Seasonal drying modulates effects of neighboring herbs on carbon gain of *Artemisia tridentata* ssp. *vaseyana* seedlings establishing after fire

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Abstract

Factors affecting establishment of *Artemisia tridentata* ssp. *vaseyana* (mountain big sagebrush) seedlings are important to succession in sagebrush steppe following fire. Mechanisms underlying interactions between seedlings of *A. t. vaseyana* and neighboring herbs were investigated following a prescribed burn in southeastern Idaho, USA. Photosynthesis and water status were measured for 1-2 year old seedlings of *A. t. vaseyana* in response to natural variation in distances to nearest herbs and seasonal soil drying. Carbon assimilation (A_{net}) was nearly twice as great for seedlings that had the greatest distances from herbs, compared to seedlings located adjacent to neighboring herbs, in June. However, distance to neighboring plants had no effects on seedlings of *A. t. vaseyana* later in the growing season, when A_{net}, stomatal conductance (g_s) and xylem pressure potentials (XPP) decreased markedly in response to seasonal soil drying. These data suggest that competitive displacement of *A. t. vaseyana* seedlings by neighboring herbs following fire may occur mainly during a short period early in the growing season, before growth processes are slowed due to water limitation. Plant interactions during the short pulse of water availability in early season may have a critical effect on establishment of *A. t. vaseyana* and on subsequent patterns of post-fire succession.

Keywords: Competition; Fire; Photosynthesis; Resource pulse; Sagebrush

1. Introduction

Fire is used to manipulate the successional status of sagebrush steppe for enhancement of forage, fuel load for wildfires, and wildlife habitat. However, compositions of sagebrush steppe communities following fire are not easily predicted and are often undesirable. For example, invasions of non-native plants are common after burns (Eliason and Allen 1997; Miller and Rose 1999), and can contribute to altered successional cycles in sagebrush steppe (Young and Evans 1978). Many studies have documented changes in plant species composition after fire (Harniss and Murray 1973; Wambolt et al. 2001; West and Hassan 1985; Young and Evans 1978), however, fewer have addressed how interactions, such as competition, might affect species change in sagebrush steppe following fire.

The role of competition in plant communities of unproductive environments is equivocal (Wiens 1977). Sagebrush steppe communities have relatively low productivity, and resource availability tends to occur in pulses, such as soil moisture recharge in the spring. In the cold deserts of the Great Basin, periods of relatively high productivity in spring and early summer results from snowmelt and spring rain, and are followed by reduced productivity as soils dry (Smith et al. 1997). Competition in low productivity environments may be most pronounced during resource pulses (Goldberg and Novoplansky 1997), and seedlings of *Artemisia tridentata* appear responsive to pulses of water availability (Gillespie and Loik 2004).

Establishment dates for *Artemisia tridentata* ssp. *vaseyana* (mountain big sagebrush) in a previous study occurred predominantly in the first growing season following fire, when herbaceous canopies are still likely to be recovering to pre-fire levels (DiCristina et al., in review). In subsequent growing seasons, distances of *A. t. vaseyana* seedlings to herbs decreased as herb cover increased in time, reflecting less microsite avoidance of herbs than in the first year after fire and putative competitive displacement of seedlings. Furthermore, root:shoot biomass of *A. t. vaseyana* seedlings decreased with proximity to neighboring herbs with, but not without water additions (DiCristina et al., in review), indicating that water might play a role in interactions between seedlings and herbs.

The objective of this research was to determine the mechanisms of competitive displacement of *A. t. vaseyana* seedlings by neighboring herbs in the second growing season following fire. We observed photosynthesis and water relations of natural seedlings of *A. t. vaseyana* in relation to distance to neighboring herbs, and during early-wet and late-dry periods of the growing season. We hypothesized that carbon assimilation of *A. t. vaseyana* would decrease with proximity to neighboring herbs and that these interactions would be modulated by water availability. A better understanding of mechanisms that govern establishment of *A. t. vaseyana* will allow more informed predictions of successional outcomes after fire.

2. Methods

2.1 Site and species

Research was conducted during the snow-free season of 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* 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 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 in 2004, two years after the fire, consisted of approximately 26% grass, 29% forbs, 11% shrub, 22% soil, 10% litter and 2% rock as assessed on 40- 1 m^2 plots. 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). There were about 13 cm of precipitation from June through September 2004. There has been light grazing (21.3 sheep days/ha) on the site from 1968-2002.

