

## CORRELATION OF NEIGHBORHOOD RELATIONSHIPS, CARBON ASSIMILATION, AND WATER STATUS OF SAGEBRUSH SEEDLINGS ESTABLISHING AFTER FIRE

Katherine DiCristina<sup>1</sup> and Matthew Germino<sup>1,2</sup>

**ABSTRACT.**—Interactions of *Artemisia tridentata* ssp. *vaseyana* (mountain big sagebrush) and neighboring herbs may affect community development following fire in sagebrush steppe. Dry mass, photosynthesis, and water relations were measured for seedlings of *A. tridentata* ssp. *vaseyana* occurring at different distances from neighboring herbs in the initial growing seasons following fire, when herbs dominate plant community cover. Seedling mass significantly increased as distance to neighboring herbs increased, although a low  $r^2$  indicated that mass was also affected by other sources of variation. Carbon assimilation ( $A_{net}$ ) was also greater for *A. tridentata* ssp. *vaseyana* seedlings in microsites farther from herbs, except during those sampling dates when  $A_{net}$  and water availability were at low levels. Contrary to our expectations, water status of seedlings was not correlated with their distances to neighboring herbs, and supplemental watering did not affect the slope of the relationship between seedling mass and distance to neighboring herbs. These findings suggest that negative relationships between *A. tridentata* ssp. *vaseyana* seedlings and herbs establishing after fire are not likely due to competition over water and may instead result from interactions over factors not measured here (e.g., nutrients).

*Key words:* sagebrush, seedling establishment, photosynthesis, plant–soil–water relations, fire, *Artemisia tridentata* ssp. *vaseyana*.

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. For example, there is considerable discrepancy in how sagebrush recovers following fire. Wambolt et al. (2001) reported much lower levels and higher variability of sagebrush (*Artemisia tridentata*) cover than expected based on previous studies (Harniss and Murray 1973) for sites burned up to 3 decades prior to their study. Lack of sagebrush recovery following fire is a major concern for sustainability of Greater Sage-Grouse (*Centrocercus urophasianus*) and other wildlife (Connelly et al. 2000). Altered rates of sagebrush reestablishment may result from changes in floristics of herb communities such as with exotic plant invasions (Brooks and Pyke 2001).

Resprouting and rapidly colonizing species (mostly herbs) tend to dominate burned sagebrush steppe in the decade 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, Schuman et al. 1998, 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 and Hassan 1985, Young et al. 1990, Tyler 1996, Chambers 2000), but less is known about factors affecting seedling success. New establishment of *A. tridentata* ssp. *vaseyana* seedlings was detected at sites burned 1–3 years prior to sampling and at sites in later stages of succession (i.e., having mature shrubs), but not at sites at intermediate stages of succession that had denser herb layers (DiCristina et al. in review, Cook and Lewis 1963, Harniss and Murray 1973, Young and Evans 1978). These temporal patterns of *A. tridentata* ssp. *vaseyana* establishment are nearly the opposite of typical changes in herb cover during disturbance-succession cycles (Harniss and Murray 1973) and

<sup>1</sup>Department of Biological Sciences, Idaho State University, Pocatello, ID 83209-8007.

<sup>2</sup>Corresponding author. E-mail: germmatt@isu.edu

indicate a potentially negative effect of herbs on *A. tridentata* ssp. *vaseyana* reestablishment following fire.

The objective of this research was to determine how physiological performance of *A. tridentata* ssp. *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 dry mass accumulation and photosynthetic carbon uptake. Moreover, we predicted that reductions in seedling growth and photosynthesis near herbs would result from water limitations, and that seedlings would therefore express the most negative relationship to neighboring herbs after midsummer, when water availability reaches yearly minimums. Seedling mass 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 previously, when herbs dominated the plant community cover.

