Contribution of Deep Soil Water to Invasion of Sagebrush Steppe by *Euphorbia esula* Following Fire

Matthew J Germino, Department of Biological Sciences, Idaho State University, Pocatello ID 83209-8007, germmatt@isu.edu, 208-282-3285

Jonathan L Horton, Biology Department, University of North Carolina, Asheville NC 27109

Steven S Seefeldt, Research Agronomist, USDA-ARS, SubArctic Agricultural Research Unit, University of Alaska Fairbanks, Fairbanks, Alaska 99775

Judson P Hill, Biology Department, Idaho State University, Pocatello ID 83209

ABSTRACT

A long-standing hypothesis for the invasive success of exotic species following disturbance is that disturbances promote invasions by increasing resource availability to the selective advantage of invasive species. Consistent with this hypothesis, efficiency of resource use is predicted to be less in invasive compared to native species. Furthermore, differences in soil resource use could lead to greater depletion of soil resources beneath invasive species, which, in turn, could be reflected in lower physiological performance of native species occurring in proximity to invaders. We examined relationships of water potentials in soils and plants, and photosynthetic gas exchange properties of *Euphorbia esula*, a forb from Eurasia, sagebrush (*Artemisia tridentata ssp. vaseyana*), and dominant native forbs (*Eriogonum heracleoides*) and grasses (*Pseudoregneria spicata*), in sagebrush steppe of Western N. America that had or had not been burned and/or invaded. Depth of water uptake was determined for all plants by comparing stable isotopes of water in stem and soils. Following snowmelt in early spring, soils were near field capacity to several m depth in all sites. As the growth season proceeded into dry summer conditions, soil water potentials decreased more in unburned compared to burned soils, particularly at depths below the main rooting zone of grasses (shallower than about 50 cm). Within burned areas, depletion of soil water at depths between about 75 and 125 cm was greater where *E. esula* occurred compared to where only native herbs occurred. Isotopic analyses revealed that *E. esula* and *A. tridentata* likely acquired water from similar depths in soils, which were consistently deeper than for native herbs and especially grasses. Predawn water potentials were similarly high (>-0.5 MPa) among species in treatments in early season, but became low in native herbs in later summer (<-1.5 MPa) in burned and invaded plots (<-2.5 MPa). In contrast, *A. tridentata* and especially *E. esula* maintained water potentials above -1.5 MPa in late summer. However, *E. esula* did not have any greater photosynthesis or photosynthetic water use efficiency than the other species. These correlations are consistent with the hypothesis that *E. esula* relies on access to relatively abundant sources of soil water below the typical rooting zone of grasses to sustain photosynthesis in this semiarid site. Fire appears to disrupt partitioning of soil water in the native community by selectively disfavoring sagebrush, thereby making deeper water more available in deep soils and providing a key resource for photosynthesis in *E. esula*.

KEYWORDS: Fire, soil water, sagebrush, stable isotopes, Euphorbia esula, photosynthesis.

INTRODUCTION

Ecological disturbance is a commonly cited factor contributing to invasion of plant communities by non-indigenous species. By disrupting resource partitioning among native plants, disturbances are thought to increase resources in ways that selectively favor exotic invaders. However, few studies have provided direct evidence that exotic plants selectively benefit from resources made available by disturbance. Such evidence would point to the potential importance of vacant niches to success of exotic plants, compared to other eminent hypotheses for success of invasive species.

Sagebrush steppe rangelands in the Great Basin cold desert of western North America are unusually vulnerable to invasion by exotic herbaceous species. Factors affecting the success of exotic annual grasses are well known in these ecosystems (eg. Chambers et al. 2007), but less is known about factors enhancing the success of the large number of species of exotic forbs that can be even more noxious problems in rangeland ecosystems (Pyke 1999). Many species in this suite of exotic forbs are tap-rooted and more persistent during water-limited periods of late summer than are native herbs, indicating a possible role for soil water to their success. Species in this suite of forbs, such as leafy spurge (*Euphorbia esula*) and thistles, knapweeds, tumbleweeds (Whitson 2002), have persisted for decades following colonizing phases of succession after disturbance (e.g. Selleck et al. 1962, Kulmatistki 2006). A greater understanding of factors promoting persistence of exotic forbs should lead to control strategies that are more effective than current emphases on eradication with chemicals or introduced insects.