2.2 Experimental design

We sampled 90 seedlings of *Artemisia tridentata* ssp. *vaseyana* that were randomly located within three, separate, belt transects that were each 5 m wide by 25 m long. We collected samples during the growing season of 2004 on three separate sampling periods: 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 sampling. Seedlings were all 1-2 years old, between 1.5 and 10 cm in height, and consisted of between 7 and 20 leaves per plant.

We measured distances from *A. t. vaseyana* seedlings to neighboring herbs, rates of carbon assimilation (A_{net}), stomatal conductance (g_s), pre-dawn and mid-day xylem pressure potentials (PDXPP and MDXPP, respectively) on each sampling date during the study. Sampling dates captured the progression of summer drought to allow comparison of responses of *A. t. vaseyana* seedlings to neighboring species at different levels of water stress.

2.3 Distances to neighboring vegetation

We measured distances between each *A. t. vaseyana* seedling and neighboring herbs on all sampling dates. Distances from the base of each *A. t. vaseyana* seedling to the base of the nearest herb and in each of four cardinal directions (NW, NE, SE, SW) were measured, for a total of four distances per seedling. The four measured distances were added together and considered the ‘sum distance’ of each *A. t. vaseyana* seedling to surrounding vegetation.

2.4 Physiological responses

We measured A_{net} and g_s, between 1300 and 1600 with a portable gas exchange system (LI-6400, LICOR Inc., Lincoln, Nebraska, USA) equipped with an artificial LED light sources and CO_2 controller. Relative humidity, temperature, and CO_2 were maintained near ambient values during measurements. 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. Photos of leaf areas were traced onto paper and scanned into a computer-imaging program (Image J, version 1.23p) that calculated leaf area.

2.5 Water status and soil moisture

Seedling PDXPP and MDXPP were measured in the field immediately after excising them, 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.

We used time domain reflectometer (TDR) probes and data loggers (models CS616 and CR10, respectively, Campbell Scientific, Logan UT, USA) to measure and record volumetric water content (VWC) of soil at 4-hour intervals from June through September. One set of probes was inserted horizontally at 5 cm and at 50 cm soil depths (n=1) in a burned area near the observational plots. Replication was low, but our objective was only to provide some indication of temporal change in soil water content. Bulk density and soil texture were similar at the TDR sampling site and vegetation plots (Germino, unpublished).

2.6 Statistical analysis

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). Where there was no significant interaction, we used a reduced ANCOVA, by removing the interaction term. Reduced ANCOVAs were used to evaluate responses of A_{net}, g_s, PDXPP and MDXPP to interactions of month and distance to neighboring plants. We normalized PDXPP by log transformation in all analyses where it was used. We calculated means (μ) ±1 standard deviation (σ) for soil VWC for each month and at each soil depth (5 cm and 50 cm). Statistical differences of VWC between months were not tested due to low replication. Least-square regressions were used to analyze relationships between A_{net} or g_s and PDXPP, after data from all months were pooled together. We combined data from all sampling dates in order to isolate the effect of water stress separate from month. 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).

3. Results

3.1 Physiological responses to proximity of neighboring herbs

In June, there was a positive relationship ($r^2 = 0.14$, $F_{29,1} = 5.6$, $P = 0.03$, Fig. 1) between net photosynthesis (A_{net}) and distance from *A. t. vaseyana* seedlings to neighboring plants. We did not detect any significant effect of sum distance on A_{net} in July or September (Fig. 1). The relative abundance of *A. t. vaseyana* seedlings that were within sum distances of 12 cm from neighboring herbs was 33% in June, compared to 10% and 0% of seedlings in July and September, respectively (Fig. 1). Mean sum distances from *A. t. vasayana* seedlings to surrounding herbs increased about 35% from June to September ($F_{89,2} = 8.7$, $P < 0.001$, Fig. 1), however distances to neighboring vegetation in July were not different from those in either June or September. By September, A_{net} ($F_{89,2} = 71.7$, $P < 0.0001$), stomatal conductance (g_s) ($F_{89,2} = 60.0$, $P < 0.0001$), pre-dawn xylem pressure potential (PDXPP) ($F_{56,2} = 112.7$, $P < 0.0001$), and mid-day xylem pressure potential (MDXPP) ($F_{20,1} = 19.4$, $P < 0.001$) were relatively low compared to measurements in June (Fig. 2). Distances to neighboring vegetation did not significantly affect g_s, or XPP of seedlings on any sampling dates, and is therefore not presented.

