposite of typical changes in herb cover during disturbance-succession cycles (eg. Harniss and Murray 1973), and indicate a potentially negative effect of herbs on *A. t. vaseyana* reestablishment following fire. The objective of this research was to determine how physiological performance of *A. t. vaseyana* seedlings is affected by their proximity to neighboring herbs, following fire and within the natural range of neighborhood spacing. We hypothesized that seedlings in microsites closest to neighboring herbs would exhibit less biomass accumulation, photosynthetic carbon uptake, and water status; and that growth limitations near herbs would result from water limitations. Moreover, we predicted that responses of *A. t. vaseyana* seedlings to neighboring herbs would be most negative in mid-late summer, when water availability reaches yearly minima. Seedling biomass was measured in response to experimental manipulations of distances to herbs, with and without supplemental water additions. We focused our sampling efforts on a site burned 1-2 years prior, when herb cover constitutes most of the plant community biomass.

METHODS

Research was conducted during the snow-free season of 2003 and 2004 in a site burned in September 2002 at the USDA, ARS, U.S. Sheep Experiment Station (USSES; 44°14’44” N Latitude, 112°12’47” W. Longitude; 1650 m a.s.l.), near Dubois, Idaho. The dominant shrub in this community is *Artemisia tridentata ssp. vaseyana* Nutt. 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* were common, as were numerous short-lived perennials such as *Achillea millefolium* L., *Antennaria sp.* Gaertn., *Erigeron sp.* L. and *Phlox sp*. L. Ground cover on 40- 1 m2 plots in 2003 and 2004 was 5 and 26% grass, 15 and 29% forb, 35 and 22 % soil, respectively, in addition to some litter and rock (DiCristina et al, in review). 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). Precipitation during our study period of January through September 2003 and 2004 was 140 and 190 mm, respectively, compared to 240 mm for mean precipitation over these months over the previous 80 years. There has been light grazing (21.3 sheep days/ha) on the site from 1968-2002.

<u>Biomass responses to experimental manipulations</u>
Seedling responses to manipulated distances to neighboring herbs and water availability (+ or – supplemental water) were examined in 2003, on seedlings that had just recently emerged (within a week or so) during the first growth season following the 2002 fire. Five replicate plots having about 20 *A. t. vaseyana* seedlings within about 6 m2 of each other were identified within different burns in a < 2 km area. Herbs were removed from *A. t. vaseyana* seedlings that had naturally established within 10 cm of herbs, to generate a range of distances of seedlings to herbs. Distances from the base of each *A. t. vaseyana* seedling were then measured to the base of the nearest herb in each of four quadrants around seedlings (NW, NE, SE, SW), for a total of four distances per seedling. The four measured distances were added together and are hereafter referred to as the 'sum distance' of each *A. t. vaseyana* seedling to surrounding vegetation. Removal of surrounding herbs was accomplished by clipping aboveground structures at least once every two weeks from July through October. We randomly selected half of each replicate plot to receive supplemental watering. Water stored in 113-liter cisterns was applied to the root zones of seedlings using electric timers (Model 3020, Melnor USA) and drip irrigation lines. Seedlings in plots with supplemental water received about 300 ml of water in early morning and late evening every day from late July through September. Validation of effects of water additions on soil water content was accomplished by measuring volumetric water content (VWC, m3/m3) of soils under all seedlings using a handheld time domain reflectometer unit (Model CS616, Campbell Scientific Logan, UT) with 12 cm probes. Soil texture and bulk density were similar among the sites (sandy loam, Germino and Seefeldt, unpublished). VWC was measured four times throughout the watering treatments: August 1 and 13, September 3, and October 3. After September, all experimental seedlings were carefully excavated, rinsed in de-ionized water, and dried in an oven at 21°C for 24 hours. Seedling biomass was then measured to 0.001 g, and there were 59 and 33 seedlings among the five replicate watered and unwatered plots, respectively. We used regression and two-way ANOVA to determine significance of differences in biomass of seedlings with different sum distances to neighboring herbs, with and without watering. Seedlings selected for this experiment were initially similar in size (< 2 cm height) and age (emerged within about one week of each other), and we assumed that their biomasses at the beginning or the experiment were comparable.