In sagebrush steppe, soil water available for plant growth results mainly from winter snow and early spring rain, when soil throughout the rooting profile of plant communities reaches water-holding capacity (Smith et al. 1997). By the mid to late growth season, partitioning of soil water uptake among plant species contributes to nearly complete utilization of extractable water in soils, at least in undisturbed, native sagebrush steppe communities (Anderson et al. 1987). Following disturbances such as fire, sites in sagebrush steppe tend to be dominated for decades by herbaceous cover, while sagebrush slowly reestablishes (Harniss and Murray 1973). The paucity of shrubs or other deep-rooted species led to less depletion of water from soils deeper than about 50 cm on a recently burned site (Link et al. 1992).

The objective of our study was to determine how changes in soil water resulting from fire might affect the water relations and corresponding photosynthesis of *E. esula*. We hypothesized that 1) water availability in soils would be greater in burned compared to unburned sites, particularly in deeper soils but except where *E. esula* had become abundant, 2) *E. esula* in burned areas would utilize soil water from similar depths as the dominant species of unburned areas (*Artemisia tridentata*), 3) *E. esula* and *A. tridentata* would utilize water from deeper and wetter soils than native herbs after midsummer, and would correspondingly have greater water status at predawn, 4) that *E. esula* would not exhibit greater photosynthesis or photosynthetic water use efficiency during seasonal drought compared to native species, which would otherwise indicate more efficient use of soil water as a mechanism contributing to its success in these desert sites, and 5) that *E. esula* would exhibit lower water potentials and greater water-related limitations to photosynthesis in the rare circumstances in which it is found adjacent to sagebrush.

METHODS

Water potentials and isotopic compositions of plants and soil were measured to determine water availability, water status, and depth of plant water uptake. Photosynthetic CO_2 and H_2O exchange of leaves was also measured as an indicator of water use that could affect plant water balance, and carbon gain that could indicate possible advantages that might result from differences in water relations. Sampling occurred twice, during June 25-30 and August 10-14. All samples for isotopic determination of depth of water uptake were collected on the same day, and all plant samples were collected within about 1 hr during late afternoon.

The experimental design consisted of a 2 x 2 factorial arrangement of twelve plots (n=3 per treatment) that differed in two factors: disturbance history (burned in 1999 or unburned in previous 70 years) and invasion by *E. esula* (invaded or not invaded). Soil water and depth of water uptake could not be measured on the three plots that were unburned and un-invaded. Plots were each about 1 m in diameter, and were separated by 20-100 m. Twelve plots were established for each of the two sampling efforts, to avoid resampling plots in August that had been disturbed during the previous sampling.

Site and species descriptions

All data were collected at the US Sheep Experimental Station (USSES; 44°14’44” N Latitude, 112°12’47” W. Longitude; 1650 m a.s.l.) near Dubois ID, USA, where most precipitation comes as winter snow and spring rain, and soils progressively dry during summer months. The dominant shrub in this community is mountain big sagebrush, *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 *Pseudoregneria spicata* (Pursh) A. Löve, *Agropyron dastychium* (Hook.) Scribn., *Festuca idahoensis* Elmer and *Poa sandbergii* Vasey were common, as were perennial forbs such as *Eriogonum heracleoides* Nutt., *Cordylanthus ramosus* Nutt., *Achillea millefolium* L., *Erigeron corymbosus* Nutt., and *Lupinus* species. 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). Annual precipitation during our study period of January through September was 190 mm, respectively, compared to 240 mm for mean precipitation over these months over the previous 80 years. There has been grazing (21.3 sheep days/ha) on the site from 1968-2002.

Water uptake, water status, and leaf physiology were measured for the exotic forb leafy spurge (*Euphorbia esula*) and the following native species: bluebunch wheatgrass (*P. spicata*), Wyeth’s or parsley-flowered buckwheat (a perennial forb, *E. heracleoides*), and sagebrush (*A t. vaseyana*). These species were the dominant cover of their respective functional groups in each of the plots, as assessed by estimating plant cover to the nearest 5% (1% below 5%) in four replicate sampling frames (0.5 m^2) positioned adjacent to the central soil cover in each replicate plot (Table 1). *Euphorbia esula* was scarce (<~3% of cover) in plots that were unburned and thus had abundant sagebrush, but was 2-fold more abundant than grasses and 5-fold more abundant than native forbs in the portions of burned areas it had invaded (Table 1). *E. esula* was present only in very small abundances at this site prior to the 1999 fire, and was the only exotic species present during our sampling.

Table 1. Mean percent cover (±1 SE) of bare soil, *Euphorbia esula*, and all species of grasses, forbs, and shrubs, in plots having different combinations of fire and invasion history (n = 3 plots; 4 sampling frames averaged per plot).