#### METHODS

Research was conducted during the snow-free season of 2003 and 2004 at a site burned in September 2002 at the USDA, Agricultural Research Service, U.S. Sheep Experiment Station (USSES; 44°14'44"N, 112°12'47"W; 1650 m ASL), near Dubois, Idaho. The larger burn site was within an area <2 km<sup>2</sup> and consisted of more than 11 burn patches ranging in size up to 100 ha. All patches burned within about 24 hours of each other. Areas we sampled had blackened soil and few woody stems after the fire. The dominant shrub in this community was *Artemisia tridentata* ssp. *vaseyana* Nutt. Less abundant shrubs were *Chrysothamnus viscidiflorus* Nutt., *Tetradymia canescens* DC. and *Purshia tridentata* (Pursh) DC. Perennial bunchgrasses such as *Agropyron dasychium* (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* spp. L., and *Phlox* spp. L. Post-fire ground cover on forty 1-m<sup>2</sup> plots in 2003 was 5% grass, 15% forb, and 35% soil, in addition to some litter and rock (DiCristina et al. in review). Cover for the same plots in 2004 was 26% grass, 29% forb, and 22% soil. Soils were

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 an average of 131 mm accumulating from May through August (Western Regional Climate Center, Desert Research Institute, Reno, NV). Precipitation from January through September was 140 mm in 2003 and 190 mm in 2004, compared to an average of 240 mm for these months over the previous 78 years. There has been light grazing (21.3 sheep days · ha<sup>-1</sup>) on the site from 1968 to 2002.

#### Responses of Dry Mass to Experimental Manipulations

In 2003 we examined seedling responses to manipulations of distance to neighboring herbs and water availability (+ or – supplemental water). The seedlings were those recently emerged (within a week or so) during the 1st growth season following the 2002 fire. We identified 5 replicate plots in the burn areas that were each about 6 m<sup>2</sup> in areal extent and had at least 20 *A. tridentata* ssp. *vaseyana* seedlings. To generate a range of distances of seedlings to herbs in each plot, we removed varying amounts of herbs from *A. tridentata* ssp. *vaseyana* seedlings that had naturally established within 10 cm of herbs. Distances from the base of each *A. tridentata* ssp. *vaseyana* seedling were then measured to the base of the nearest herb in each of 4 quadrants around seedlings (NW, NE, SE, SW), for a total of 4 distances per seedling. The 4 distances were added together and are hereafter called the “sum distance” of each *A. tridentata* ssp. *vaseyana* seedling to surrounding vegetation. Sum distance to nearest neighbor was chosen over other measures of neighborhood spacing, such as distance to nearest neighbor, because it provides representation of >1 neighbor, yet can be measured quickly enough in the field to allow sufficient replication. Moreover, sagebrush seedling measures were correlated more strongly to the sum distance to neighbors than to other calculations of neighborhood spacing. It is likely that herb species can differ in their relationship to sagebrush seedlings, as could be revealed if our data collections were replicated for separate species. We did not have sufficient replication to elucidate seedling relationships to different species of herbs.

We removed surrounding herbs by clipping aboveground structures at least once every 2 weeks from July through October. We also randomly selected half of each replicate plot to receive supplemental watering. Water stored in 113-L cisterns was applied to the root zones of seedlings via drip irrigation lines on electric timers (Model 3020, Melnor USA). Seedlings in plots with supplemental water received about 300 mL of water in early morning and late evening, every day from July through September. We measured volumetric water content (VWC,  $\text{m}^3 \cdot \text{m}^{-3}$ ) 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 data). VWC was measured 4 times throughout the watering treatments: 1 August, 13 August, 3 September, and 3 October.

After September, all experimental seedlings were carefully excavated, rinsed in deionized water, and dried in an oven at 21°C for 24 hours. Seedling mass was then measured to 0.001 g. There were 59 and 33 seedlings among the 5 replicate watered and unwatered plots, respectively. We used regression and 2-way ANOVA to test for differences in seedling mass with different sum distances to neighboring herbs with and without watering. Seedlings selected for this experiment were initially similar in height (<2 cm) and age (emerged within about 1 week of each other), and we assumed their masses at the beginning of the experiment were within 0.01 g and 0.05 g dry mass, based on height measurements and mass:height relationships (K. DiCristina unpublished data).