<u>Ecophysiological responses to neighboring herbs</u>
Photosynthesis, water relations, and distance to neighboring herbs were measured in 2004 on seedlings of *Artemisia tridentata ssp. vaseyana* that we detected within three, separate, belt transects that were each 5 m wide by 25 m long, positioned in one ~ 100 ha burn patch. Data were collected on three separate sampling periods in 2004: 24-25 June, 17-18 July, and 4-5 September. Thirty seedlings were harvested at each sampling date, requiring selection of 30 new seedlings for each subsequent sampling. Seedlings were in their first or second season of growth and were between 1.5 and 10 cm in height, and consisted of between 7 and 20 leaves per plant. Sum distance to neighboring herbs (see methods above), photosynthetic gas exchange, and water status were measured for each seedling. We measured net photosynthetic carbon assimilation (Anet) and gs with a portable gas exchange system (LI-6400, LICOR Inc., Lincoln, Nebraska, USA) equipped with an artificial LED light sources and CO2 controller. Relative humidity, temperature, and CO2 were maintained near ambient values during measurements. Measurements were made during mid-morning to midday during the hours of maximal photosynthesis, and no daily time effects were evident in our data. Light intensity was 1000

µmol $m^{-2}s^{-1}$ for all measurements. All values were reported on silhouette leaf area basis according to recommendations of Smith et al. (1991). We quantified silhouette leaf area of each seedling by taking a digital photo of leaf area as it was naturally configured in the measurement chamber, perpendicular to the artificial light source and with objects of known size in view for calibration. Leaf areas and calibration objects in photos were traced onto paper and scanned into a computer-imaging program (Image J, version 1.23p) for calculation of leaf area.

Pre-dawn and midday xylem pressure potentials (PDXPP and MDXPP, respectively) were measured in the field immediately after excising shoots at the root interface, using a Scholander-type pressure chamber (Model 1000, PMS Instrument Co., Corvallis, Oregon, USA). We measured PDXPP between 0530 and 0630 on all sampling dates for half (n=15) of each sample population, except in June, when we measured the entire sample population (n=30) before dawn. We measured MDXPP between 1130 and 1400 for half (n=15) of each sample population in July and September only.

Time domain reflectometer (TDR) probes and data loggers (models CS616 and CR10, respectively, Campbell Scientific, Logan UT, USA) were used to measure and record VWC at one central location in the burn area. VWC was recorded at 4-hour intervals from June through September on two sets of 30 cm length probes inserted horizontally at 5 cm and at 50 cm soil depths. Soil water contents can vary considerably in space, and the TDR data were therefore used only to estimate how the timing of our physiological measurements corresponded to general seasonal trends in drying, or summer rains that led to soil wetting.

We used analysis of covariance (ANCOVA) to determine if month (main effect) affected the relationship between physiological responses of *A. t. vaseyana* and distances to neighbors (covariate). PDXPP values were log-transformed for statistical calculations. Statistical differences of VWC between months were not tested due to low replication, and we report only mean ± SD for monthly values for each soil depth. Least-square regressions were used to analyze relationships between A_{net} or g_s and PDXPP over all sampling dates. Significant differences between specific means were determined with Tukey-Kramer tests at the $P < 0.05$ level. All analyses were conducted using SAS version 8, and JMP version 3.1 statistical software (SAS Institute Inc., Cary, North Carolina, USA).

RESULTS

<u>Biomass responses to neighboring herb proximity and water additions</u>

Biomass of *A. t. vaseyana* seedlings in unwatered plots was negatively correlated to proximity of neighboring herbs, though distances to herbs could explain only a small amount of the variation in seedling biomass (slope = 0.006 g/cm, $r^2 = 0.12$, $F_{1,57} = 7.6$, $P < 0.001$; Fig. 1). Supplemental watering led to a more negative but less significant correlation of seedling biomass and proximity to herbs (slope = 0.009, $r^2 = 0.09$, $F_{1,31} = 3.16$, $P = 0.08$; Fig. 1). Supplemental watering thus did not appear to ameliorate the negative relationship of seedling growth and distance to herbs, even though watering led to nearly a doubling of biomass ($F_{1,88} = 4.03$, $P<0.001$).