	Burned, invaded	**Unburned, uninvaded**	**Burned, uninvaded**
Grass	14.0 ± 4.3	10.8 ± 0.4	35.4 ± 7.0
Forb	4.5 ± 3.5	16.5 ± 3.1	11.9 ± 2.7
Shrub	0.6 ± 0.4	38.6 ± 3.9	1.5 ± 0.6
E. esula	26.7 ± 2.5	0	0
Bare ground	55.4 ± 8.1	35.8 ± 2.6	50.7 ± 6.1

Euphorbia esula is a rhizomatous perennial herb native to Eurasia that commonly can have abundant root mass at 2.4 m deep in soil, and maximum rooting depths are between 4.6 to 9 m (Raju et al. 1963, Raju 1985). Proliferation of *E. esula* after fire occurs through seedling establishment and resprouting. The shrub *A. tridentata* is among the deepest-rooted native species in sagebrush steppe, with rooting depths commonly reaching 2 m or frequently deeper (Richards and Caldwell 1987, Welch and Jacobson 1988). *Artemisia tridentata* has both evergreen and deciduous leaves that collectively enhance water relations and carbon gain as soil water availability decreases during summer. *A. tridentata* reproduces only by seed. The native *P. spicata* is a perennial grass that can reproduce through tillers, and resprouts vigorously after fire. Root depths of *P. spicata* are commonly deeper than other, co-occurring grasses (< 0.5 m), but the maximum rooting depth of *P. spicata* (1.4 m) is much less than that of *E. esula* and *A. t. vaseyana* (Cline et al. 1977, Canadell et al. 1996).

Isotopic determination of depth of water uptake

In each plot, we extracted 1 soil core from the soil surface to bedrock (lava) using a tractor-mounted hydraulic corer (2.5 cm diameter, Giddings Inc, Ft. Collins, CO). Cores were extracted, divided into 5-10 cm increments that were sealed in thick plastic bags and stored in a cooler on ice, within a 10-minute period. Each increment samples was frozen at the end of the day, and later thawed, mixed, and separated into fractions to be used for isotopic analysis or measurement of water potential and content. Water potential and content were measured immediately, and soils for isotopic analysis were repackaged in sealed glass vials and frozen until analysis.

Two samples of non-photosynthetic tissue were collected per species from around each core, and were bulked to form each replicate for plant isotopic analysis. Woody stem was sampled from sagebrush, non-photosynthetic culms were sampled in the grass, tissue near the root stem interface was sampled from *E. esula*, and woody fibrous tillers from litter were sampled for the native forb. Samples were stored in glass vials and sealed with parafilm and then frozen until extraction of water for isotopic analysis.

Water was extracted from soil and plant samples using cryogenic vacuum distillation (Ehleringer and Osmond 1989), and analyzed for stable isotopes of hydrogen and oxygen by the Stable Isotope Ratio Facility for Environmental Research at the University of Utah. The ratio of deuterium to hydrogen and ^{18}O to ^{16}O in each sample was expressed relative to Standard Mean Ocean Water (SMOW) as follows:

$$\delta_{sample} = ((\mathrm{Ratio}_{sample}/\mathrm{Ratio}_{standard})-1)*1000$$

where R_{sample} is the ratio of the heavy to light isotope in the sample and $R_{stnadard}$ is the ratio of heavy to light isotopes in SMOW.

Mean isotopic ratios were calculated for each soil depth and plant species across treatments and sampling times (n = 3 for each treatment * sampling period). Plots were made of soil water potential (*see below*) and isotopic ratio as a function of soil depth. Plant isotopic values were compared to these graphs to determine the potential depths of water uptake.

Determination of water potential

Soil water potentials were determined for each increment of soil cores in the laboratory, using a temperature-controlled, WP4-T dewpoint hygrometer (Decagon, WA). Plant water potentials were determined at predawn and midday, on excised stems or grass blades, using a field-portable pressure chamber (Model 1000, PMS Instrument Co., Corvallis, Oregon, USA).

Photosynthetic gas exchange

Photosynthetic gas exchange was measured under clear sky conditions, using a portable photosynthesis instrument equipped with an artificial light source and a CO_2 controller (model 6400, LiCOR, NE). Light levels during measurement were 1000 μmol m^{-2} s^{-1} (400-700 nm), which was sufficient to saturate photosynthesis in all species, and [CO_2] was controlled at 370 μl l^{-1}. Humidity and temperature during measurement were maintained within about10-15% of ambient levels. Photosynthesis and stomatal conductance were reported on a projected leaf area basis. Leaf areas were determined using digital photography with objects of known size in the field-of-view, and image processing software (ImageJ, National Institute for Health) to calculate areas.