#### Ecophysiological Responses to Neighboring Herbs

Photosynthesis, water relations, and distance to neighboring herbs were measured in 2004 on seedlings of *Artemisia tridentata* ssp. *vaseyana* that we detected within 3 separate belt transects, each 5 m wide by 25 m long and positioned in one ~100-ha burn patch. Data were collected in 3 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 1st (or possi-

bly 2nd) season of growth and were between 1.5 cm and 10 cm (most were 4–7 cm) in height, with 7–20 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 ( $A_{net}$ ) and  $g_s$  with a portable gas exchange system (LI-6400, LICOR Inc., Lincoln, NE) equipped with an artificial LED light source and CO<sub>2</sub> controller. Relative humidity, temperature, and CO<sub>2</sub> were maintained near ambient values during measurements. Measurements were made during midmorning to midday during the hours of maximal photosynthesis; no daily time effects were evident in our data. Light intensity was 1000  $\mu\text{mol} \cdot \text{m}^{-2}\text{s}^{-1}$  for all measurements. All values were reported as silhouette leaf area according to recommendations of Smith et al. (1991). We quantified silhouette leaf area of each seedling by taking a digital photo of leaf area, with the seedling naturally configured in the measurement chamber, perpendicular to the artificial light source, and next to objects of known size for calibration. Leaves 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.

Predawn xylem pressure potentials (PDXPP) and midday xylem pressure potentials (MDXPP) were measured in the field immediately after excising shoots at the root interface (Scholander-type pressure chamber, Model 1000, PMS Instrument Co., Corvallis, OR). We measured PDXPP between 0530 hours and 0630 hours 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 hours and 1400 hours 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) were used to measure and record VWC at 1 central location in the burn area. VWC was recorded at 4-hour intervals from June through September on 2 sets of 30-cm-long probes inserted horizontally at soil depths of 5 cm and 50 cm. Soil water contents can vary considerably in space, and the TDR data were

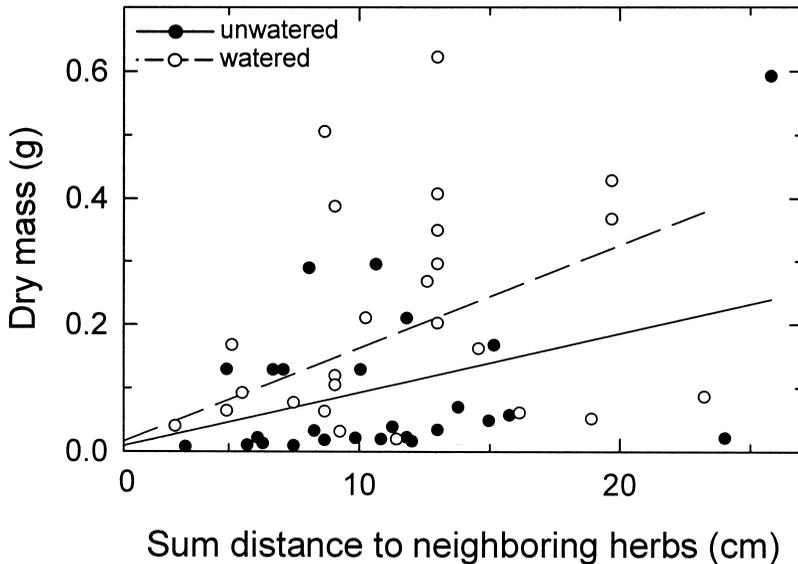


Fig. 1. Correlations of dry mass of *Artemisia tridentata* ssp. *vaseyana* seedlings and their sum distance to neighboring herbs in watered and unwatered plots in 2003. The coefficient of determination ( $r^2$ ) was 0.19 ( $P = 0.02$ ) for unwatered seedlings (open symbols and dashed line) and 0.09 ( $P = 0.10$ ) for watered seedlings (solid symbols and solid line). Dry mass was determined at the end of September, following 3 months of treatment application. Each point is a replicate seedling ( $n = 27$  for watered plots,  $n = 27$  for unwatered plots).

therefore used only to estimate how the timing of our physiological measurements corresponded to general seasonal trends in drying or to summer rains that could potentially wet soils.