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 2003 were 11.0 ± 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 about 13 mm of precipitation during the month of September, compared to a mean of 6.3 mm for each of the previous three months.

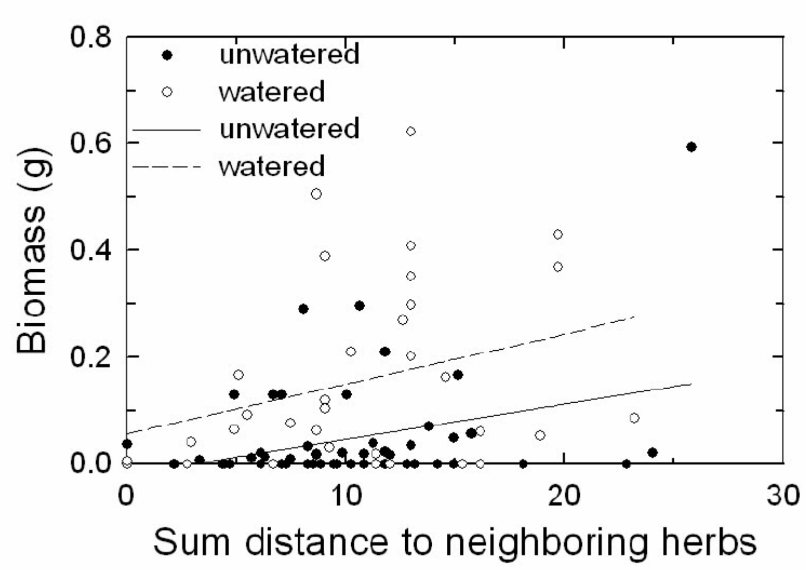

Figure 1. Correlation of biomass of *A. t. vaseyana* seedlings and sum distance to neighboring herbs in watered and unwatered plots in 2003. N = 59 seedlings in the watered and 33 in the unwatered plots.

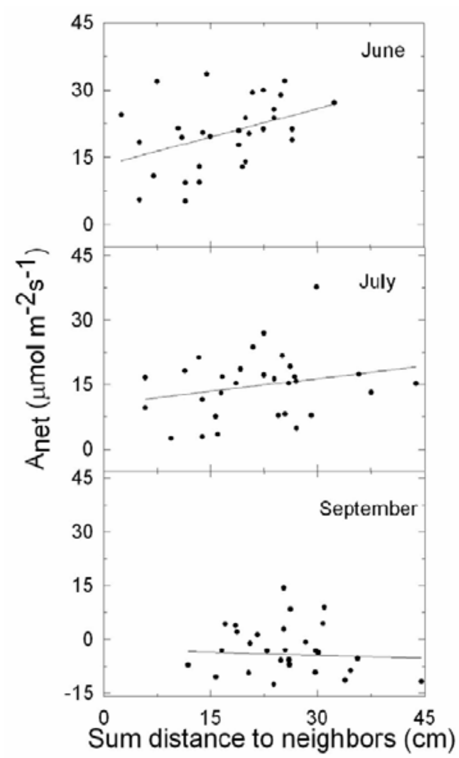

Figure 2. Relationship of distance to herbs and photosynthesis in *A. t. vaseyana* seedlings in June, July, and September 2004.