3.2 Effects of soil drying over the growing season

At 5 cm soil depth, volumetric water content (VWC; m^3 water/m^3, reported as a percentage) was highest in June (19.0% ± 4.2%, $\mu \pm \sigma$) of all months sampled and decreased until reaching seasonal minimum in August (7.8% ± 1.0%, Fig. 3). At 50 cm depth, VWC was highest in June (33.4% ± 0.6%) and decreased consecutively in July (27.6% ± 2.8%), August (21.8% ± 0.9%), and September (20.1% ± 0.5%, Fig. 3). VWC at 5 cm, on the days in which physiology was measured, was 15% on 24-25 June, 12% on 17-18 July, and 8% on 4-5 September. For all months combined, A_{net} ($r^2 = 0.61$, $P < 0.0001$) increased and g_s increased ($r^2 = 0.50$, $P < 0.0001$) with decreasing water stress (Fig. 4). Maximum levels of A_{net} and g_s occurred when PDXPPs were between –0.5 MPa and –1.0 MPa, and additional water availability did not appear to increase A_{net} and g_s any further (Fig. 4).

4. Discussion

We detected negative effects of nearby herbs on carbon assimilation in seedlings of *A. t. vasayana* in June, but not in July or September, when water stress appeared to cause major reductions in photosynthesis (Figs. 1 & 4). These results are consistent with the hypothesis of Goldberg and Novoplansky (1997), that competition in sites of low annual productivity is most evident during brief periods of increased resource availability, rather than when resources are relatively scarce. Increased availability of soil resources is most apparent in sagebrush steppe as a spring pulse, generated by snowmelt and rains that occur in early summer. The spring pulse of soil resources was most likely still affecting *A. t. vasayana* seedlings in June when stomatal conductance and photosynthesis were greater compared to July and September (Fig. 2). Comparisons of VWCs reported here with water retention curves for soils around our TDR probes (Germino, unpublished) indicate that VWCs likely fell below the minimum level for extraction by most plants after the first week of August, and only at 5 cm soil depths. Water potentials for these soils decreased to –1.5 MPa at 10-12% VWC, and –1.5 MPa is a typical threshold for water uptake in many plant species (i.e. water is typically unavailable to plants when soils become drier than –1.5 MPa.). Furthermore, Bilbrough and Caldwell (1997) found that *A. t. vasayana* had greater vegetative growth in response to experimentally applied pulses in early May and June, when vegetative growth was at its peak of the season, than in late June. These findings indicated that the magnitude of plant responses to resource pulse depends on concurrent high growth rates and background resource availability. Rapid growth early compared to late in the growing season is common among many Great Basin plants, which could lead to greater competition for soil resources during this period (Bilbrough and Caldwell 1997).

Growth rates are affected by rates of carbon uptake in photosynthesis. Increases in photosynthetic rates per unit area and time result from either increases in diffusive supply of CO_2 through stomata, or increases in physiological/biochemical demand for CO_2 in carboxylation reactions. Stomatal conductance and xylem pressure potential did not appear responsive to proximity to neighboring herbs, which we would have expected to observe if decreased photosynthesis of seedlings near herbs was due to limited water uptake resulting from competition. Specifically, there was no evidence that seedlings closed stomata to prevent further water loss in response to water stress near herbs, and thus, no evidence that diffusion of CO_2 into leaves decreased rates of photosynthesis. These results do not support our initial expectation that the competitive displacement of *A. t. vasayana* by herbs (DiCristina et al., in review) was attributable to preemption of water by neighboring herbs. An alternative explanation for lower photosynthesis in microsites closer to herbs could be that biochemical demands for CO_2 decreased, rather than experiencing greater hydraulic constraints on diffusive supply of CO_2. Nitrogen (N) is an important constituent of chloroplasts that is necessary for carbon assimilation, and can be an important limiting resource in many arid environments (Dobrowolski et al. 1990, Gutierrez and Whitford 1987). Although we made no measurements of N, competition for nutrients appears to be a likely way that herbs affected photosynthesis of seedlings. N levels returned to pre-fire levels after about 10 months following fire in sagebrush (Hobbs and Schimel 1984), leading us to speculate that N availability was not unusually high during our study. N availability and uptake increase with moisture pulses