We used analysis of covariance (ANCOVA) to determine if month (main effect) affected the relationship between physiological responses of *A. tridentata* ssp. *vaseyana* and distances to neighbors (covariate). PDXPP values were log-transformed for statistical analyses. Statistical differences among periodic measures of VWC (i.e., not the continuous data logger readings) between months were not tested due to low replication, and we report only means and standard deviations ( $\bar{x} \pm s$ ) for monthly values for each soil depth under the watered and control plots. Least-square regression analyses were used to characterize relationships between  $A_{net}$  or  $g_s$  and PDXPP over all sampling dates. Differences between specific means were tested with Tukey-Kramer tests and deemed significant when  $P < 0.05$ . All analyses were conducted using SAS version 8 and JMP version 3.1 (SAS Institute, Inc., Cary, NC).

## RESULTS

Seedling mass was negatively correlated to proximity of neighboring herbs, though distances to herbs explained only a small amount of variation in seedling mass (slope =  $0.001 \text{ g} \cdot \text{cm}^{-1}$ ,  $r^2 = 0.19$ ,  $F_{1, 26} = 5.9$ ,  $P < 0.05$ ; Fig. 1). Supplemental watering led to a more negative but less significant correlation of seedling mass and proximity to herbs (slope =  $0.016 \text{ g} \cdot \text{cm}^{-1}$ ,  $r^2 = 0.09$ ,  $F_{1, 26} = 3.0$ ,  $P = 0.10$ ; Fig. 1,  $P = 0.05$  for differences in slope). Supplemental watering thus did not appear to ameliorate the negative relationship of seedling growth and proximity to herbs, even though watering increased the mean dry mass of seedlings considerably ( $F_{1, 53} = 4.03$ ,  $P < 0.001$ ).

On all dates measured, VWCs in plots with supplemental water were 8%–48% greater than in unwatered plots ( $F_{1, 335} = 92.43$ ,  $P < 0.0001$ ). Mean VWC values of unwatered plots for monthly sampling dates from June 2003 to September 2003 were  $11.0 \pm 1.0$ ,  $9.8 \pm 0.3$ ,  $10.3 \pm 0.6$ , and  $13.9 \pm 0.4$ ; whereas mean VWC values of watered plots were  $17.9 \pm 1.0$ ,  $16.2 \pm 1.4$ ,  $20.0 \pm 1.3$ , and  $15.1 \pm 0.5$ , respectively.

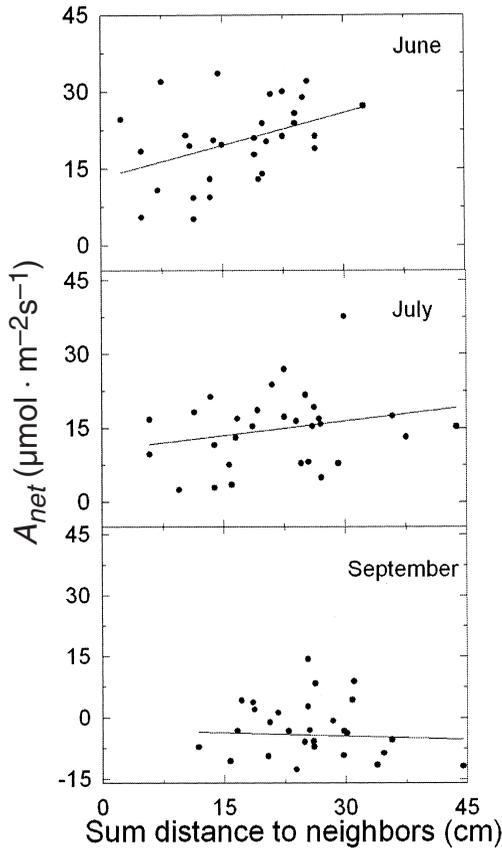


Fig. 2. Relationship of photosynthesis ( $A_{net}$ ) in *Artemisia tridentata* ssp. *vaseyana* seedlings to their sum distance to neighboring herbs in June, July, and September 2004. The correlation is significant only in June ( $r^2 = 0.14$ ,  $P = 0.03$ ). Each point is a replicate seedling ( $n = 28$ – $30$  separate seedlings for each sampling date).