In June, there was a positive relationship (r2 = 0.14, F1,29 = 5.6, P = 0.03, Fig. 2) between net photosynthesis (Anet) and distance from *A. t. vaseyana* seedlings to neighboring plants. We did not detect any significant effect of sum distance on Anet in July or September (Fig. 2). The percent of *A. t. vaseyana* seedlings having sum distances to neighboring herbs of 12 cm or less was 33% in June, 10% in July, and 0% in September, respectively (Fig. 2). Mean sum distances from *A. t. vasayana* seedlings to surrounding herbs increased about 35% from June to September ($F_{2,89} = 8.7$, $P < 0.001$, Fig. 2). No correlations of gs, or XPP and sum distances of seedlings to neighboring herbs were detected on any sampling dates, and therefore are not presented.

By September, Anet ($F_{2,89} = 71.7$, $P < 0.0001$), stomatal conductance (gs) ($F_{2,89} = 60.0$, $P< 0.0001$), pre-dawn xylem pressure potential (PDXPP) ($F_{2,56} = 112.7$, $P < 0.0001$), and mid-day xylem pressure potential (MDXPP) ($F_{1,20} = 19.4$, $P < 0.001$) were considerably lower than measurements in June (Fig. 3). At 5 cm soil depth, volumetric water content (VWC; m^3 water/m^3, reported as a percentage) in 2004 were highest in June (19.0% ± 4.2% SD) but decreased to 15% on 24-25 June, 12% on 17-18 July, and 8% on 4-5 September, which were days in which physiology was measured (Fig. 4). VWC was relatively more abundant at 50 cm depth, but also decreased from June (33.4% ± 0.6% VWC) to September (20.1% ± 0.5%, Fig. 4).

For all months combined, Anet ($r^2 = 0.61$, $P < 0.0001$) and gs increased ($r^2 = 0.80$, $P < 0.0001$) considerably with PDXPP (Fig. 5). Maximum levels of Anet and gs occurred when PDXPPs were above about –0.5 MPa (Fig. 5). Anet decreased less than gs as PDXPP decreased below about 0.5 MPa in the latter sampling dates (linear decline for Anet compared to exponential decrease in gs), reflecting increases in water use efficiency (A/gs) as soils dried in mid-late summer.

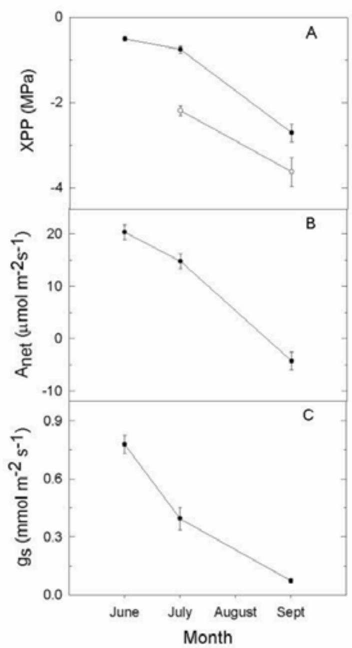

Figure 3. Mean (+/- 1 SE) pre-dawn (solid circles) and mid-day (open circles) xylem pressure potential (XPP) (A), photosynthesis (B), and stomatal conductance (C) of *A. t. vaseyana* in each of 3 months sampled in 2004.

DISCUSSION

Seedlings of *A. t. vaseyana* had less biomass at the end of their first growth season in microsites closest to neighboring grasses, but less carbon assimilation (Anet) near neighboring herbs in June only, and not in subsequent, drier months (Figs. 1 and 2). Relatively greater distances of *A. t. vaseyana* to neighboring herbs also occurred in months following June (Fig. 2), which could have resulted from mortality of *A. t. vaseyana* seedlings or senescence of herbs. Seasonal changes in neighborhood spacing could contribute to - but not completely explain – seasonal decreases in photosynthetic responses of *A. t. vaseyana* seedlings to proximity of neighboring herbs, because sum distances >15 cm were observed on all sampling dates (Fig. 2). Thus, photosynthetic and growth responses of *A. t. vaseyana* to proximity of neighboring herbs could possibly reflect growth limitations in microsites adjacent to herbs.