RESULTS

Soil water availability

During the June sampling, soil water was generally above typical minimum levels (-1.5 MPa) for plant uptake, at nearly all depths and in all plots (Figure 1). Soil water potentials during this period were greatest in plots in the unburned, uninvaded areas that had intact vegetation communities. Soil water potentials decreased considerably from the June to August sampling dates, and only soils deeper than about 75-125 cm had water potentials above about -3 MPa by August. In August, water potentials in soils at approximately 50-150 cm depths were several times greater in burned compared to unburned plots, except where *E. esula* was abundant (Figure 1).

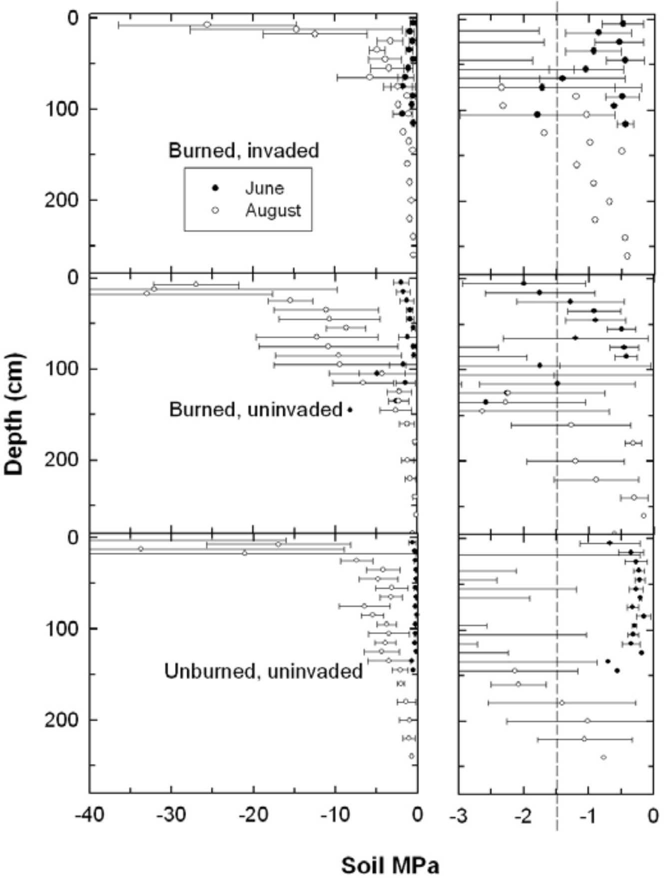

Figure 1. Soil water potential of soil in each treatment. Panels on the right are an expanded view of the plant-relevant values of soil water potential. The vertical dashed line shows the nominal value for permanent wilting point for crops (-1.5 MPa).

Isotopic evidence for depth of water uptake

In all plots, soils located between the surface and approximately 25 cm depth consistently had greater δD and δ^{18}O values than soils located deeper than ~25 cm (Figures 2-3). Below these depths, there were no consistent trends in isotopic ratios in soil water that could indicate depth of water uptake in plants. Despite the lack of inconsistent trends in isotopic ratios in soil, both δD and δ^{18}O were always greatest in the native grass (*P. spicata*), less in the native forb (*E. heracleoides*), and least in sagebrush (*A. tridentata*) and *E. esula*. No differences in δD and δ^{18}O were detected between *A. tridentata* and *E. esula*.

δD and $\delta^{18}O$ decreased in plants relative to maximum δD and $\delta^{18}O$ in soils at 0-25 cm depths (Figures 2-3), from June to August, due to both seasonal decreases in δD and $\delta^{18}O$ in plants and increases in δD and $\delta^{18}O$ in soils. Slightly greater δD and $\delta^{18}O$ in grasses than any soil values in June could be due sampling artifacts, such as accidental inclusion of transpiration-affected water in plant samples, or from possible plant uptake of water from the top few cm of soils. There were likely gradients of δD and $\delta^{18}O$ within each 10 cm increment of bulk soil we analyzed, and it is likely that such gradients would have been most pronounced in the shallowest soil depths, in which δD and $\delta^{18}O$ would were likely greater at a 1 cm than at 10 cm depth, for example (Figures 2-3).

