Advantages in Water Relations Contribute to Greater Photosynthesis in *Centaurea maculosa* Compared with Established Grasses

Judson P. Hill, Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209-8007

Matthew J. Germino, Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209-8007

John M. Wraith, Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana 59717-3120.

Bret E. Olson, Department of Animal and Range Sciences, Montana State University, Bozeman, Montana 59717-2900.

Megan B. Swan, Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana 59717-3120.

ABSTRACT
Semiarid steppe communities in North America appear particularly vulnerable to persistent infestations by exotic, taprooted forbs, such as European spotted knapweed (*Centaurea maculosa*). We determined whether species differences in ecophysiological response to water availability could help link traits of *Centaurea* with invasibility of steppe communities. Plant–soil water relations and photosynthesis were measured under three water levels in a greenhouse and at two sites over two years in the field for *Centaurea* and dominant rangeland species of southwestern Montana: *Pseudoregneria spicata*, *Pascopyron smithii*, and *Bromus inermis*. *Centaurea* had greater and more seasonally persistent photosynthesis than the other species under field conditions but not in the greenhouse, where water availability was similar for the species. *Centaurea* had no greater water use efficiency, except under unusually dry conditions, but maintained greater water potentials despite greater transpiration than the grasses. Changes in soil water indicated uptake from deeper and wetter soils in *Centaurea* than in grasses. Greater photosynthesis in *Centaurea* compared with grasses may result from uptake of deeper soil water and corresponding drought avoidance. Interspecific differences in resource use may therefore contribute to the success of *Centaurea*, and *Centaurea*'s ecological requirement for water matches an available resource niche in the communities we examined.

Keywords: exotic plants, grasslands, photosynthetic gas exchange, water relations.

INTRODUCTION

Replacement of native species by exotic annual grasses and perennial forbs has occurred in many areas of semiarid steppe in western North America, especially in areas converted to steppe through exclusion of woody species. The persistence of *Bromus tectorum* and similar invasive grasses in these semiarid rangelands has been attributed to differences in their phenology and soil resource use compared to native species, which, along with altered fire frequencies, can lead to site modifications that favor traits of invasive over those of native species (Booth et al. 2003). However, less is known about factors contributing to the invasiveness of the numerous species of exotic perennial forbs (e.g., thistles, *Centaurea* sp.) that are commonly taprooted members of the Asteraceae and are noxious invaders of semiarid grasslands and disturbed shrublands (Taylor 1992; Pyke 1999). These species can both colonize and persistently dominate sites for decades or longer. *Centaurea maculosa* Lam. (European spotted knapweed) is a particularly noxious, taprooted, and exotic forb that was introduced to the San Juan Islands in the late 19th century and has since expanded its range to much of North America, especially grasslands of the Pacific Northwest (Sheley et al. 1998).

Soil resource availability may contribute to invasions, provided that interspecific variation in soil resource use leads to selective advantages for exotic invaders compared to native species (e.g., Lonsdale 1999; Davis et al. 2000). *Centaurea maculosa* did not appear to use nitrogen more efficiently than native grasses it competes with (Olson and Blicker 2003) and did not appear to alter soil physical characteristics (Sperber et al. 2003). However, *C. maculosa* and other exotic forbs frequently have deeper roots and can emerge earlier and persist longer during seasonal drought than native or naturalized (hereafter ''established'') steppe herbs. Soil water within steppe is usually replenished by snowmelt and spring rain but then becomes depleted to low levels during warm summers, particularly in the shallow root zones of grasses (Smith et al. 1997). While several studies have addressed allelopathy as a factor contributing to invasiveness of *C. maculosa* (Ridenour and Callaway 2001; Bais et al. 2003), differential use of soil water during seasonal drought could also be a key factor affecting the success of *C.maculosa*.

Invasive species in forests and grasslands that are more productive than semiarid steppe typically had greater growth and photosynthesis or photosynthetic efficiency than native plants, and these advantages were frequently related to properties that enhance sunlight use (e.g., Williams and Black 1993; Williams et al. 1995; Pattison et al. 1998; Baruch and Goldstein 1999; Durand and Goldstein 2001; Myers and Anderson 2003; Nagel and Griffin 2004). Surveys of traits related to resource utilization and carbon gain across groups of exotic invasive and native species have not always revealed differences (e.g., Smith and Knapp 2001). Matching differences in resource use between exotic and native species to the specific ways that resources become available in time and space may lead to more comprehensive linkages between species invasiveness and community invasibility. Photosynthetic differences among species in semiarid steppe can result from variation in plant–soil water relations, and greater photosynthesis might increase plant fitness. Determining whether suites of traits in exotic forbs such as *C. maculosa* reflect relatively greater drought avoidance, tolerance, or water conservation than native plants could yield important insight on the invasiveness of *C. maculosa* as well as the susceptibility of steppe communities to invasion.