The intensity of plant interactions in communities with low water availability and productivity is expected to be greatest during brief periods of increased resource availability, rather than when resource scarcity leads to reductions in background growth levels (Goldberg and Novoplansky 1997, see also Bilbrough and Caldwell 1997). Availability of soil water is typically greatest in sagebrush steppe during spring and early summer, following snowmelt and spring rain (Fig. 4). Although drought-adapted species might be capable of extracting water from drier soils, water potentials near –1.5 MPa are typical thresholds for water uptake in many plant species (Lambers et al. 1998). Comparisons of VWCs (Fig. 4) with water retention curves (Germino and Seefeldt, unpublished) indicated that VWCs around our TDR probes likely became less than –1.5 MPa (10-12% VWC), at the end of July and only at 5 cm soil depths. Although we did not measure VWC directly under seedlings, sharp reductions in stomatal conductance in seedlings occurred as plant water potentials at predawn decreased to and below –1.5 MPa, and were also somewhat synchronous with decreases in water content to below 10-12% VWC and –1.5 MPa in soils around our TDR probes (Figs. 3-5). Despite apparent increases in water use efficiency, stomatal limitations likely led to appreciable decreases in Anet as water potentials of plants and soils around TDR probes decreased to below about –1.5 MPa (Figs 3-5). Anderson et al. (1987) found that water consumption ceased at 10-12% VWC in older *A. t. wyomingensis* in a nearby site with similar soil textures (Anderson et al. 1987), and *A. t. wyomingensis* typically occurs in drier sites than *A. t. vaseyana* (reviewed in Smith et al. 1997). Responses of Anet in *A. t. vaseyana* seedlings to proximity of neighboring herbs in June, but not in subsequent months, corresponds with drought-induced reductions in Anet in the later months (Figs. 3 and 5; see Gillespie and Loik 2004 for drought responses in seedlings of other subspecies of Artemisia), and therefore matches the predictions of Goldberg and Novoplansky (1997). Community relationships of A. t. vaseyana seedlings and neighboring herbs may result largely from their interactions before the onset of seasonal water limitations to photosynthesis and growth.

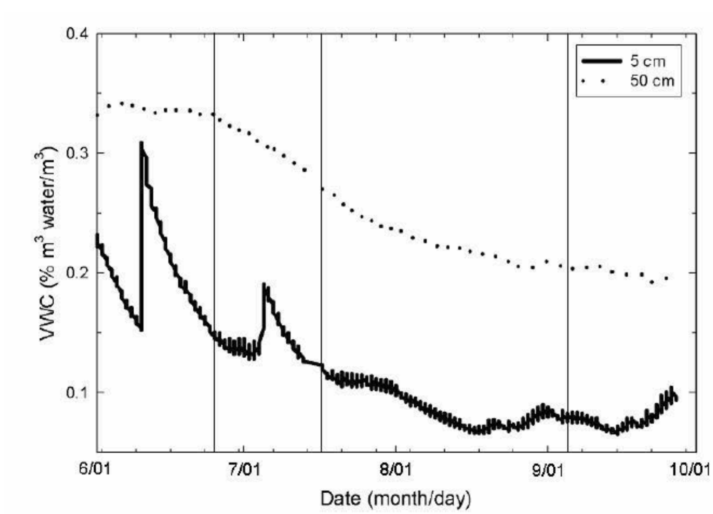

Figure 4. Volumetric soil water content from 1-June through 30-September 2004 at 5 and 50cm depths in soil. Data are plotted as recorded, in 4-hr intervals. Minor ticks on X-axis represent 7-day intervals. Vertical lines indicate sampling dates.