There was  $\sim 13$  mm of precipitation during the month of September, compared to a mean of 6.3 mm for each of the previous 3 months.

In June there was a positive relationship ( $r^2 = 0.14$ ,  $F_{1, 29} = 5.6$ ,  $P = 0.03$ ; Fig. 2) between net photosynthesis ( $A_{net}$ ) and distance from *A. tridentata* ssp. *vaseyana* seedlings to neighboring plants. We did not detect any significant effect of sum distance on  $A_{net}$  in July or September (Fig. 2). The percent of *A. tridentata* ssp. *vaseyana* seedlings having sum distances to neighboring herbs of  $\leq 12$  cm was 33% in June, 10% in July, and 0% in September (Fig. 2). Mean sum distances from *A. tridentata* ssp. *vaseyana* seedlings to surrounding herbs increased  $\sim 35\%$  from June to September ( $F_{2, 89} = 8.7$ ,  $P < 0.001$ ; Fig. 2). No correlations of

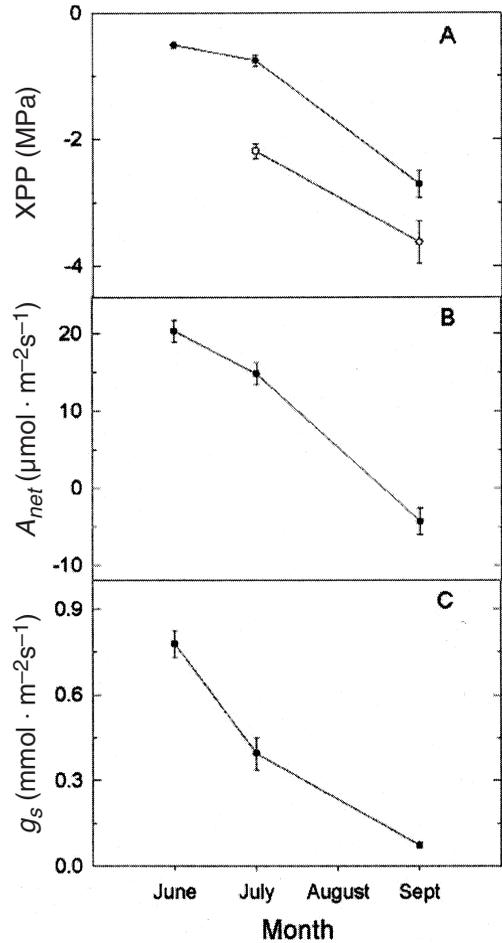


Fig. 3. (A) Xylem pressure potential (XPP), (B) photosynthesis ( $A_{net}$ ), and (C) stomatal conductance ( $g_s$ ) of *Artemisia tridentata* ssp. *vaseyana* in each of 3 months sampled in 2004. In panel A, XPP is shown for measurements made both at predawn (solid circles) and midday (open circles). Bars represent 1  $s_d$  around the mean ( $n = 15$ – $30$ ).

stomatal conductance ( $g_s$ ) or the xylem pressure potential measure of water status (XPP) and sum distances of seedlings to neighboring herbs were detected on any sampling dates (results not presented).

By September,  $A_{net}$  ( $F_{2, 89} = 71.7$ ,  $P < 0.0001$ ),  $g_s$  ( $F_{2, 89} = 60.0$ ,  $P < 0.0001$ ), PDXPP ( $F_{2, 56} = 112.7$ ,  $P < 0.0001$ ), and MDXPP ( $F_{1, 20} = 19.4$ ,  $P < 0.001$ ) were considerably lower than measurements in June (Fig. 3). At 5 cm soil depth, VWC ( $\text{m}^3 \text{H}_2\text{O} \cdot \text{m}^{-3}$ , reported as a percentage) in 2004 was highest in June ( $19.0\% \pm 4.2\%$  [ $s$ ]) but decreased to 15% on