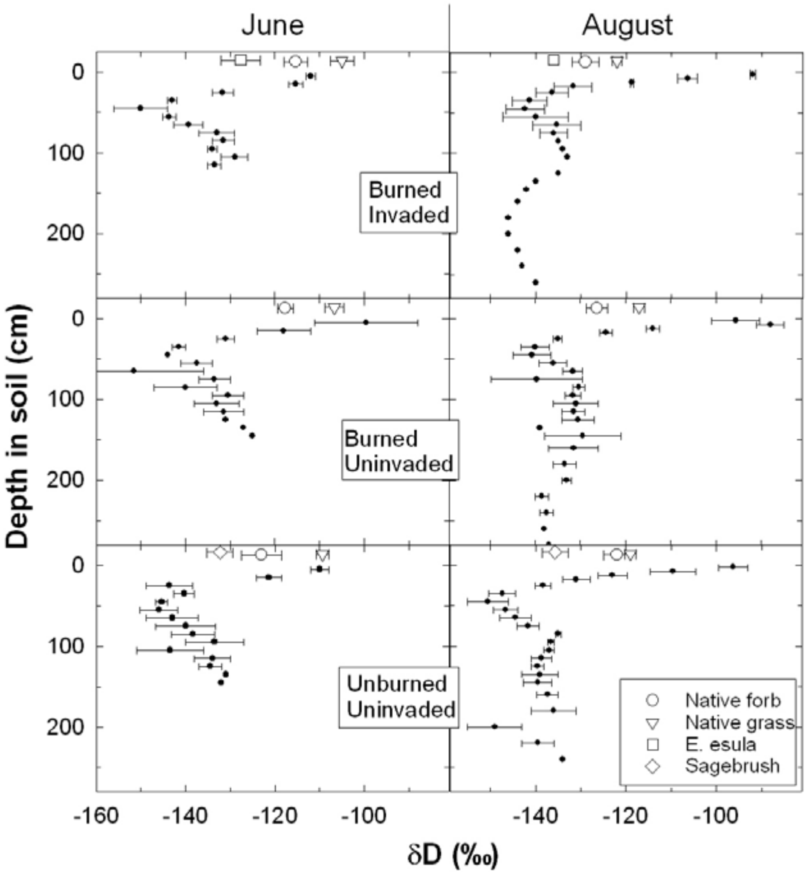

Figure 2. D/H in each treatment. Dark symbols show values in soil, and open symbols above the 0 cm depth in soil show the different plant species sampled.

Soil water uptake in *E. esula* and *A. tridentata* in August appeared possible from two depths in soil, at approximately 25 and 100 cm depths, based on comparisons of plant and soil δD and $\delta^{18}O$ (Figure 2, and top panel only of Fig. 3). Assuming that plants can only extract water from soils that have water potentials than the plants, these species were likely extracting soil water from the deeper depths (Figs. 1,4). Isotopic ratios of *P. spicata* and *E. heracleoides* were similar to ratios of soil water only in the dry soils from about 15-25 cm depth.

Plant water status

Predawn plant water potentials decreased by nearly three fold or more from June to August (Figure 4). The native grass *P. spicata* tended to have lower water potentials than the forb, and sagebrush and *E. esula* tended to have greater water potentials than the native herbs at predawn. The native grass and forb both had higher water potentials in plots that did not have *E. esula*, compared to plots that did have *E.*

esula. Daily decreases in water status from predawn to midday were greater in sagebush and *E. esula* than in the native herbs (Figures 4-5).