Differences in photosynthesis (when normalized for area and time) result from increases in diffusive supply of CO2 through stomata, or physiological demand for CO2 in carboxylation reactions. Although water availability strongly affected biomass and temporal patterns of gs and Anet in *A. t. vaseyana* seedlings (Figs. 1 and 2), plant water status and gs were not correlated with proximity of neighboring herbs on any sampling date, and were therefore unlikely to explain lower Anet in seedlings nearest herbs, in June (Fig. 2). Moreover, negative relationships of biomass and proximity of neighboring herbs were not alleviated by supplemental watering (Fig. 1). Less Anet and growth of *A. t. vaseyana* in microsites closest to neighboring herbs were therefore not likely to have resulted from preemption of soil water for seedlings by neighboring herbs. Alternative explanations for reduced Anet in *A. t. vaseyana* seedlings near herbs could include factors that affect photosynthetic demand for CO2, such as less sunlight or soil nutrient availability in microsites closer to herbs. Seedlings we studied were only rarely overtopped by neighboring herbs, and often did not appear located closely enough to herbs to be shaded by them (dividing sum distances in Figs. 1 and 2 by four gives mean proximities). Moreover, DiCristina et al. (in review) found distances of *A. t. vaseyana* seedlings to neighboring herbs were not affected by whether seedlings were located on the north or south sides of herbs, which would otherwise indicate shading effects.

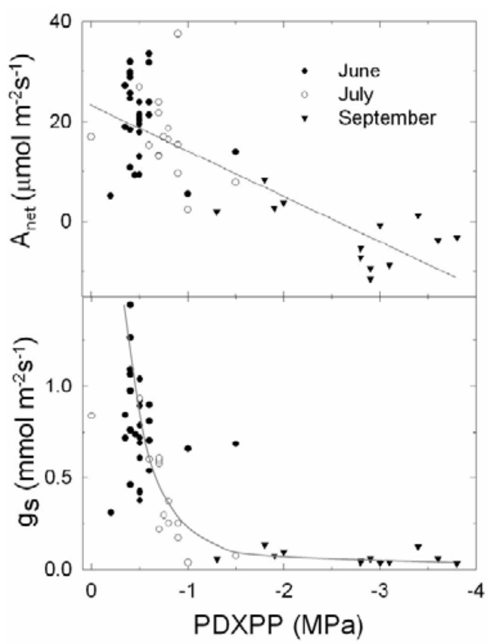

Figure 5. Relationship of pre-dawn xylem pressure potential (PDXPP) to photosynthesis (top) and stomatal conductance (bottom) of *A. t. vaseyana* seedlings in 2004.

High nutrient levels commonly occur after fires and could diminish the role of nutrients in plants interactions. However, nitrogen levels returned to pre-fire levels after about 10 months following fire in sagebrush (Hobbs and Schimel 1984), leading us to speculate that nutrient availability was not unusually high during years of our study. Several studies indicated greater nutrient uptake during moisture pulses in semiarid communities (Cui and Caldwell 1997; Ivans et al. 2003), and high uptake rates in June by herbs, and corresponding depletion of soil nutrients near herbs, would be consistent with our results. Our study was not designed to experimentally isolate the importance of specific resources on seedling Anet, but we speculate that nutrient limitations could be an important factor contributing to less Anet and growth of *A. t. vaseyana* seedlings located near herbs.

Summary and implications

Biomass gain and early-season photosynthesis in *A. t. vaseyana* establishing following fire was negatively correlated with proximity to neighboring herbs. Nearly inverse relationships of *A. t.*

vaseyana establishment and herb cover during disturbance-succession cycles, and much larger distances of *A. t. vaseyana* seedlings to neighboring herbs after fire than could occur randomly (DiCristina et al. in review), may therefore be partly attributable to physiological responses of *A. t. vaseyana* to herbs. Interactions between *A. t. vaseyana* and herbs in early season may be particularly important to post-fire establishment of *A. t. vaseyana*, and are more likely to be mediated by factors such as nutrients than soil water, in contrast to our initial predictions. Studies have investigated competitive relationships between adult sagebrush and herbs, but our study indicates a potential for competitive effects of lush, post-fire herb cover on establishment of young *A. t. vaseyana*, that is worthy of further experimental verification. The composition and abundance of herb communities following fire in sagebrush steppe is sensitive to management actions such as grazing, seeding, and herbicide applications (eg. Seefledt et al. 2002), and how changes in herb communities affect longer-term community development through their effect on sagebrush establishment should received greater consideration.

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