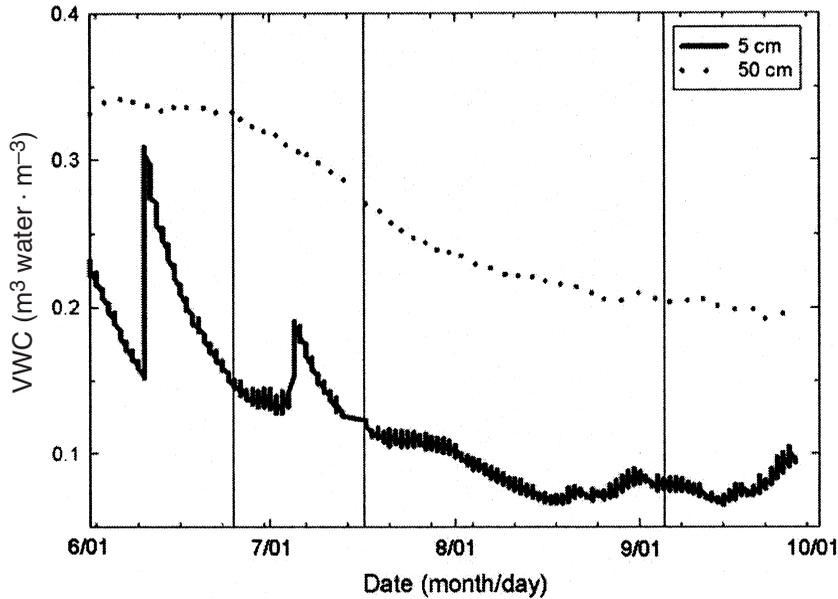


Fig. 4. Volumetric soil water content from 1 June 2004 through 30 September 2004 at 5 cm and 50 cm depth. Data are plotted as recorded in 4-hour intervals. Minor ticks on the x-axis represent 7-day intervals. Vertical lines indicate dates on which seedling physiology was measured. Two sensors were at each sampling depth.

24–25 June, 12% on 17–18 July, and 8% on 4–5 September, which were days when physiology was measured (Fig. 4). VWC was relatively higher at 50 cm depth, but also decreased from June ( $33.4\% \pm 0.6\%$ ) to September ( $20.1\% \pm 0.5\%$ ; Fig. 4).

For all months combined,  $A_{net}$  ( $r^2 = 0.61$ ,  $P < 0.0001$ ) and  $g_s$  ( $r^2 = 0.80$ ,  $P < 0.0001$ ) increased considerably with PDXPP (Fig. 5). Maximum levels of  $A_{net}$  and  $g_s$  occurred when PDXPPs were above about  $-0.5$  MPa (Fig. 5). As PDXPP decreased below about  $-0.5$  MPa in the latter and drier sampling dates,  $A_{net}$  decreased less than the exponential decrease observed in  $g_s$ . These different responses of  $A_{net}$  and  $g_s$  to the seasonal drying trend led to progressive increases in water use efficiency ( $A \cdot g_s^{-1}$ ).

#### DISCUSSION

Seedlings of *A. tridentata* ssp. *vaseyana* had less dry mass at the end of their 1st growth season in microsites closest to neighboring herbs. Carbon assimilation ( $A_{net}$ ) was also lower for seedlings nearer to herbs, but in June only and not in subsequent drier months. Relationships of *A. tridentata* ssp. *vaseyana* seedlings and neighboring herbs may result largely from

their interactions in early summer, before the onset of seasonal water limitations to growth and when a significant amount of yearly carbon gain likely occurs for seedlings (Fig. 2). Decreases in seedling sensitivity to herbs after June could partly reflect progressive increases in spacing between them in months following June. We did not determine the precise causes of plant spacing (e.g., with repeated observations), and we speculate that increases in plant spacing during summer could have resulted from mortality of *A. tridentata* ssp. *vaseyana* seedlings near herbs or from senescence of herbs. Regardless of their causes, increases in neighborhood spacing could not completely explain decreases in sensitivity of seedling photosynthesis to proximity of neighboring herbs at mid- or late-summer, because there was still substantial overlap of sum distance values among all sampling dates (i.e., values  $>15$  cm; Fig. 2). Thus, seedling responses to proximity of neighboring herbs likely reflect limitations to growth processes in microsites adjacent to herbs. Photosynthetic carbohydrate production is one of the primary determinants of growth rates, but we need to exercise caution when inferring how changes in photosynthesis might affect growth near herbs, because