(Cui and Caldwell 1997; Dobrowolski et al. 1990; Ivans et al. 2003). Therefore, a hypothetical explanation for our findings is that competition between *A. t. vasayana* seedlings and neighbors is primarily for N, and as soils dry, herbs are less likely to preempt N from root zones of neighboring *A. t. vasayana* seedlings. Thus, decreases in early-season photosynthesis without corresponding decreases in stomatal conductance or water relations, in microsites near, compared to away from herbs, may be attributable to effects of water levels on plant-soil nutrient relations. However, since we did not address N uptake in this study, we can only speculate on the role of N in competition. Furthermore, greater distances between *A. t. vasayana* seedlings and herbs in July and especially September compared to June (Fig. 1) may reflect selective survival of seedlings away from herbs, and seedlings surviving to September might be distant enough from herbs to escape competitive pressures that lead to reductions in carbon gain.

Negative responses of photosynthesis in *A. t. vasayana* seedlings to neighboring herbs following fire indicate that seedling growth should be greater in microsites with little or no herbaceous cover. Herbaceous cover is usually reduced in the first growing season following fire compared to pre-fire levels, but surpasses pre-fire levels in the second and subsequent growing seasons for up to about a decade (DiCristina et al., in review). Therefore, establishment of *A. t. vasayana* requires both open microsites that become available when herb cover is reduced, and a pulse of soil resources that occur with relatively large inputs of soil water. The combination of these conditions appears primarily in years following fire, and primarily early in the growing season, resulting in a narrow temporal window of establishment for *A. t. vasayana*.

Soil water appeared to modulate, rather than mediate, competitive interactions between *A. t. vasayana* seedlings and neighboring herbs. Significant growth of *A. t. vasayana* and apparent competitive pressure from neighboring herbs occurred during the early-season pulse of water availability. In the second and subsequent years following fire, when herb canopies tend to be greater than in the first year after fire or the most advanced stages of succession, competitive displacement from increasing cover of herbs may limit the ability of *A. t. vasayana* to establish. Thus, management activities that affect herb communities following fire, such as selective grazing in spring or fall (Seefeldt and McCoy 2003) or herbicide use, are also likely to affect reestablishment of *A. t. vasayana*.

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Figure captions

Figure 1. Relationship of the effect of sum distance from *A. tridentata* seedlings to surrounding vegetation and photosynthesis of *A. tridentata* seedlings for June, July, and September.

Figure 2. 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. tridentata* in each of 3 months sampled over the growing season of 2004.

Figure 3. Volumetric soil water content from 1 June through 30 September 2004 at 5 and 50 cm depths in soil. Minor ticks on X-axis represent 7-day intervals. Vertical lines indicate sampling dates.

Figure 4. Relationship of pre-dawn xylem pressure potential (PDXPP) to photosynthesis (top), and stomatal conductance (bottom) of *A. t. vaseyana* seedlings.