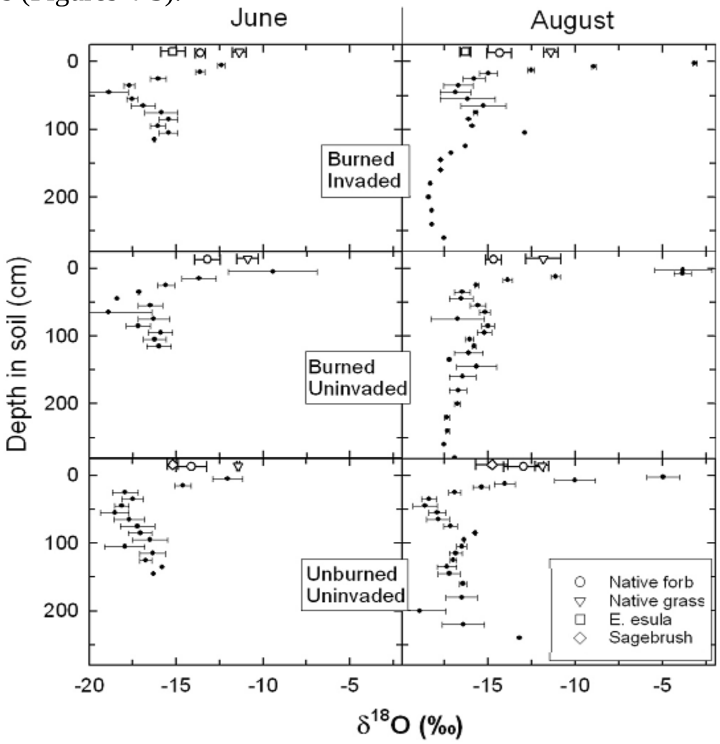

Figure 3. $^{18}O/^{16}O$ in each treatment Dark symbols show values in soil, and open symbols above the 0 cm depth in soil show the different plant species sampled.

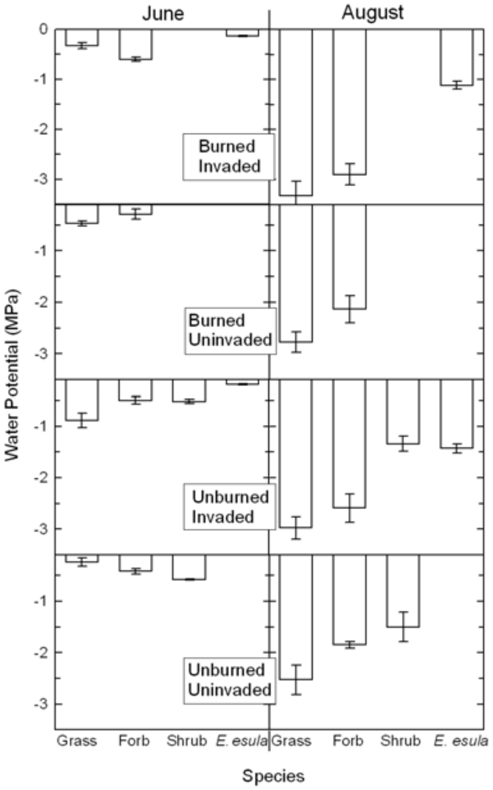

Figure 4. Predawn water potentials of the species sampled in each treatment.

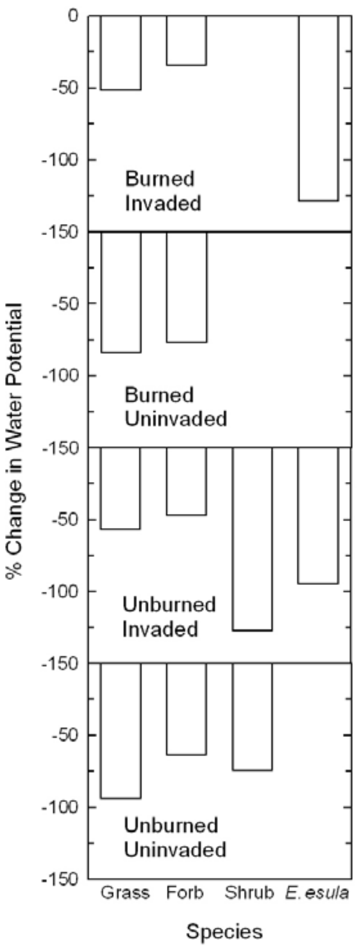

Figure 5. Percent change in water potentials from predawn to midday, in August.

Photosynthetic gas exchange
Leaf-level photosynthesis decreased 96% from June to August in *E. esula*, compared to decreases of 70% in sagebrush, 78% in the native forb, and 92% in the native grass (Table 2). Photosynthesis in *E. esula* was similar to or significantly less than in any native species, during both sampling periods. In the unburned plots, photosynthesis was least of all species in *E. esula*, with the native forb and sagebrush having nearly 5-fold greater photosynthesis. In burned plots during June, photosynthesis was 30% greater in the native forb compared to *E. esula*, but by August the forb had 5-fold greater photosynthesis. Photosynthesis was similar in *E. esula* and the native grass in the burned plots. Stomatal conductances in *E. esula* were similar or greater than in the native grass, but less than in the other native species. Water-use efficiency was similar or less in *E. esula* than in adjacent native species, except in unburned plots where photosynthesis was exceptionally low.