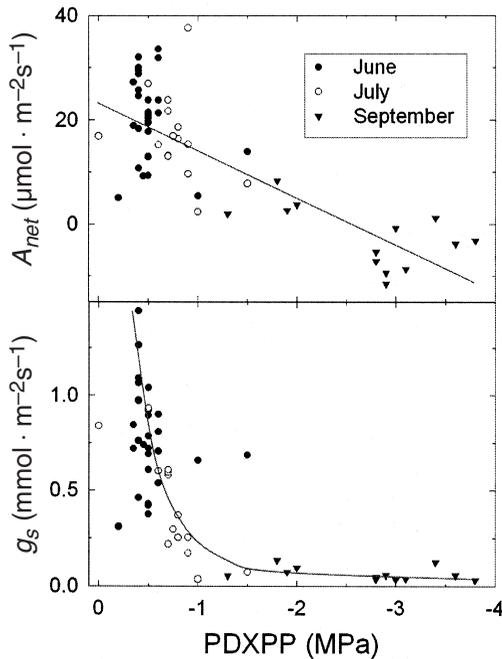


Fig. 5. Relationship of predawn xylem pressure potential (PDXPP) to photosynthesis ( $A_{net}$ , top), and stomatal conductance ( $g_s$ , bottom) of *Artemisia tridentata* ssp. *vaseyana* seedlings in 2004. Each point is a replicate seedling. The correlation of  $A_{net}$  with PDXPP is significant ( $r^2 = 0.61$ ,  $P < 0.0001$ ), as is  $g_s$  with PDXPP ( $r^2 = 0.80$ ,  $P < 0.0001$ ).

dry mass and photosynthesis were measured on different seedlings and in different years.

Decreases in photosynthesis (when normalized for area and time) result from either decreases in diffusive supply of  $\text{CO}_2$  through stomata into leaves or from reductions in the physiological demand for  $\text{CO}_2$  in carboxylation reactions (i.e., biochemical capacity to use  $\text{CO}_2$  inside leaves for carbohydrate production). Plants commonly close stomata (reduce  $g_s$ ) to conserve water at the expense of a less diffusive supply of  $\text{CO}_2$  for carboxylation in photosynthesis (Smith et al. 1997). Reductions in  $g_s$  can decrease  $A_{net}$  if  $\text{CO}_2$  within leaves becomes scarce. If lower  $A_{net}$  in seedlings near herbs were due to competition for water, we would have expected to observe lower water status and corresponding reductions in  $g_s$  compared to seedlings with greater distances to herbs. Plant water status and  $g_s$  were not correlated with proximity of neighboring herbs on any sampling date and were therefore un-

likely explanations for lower  $A_{net}$  in seedlings nearest to herbs. Although water availability strongly affected growth and photosynthesis (Figs. 1, 3, 5), lower  $A_{net}$  and growth of *A. tridentata* ssp. *vaseyana* in microsites closest to neighboring herbs were therefore not likely to have resulted from preemption of soil water for seedlings by neighboring herbs. Additional support for excluding the direct role of water in seedling responses to herbs comes from experimental water additions; if herbs preempted water for seedlings as we hypothesized, supplemental watering would have alleviated negative relationships of seedling mass and proximity to herbs. We observed the opposite outcome.

Alternative explanations for reduced  $A_{net}$  in *A. tridentata* ssp. *vaseyana* seedlings near herbs could include factors that affect photosynthetic demand for  $\text{CO}_2$ , such as less sunlight or soil nutrient availability in microsites closer to herbs. Whereas sunlight provides the energy for reducing  $\text{CO}_2$  into carbohydrates, enzymes used in carboxylation require a substantial proportion of plant nitrogen (Lambers et al. 1998). Seedlings we studied were only rarely overtopped by neighboring herbs and often did not appear to be located closely enough to herbs to be shaded by them. Moreover, DiCristina et al. (in review) found that distances of *A. tridentata* ssp. *vaseyana* seedlings to neighboring herbs in sites burned 1–8 years prior to sampling were not affected by whether seedlings were located on the north or south sides of herbs; this outcome did not indicate shading effects.