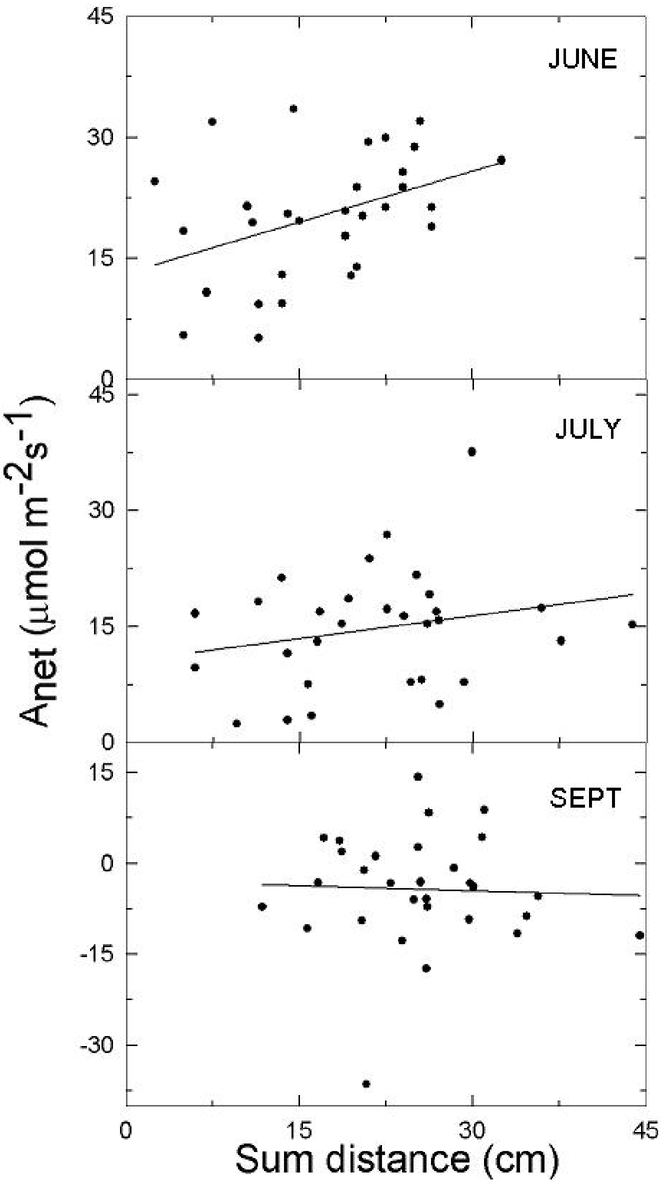
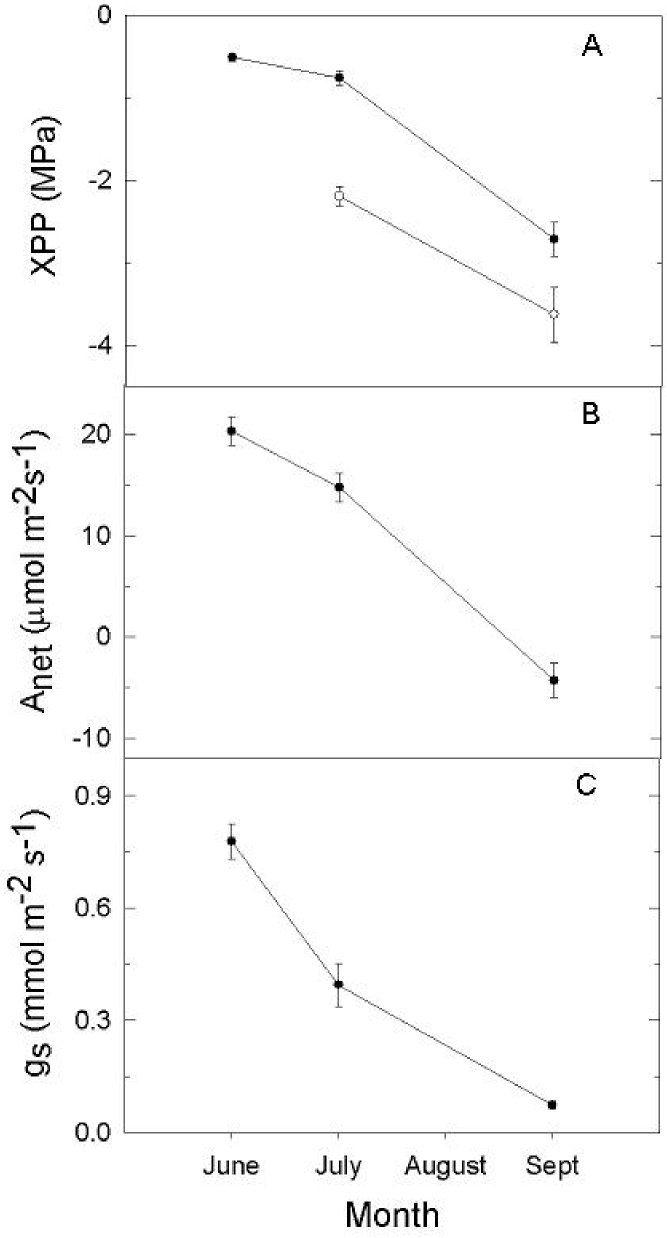

JUNE
JULY
SEPT
Anet (μmol m-2s-1)
Sum distance (cm)
45
30
15
0
-15
-30
0
15
30
45

Figure 1



A
B
C
XPP (MPa)
0
-2
-4
Anet (μmol m-2s-1)
20
10
0
-10
gs (mmol m-2 s-1)
0.9
0.6
0.3
0.0
June
July
August
Sept
Month