Comparisons of photosynthesis in native plants among plots that did or did not have *E. esula* did not indicate any negative effects of *E. esula* on photosynthesis or conductance in neighboring native species (Table 2). However, water-use efficiency was 77% greater in native species in plots with *E. esula* (3.22 μmol/mol) compared to plots that had no *E. esula* (1.82 μmol/mol; Paired T = 2.06, P = 0.05, using means for each species x treatment as replicates).

Table 2. Photosynthesis (μmol CO_2 m^{-2} s^{-1}), stomatal conductance (mol H_2O m^{-2} s^{-1}), and water-use efficiency (WUE, photosynthesis/evapotranspiration, mol/mmol) among the species in each treatment type.

	Period	Species	Photosynthesis (μmol m^{-2} s^{-1})	Conductance (mol m^{-2} s^{-1})	WUE (μmol/mmol)
Burned, invaded	June	Native forb	17.0 ±2.6	0.406 ±0.069	1.3 ±0.1
		Native grass	11.0 ±1.3	0.158 ±0.015	1.8 ±0.3
		E. esula	12.8 ±2.7	0.260 ±0.064	1.6 ±0.1
	August	Native forb	3.6 ±0.7	0.053 ±0.017	1.8 ±0.3
		Native grass	0.9 ±0.2	0.003 ±0.003	4.2 ±0.8
		E. esula	0.6 ±0.3	0.003 ±0.003	1.4 ±4.8
Unburned, uninvaded	June	Native forb	20.3 ±1.5	0.421 ±0.029	1.0 ±0.1
		Native grass	10.0 ±1.3	0.203 ±0.036	0.9 ±0.1
		Sagebrush	13.2 ±1.9	0.376 ±0.041	0.9 ±0.1
	August	Native forb	4.5 ±1.8	0.080 ±0.045	1.6 ±0.3
		Native grass	0.9 ±0.3	0.008 ±0.005	2.2 ±0.6
		Sagebrush	3.9 ±1.4	0.078 ±0.048	1.4 ±0.3
Burned, uninvaded	August	Native forb	2.9 ±1.6	0.045 ±0.033	0.6 ±1.0
		Native grass	0.9 ±0.5	0.005 ±0.003	3.3 ±1.2
Unburned, invaded	August	Native forb	5.3 ±1.6	0.078 ±0.028	1.6 ±0.6
		Native grass	1.1 ±0.1	0.003 ±0.003	6.2 ±2.9
		Sagebrush	4.9 ±2.1	0.070 ±0.047	2.3 ±0.4
		E. esula	0.8 ±0.1	0.003 ±0.003	5.3 ±7.7

DISCUSSION

Whether interspecific difference in soil resource contribute to invasions of semiarid communities is a critical question not only for understanding community stability, but also for land management practices that affect soil resources through altering species compositions and abundances. For example, sheep grazing has affected the relative abundance of forbs within the herbaceous component of the mountain sagebrush communities we examined (Seefeldt et al. 2007). Prescribed burning practices, aside from promoting invasive, exotic species, are perceived as have little impact on the composition of herbaceous communities. One potentially important exception has been that prescribed fires have selected against *Cordylanthus racemosus*, one of the few late-season native forbs that presumably persists on deeper soil water reserves and has been promoted by domestic grazing activities (Seefeldt and McCoy 2001; Seefeldt et al. 2007).

Euphorbia esula dominated burned areas but was scarce in the undisturbed sagebrush steppe we evaluated, and correspondingly tended to have lower photosynthesis than native species despite having greater or equal water potentials than the natives (Tables 1-2, Figure 4). Moreover, *E. esula* tended to have lower photosynthetic water use efficiency, and exhibited no greater ability to photosynthesize under its low midday water potentials than native species (Table 2, Figure 5). Depth of water uptake was similar in *E. esula* and sagebrush, and both acquired water from deeper soils than the native forb and especially grass. Water availability was greater in deep soils, especially in burned areas in which sagebrush was absent. Correspondingly, both sagebrush and *E. esula* tended to have greater water status at predawn, compared to the native herbs. *E. esula* had lower predawn water potential in unburned areas having sagebrush compared to burned plots, and greater water-use efficiency. These differences point to greater water stress for *E. esula* in the rare cases in which we observed it near sagebrush. Interestingly, water potentials of native herbs were lower when herbs occurred near *E. esula*, which could also indicate belowground interactions in shallower soils. These findings suggest a greater reliance on soil water availability in *E. esula* than native herbs that recolonize burn sites. *E. esula* needs the deep soil water used by sagebrush, and increases in deep soil water that result from the temporary loss of sagebrush appear to be a mechanism contributing to the persistence of *E. esula* on the sites we examined.