High nutrient levels commonly occur after fires and could diminish the role of nutrients in plant 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 the years of our study. Several studies indicated greater nutrient uptake by plants during moisture pulses in semiarid communities (Cui and Caldwell 1997, Ivans et al. 2003). Elevated rates of nutrient uptake and corresponding depletion of soil nutrients near herbs during periods of relatively high growth rate (i.e., June) would be consistent with the sensitivity of seedlings to herbs in June but not in later summer. Photosynthesis in other subspecies of sagebrush (*A. tridentata*

ssp. *wyomingensis*) was highly responsive to manipulations of nitrogen availability (Doescher et al. 1990). Our study was not designed to experimentally isolate the importance of nutrients on  $A_{net}$  of seedlings, but we speculate that nutrient limitations could be an important factor contributing to lower  $A_{net}$  and growth of *A. tridentata* ssp. *vaseyana* seedlings located near herbs.

Although water did not appear to mediate seedling responses to neighboring herbs, water availability did appear to positively modulate the sensitivity of seedlings 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 periods when resource scarcity leads to reductions in background growth levels (Goldberg and Novoplansky 1997, see also Billbrough and Caldwell 1997). The sensitivity of seedlings to neighboring herbs (Fig. 2) corresponded with strong reductions in seedling carbon uptake as soil water deficits increased during summer (Figs. 3, 5). Soil water availability is typically greatest in sagebrush steppe during spring and early summer, following snowmelt and spring rain (Fig. 4). Seedling responses to this seasonal drying were reflected in decreases in  $g_s$  to minimum values in seedlings as (1) pre-dawn water potentials of seedlings decreased to  $\leq -1.5$  MPa and (2) volume water content decreased below 10%–12% and  $-1.5$  MPa in soils around our TDR probes (Figs. 3–5; MPa estimate based on water retention curves; Germino and Seefeldt unpublished data). Water potentials near  $-1.5$  MPa are typical thresholds for water uptake in many plant species (Lambers et al. 1998; though desert plants can have lower thresholds). Significant water consumption ceased at 10%–12% VWC in a related sagebrush subspecies adapted to drier conditions than *A. tridentata* ssp. *vaseyana*, in a site near ours with similar soil textures (*A. tridentata* ssp. *wyomingensis*; Anderson et al. 1987, Smith et al. 1997). The possible effect of seasonal onset of drought-induced growth limitations on the progressive decrease in sensitivity of *A. tridentata* ssp. *vaseyana* seedlings to herbs (Fig. 2) is further supported by the less negative responses of seedling mass to drier soils in unwatered compared to water-supplemented treatments (Fig. 1). Supplemen-

tal watering intensified the negative relationship of seedling mass and proximity to herbs. Our finding of greater negative responses of *A. tridentata* ssp. *vaseyana* seedlings to neighboring herbs when soil resources and growth processes were at seasonal maximums matches the prediction that the intensity of plant interactions in arid environments is greatest when growth resources are most abundant.

#### Summary and Implications

Dry mass gain and early season photosynthesis in *A. tridentata* ssp. *vaseyana* establishing following fire was negatively correlated with proximity to neighboring herbs. Nearly inverse relationships of *A. tridentata* ssp. *vaseyana* establishment and herb cover during disturbance-succession cycles, and much larger distances of *A. tridentata* ssp. *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. tridentata* ssp. *vaseyana* to herbs. Contrary to our predictions, negative responses of seedlings to neighboring herbs did not appear attributable to interactions over water availability, but more likely resulted from interactions over factors such as nutrients. Although water did not have a direct role in mediating sagebrush seedling relationships with neighboring herbs, water availability indirectly affected the relationships by influencing the intensity of seedling responses to herbs.

The herbaceous flora of sagebrush steppe is changing rapidly due to exotic plant invasions, selective use of species in plantings, and management activities. Determining how herbaceous species differ in their effects on young sagebrush seedlings is an important research need, particularly in light of changes in precipitation and other aspects of environmental change.

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