Figure 2

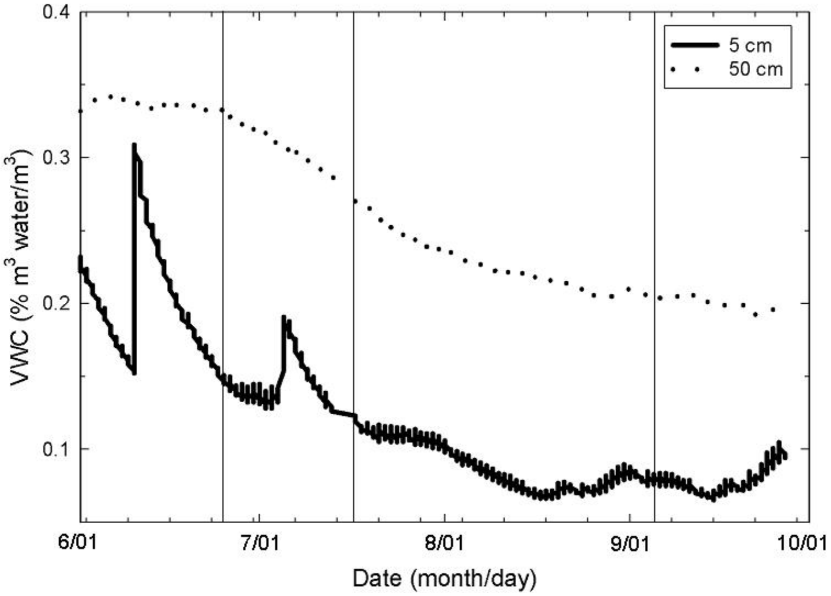

0.4
0.3
0.2
0.1
VWC (% m^3 water/m^3)
5 cm
50 cm
6/01
7/01
8/01
9/01
10/01
Date (month/day)

Figure 3

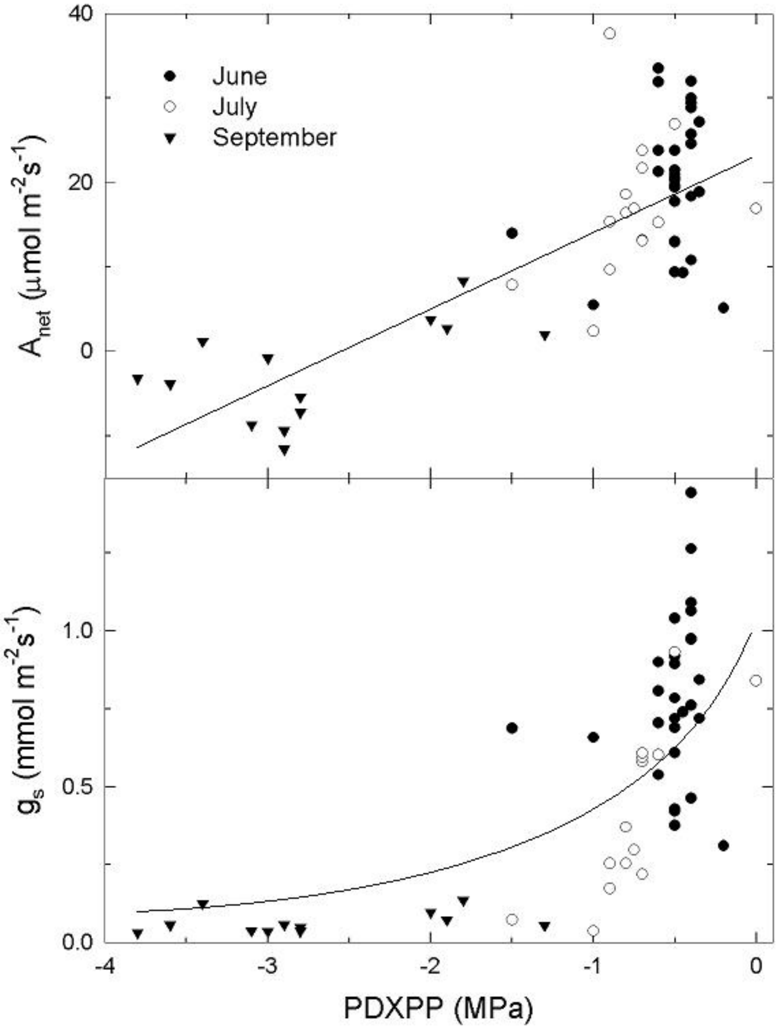

40
20
0
A_{net} (µmol m^{-2}s^{-1})
● June
○ July
▼ September
1.0
0.5
0.0
g_s (mmol m^{-2}s^{-1})
-4
-3
-2
-1
0
PDXPP (MPa)

Figure 4