Differences in water source have been demonstrated for exotic forbs and native shrub-steppe species (Kulmatiski et al. 2007), and were the basis of surmising a "tap-root advantage" for the exotics. However, use of a water source does not alone indicate the importance of the water source to a plant. Here, we demonstrate that leafy spurge appears to have a marginal photosynthesis and water status in cold desert. In the absence of conservative water use abilities, use of more abundant supplies of water available beneath the rooting zone of native herbs is likely critical for its persistence in cold desert. Restoration of abandoned dry farms and stabilization of burn areas often focuses on promoting grass cover, which should render sites vulnerable to infestation of leafy spurge. Efforts to prevent or restore infestations of leafy spurge could benefit from promotion of native forbs and especially shrubs like sagebrush. Deep-rooted perennials that persist though seasonal drought are clearly better poised to preempt the soil resources required by leafy spurge.

ACKNOWLEDGEMENTS

This study was made possible by a grant from the National Aeronautics and Space Administration Goddard Space Flight Center which was made possible through efforts of the Idaho congressional delegation.

LITERATURE CITED

Anderson J. E., Shumar M.L., Toft N.L., Nowak R. S. 1987. Control of the soil water balance by sagebrush and three perennial grasses in a cold-desert environment. Arid Soils Research and Rehabilitation 1:229-244.

Canadell, J., Jackson, R. B.; Ehleringer, J. R.; [and others]. 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia. 108(4): 583-595. [27670]

Chambers J. C., Roundy B.A., Blank R.B., Meyer S.E., Wittaker A. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117-145.

Cline, J. F.; Uresk, D. W.; Rickard, W. H. 1977. Comparison of soil water used by a sagebrush-bunchgrass and a cheatgrass community. Journal of Range Management. 30(3): 199-210

Ehleringer, J.R. and C.B. Osmond. 1989. Stable Isotopes. pp. 281-300 *in* Pearcy, R.W., J.R. Ehleringer, H.A. Mooney, and P.W. Rundel (eds). Plant Physiological Ecology. Chapman & Hall, London.

Kulmatiski, A. 2006. Exotic plants establish persistent communities. Plant Ecology 187:261-275.

Kulmatiski, A. Beard K.H., Stark, J.M. 2006. Exotic plant communities shift water-use timing in a shrub-steppe ecosystem. Plant Soil 288:271-284

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

Hill J.P., Germino M.J., Wraith J.M., Olson B.E., Swan M.B. 2006. Advantages in water relations contribute to greater photosynthesis in *Centaurea maculosa* compare with established grasses. International Journal of Plant Sciences 167: 269-277.

Link S, Gee G.W., Thiede M.E., Beedlow P.A. 1990. Response of a shrub-steppe ecosystem to fire: soil water and vegetational change. Arid Soils Research and Rehabilitation 4: 163-172.

Pyke D.A. 1999. Invasive exotic plants in sagebrush ecosystems of the Intermountain west. Pages 43-45 in PG Entwistle et al. (eds) Proceedings: sagebrush steppe ecosystems symposium. Publication BLM/ID/PT-001001+1150. Bureau of Land Management, Boise ID.

Seefeldt, S.S. Germino, M.J. DiCristina, K. 2007. Prescribned fires in *Artemisia tridentata* ssp. *vaseyana* steppe have minor and transient effects on herb cover and composition. Applied Vegetation Science 10: 249-256

Selleck, G. W.; Coupland, R. T.; Frankton, C. 1962. Leafy spurge in Saskatchewan. Ecological Monographs. 32(1): 1-29.

Smith S.D., Monson R.K., Anderson J.E. 1997. Physiological Ecology of North American Desert Plants. Springer NY.

Raju, M. V. S. 1985. Morphology and anatomy of leafy spurge. In: Watson, Alan K., ed. Leafy spurge. Monograph Series No. 3. Champaign, IL: Weed Science Society of America: 26-41.

Raju, M. V. S.; Steeves, T. A.; Coupland, R. T. 1963. Developmental studies on *Euphorbia esula* L.: morphology of the root system. Canadian Journal of Botany. 41: 579-588.

Richards, J. H.; Caldwell, M. M. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata*. Oecologia. 73(4): 486-489.

Welch, B. L., Jacobson, T. L. C. 1988. Root growth of *Artemisia tridentata*. Journal of Range Management. 41(4): 332-334.

[THIS PAGE LEFT BLANK INTENTIONALLY]