The objective of this study was to determine whether inter-specific differences in net carbon assimilation rates (A_{net}) and soil-plant water relations between *C. maculosa* and established species exist, and could contribute to the success of *C. maculosa* in semiarid steppe. We hypothesized that *C. maculosa* would have greater A_{net} than grasses that otherwise dominate sites frequently invaded by *C.maculosa*. Moreover, we predicted that the greater A_{net} in *C. maculosa* would be the result of persistent water acquisition and flexibility in the utilization of water as

water availability decreased from early to late season. Greater flexibility or plasticity in ecophysiological characteristics in exotic plants can contribute to their success in different environments (Williams et al. 1995). From its widespread distribution and relatively extended phenology, we also hypothesized that *C. maculosa* would be more flexible in its carbon assimilation and water relations among sites and times, compared with established species.

METHODS
Photosynthesis and water relations were measured under controlled soil water levels in a greenhouse experiment in the summer of 2001 and under natural field conditions in the summers of 2002 and 2003. Measurements were performed on *Centaurea maculosa* and the dominant native rangeland grasses *Pascopyron smithii* Rydb. (western wheatgrass), *Pseudoregneria spicata* Pursh A. Love ssp. *spicata*(bluebunch wheatgrass), and the nonnative but established *Bromus inermis* Leyss. (smooth brome).

FIELD OBSERVATIONS
Plants were monitored in monocultures at two sites: in Leverich Canyon, 10 km south of Bozeman, Montana, and another site ca. 16 km east of Helena, Montana. Four 2 3 2-m monocultures were created for each species at each site by painting glyphosphate herbicide (Roundup, Monsanto, Columbus, OH) onto leaves of other species in each plot during the year before the experiment. Ground litter was removed from the plots once the nontarget species had died to prevent the species from receiving extra nutrients. Soils at Bozeman were a silty loam overlaying gravelly and sandy loams below ca. 25 cm. Soils at Helena were silty clay loam overlaying clay below ca. 25 cm, as described in Swan (2004).

MICROCLIMATE
Field microclimate conditions were continuously recorded at both sites using dataloggers (CR10X, Campbell Scientific, Logan, UT) throughout both growth seasons. Air temperatures were measured with fine-wire, radiation-shielded thermocouples positioned at 5 cm ($n= 4$) and 100 cm ($n= 2$) above ground, and averages of readings made at 5-min intervals were recorded every 30 min (24-gauge, Omega, Stamford, CT). The different heights were chosen for their comparability to rosette foliage and regional weather stations, respectively. Long-term maximum and mean temperatures during the summer months were determined for both sites from the three Western Regional Climate Center (WRCC; Desert Research Institute, Reno, NV) monitoring stations located closest (<20 km) to each site. These climate stations have reported monthly averages of daily minimum, maximum, and mean temperatures over the past 40–60 yr.

During the 2003 season, 32 time-domain reflectometry (TDR) probes (model TDR 100, Campbell Scientific) were permanently inserted vertically into soil, from the surface to 30 cm deep, to provide continuous monitoring of soil water. TDR was measured every 6 h at the Bozeman and Helena field sites from June through August. Volumetric soil water contents were also determined under four monospecific stands of *C. maculosa* or four plots of grasses only at each site, at incremental depths of 20 down to 120 cm at Bozeman and to 100 cm at Helena, during the 2002 and 2003 seasons using a neutron moisture meter (503DR, California Pacific Nuclear, Martinez, CA). Neutron probe readings were made in one PVC-lined access hole per plot at midday on one day in the second week of each summer month.

Soil water retention curves (plots of soil water potential and water content) were determined for the two different soils found at the two different sites. Three soil cores were extracted at each site, and samples were collected at 10-cm intervals to the 50-or 70-cm depth. Each 10-cm sample increment was saturated in the lab with distilled water, and a subsample of ca. 8–10 g of soil was taken for measurement. Water potential was measured using a WP4-T model dew point

potentiometer (Decagon, Pullman, WA), and water content was determined using the mass-based gravimetric method on each subsample at 15–30-min intervals as samples dried at room temperature. After ca. 8 h of drying, soil samples were then dried in an oven for 24 h and weighed. We then calculated $(gH_2O)/(gdrysoil)$ and $(mLH_2O)/(mLdrysoil)$ for each interval measurement during the dry-down. Additional subsamples were taken from the 10-cm incremental samples and used to determine soil bulk density ($m^3 m^{-3}$).

GAS EXCHANGE MEASUREMENTS

Leaf-level gas exchange measurements were made at both sites on *C. maculosa*, on *P.spicata* at the Helena site, and on *B. inermis* at the Bozeman site, in 2002 and 2003. Bromus inermiswas also measured in 2003 at the Helena site. *Pascopyron smithii* was a relatively less abundant species at the sites, and although we examined it in our greenhouse study, we did not generate enough field data for meaningful statistics or presentation. Measurements were made at each site three times during the growing season, at ca. 6-wk intervals, to evaluate temporal variations in carbon assimilation as soil water decreased from seasonal maximum to minimum availability by late summer. Seasonal variation in water results from high water inputs during snowmelt and early spring rain, when plants are dormant, followed by little precipitation as temperatures and vapor deficits increase during the summer growing season. Gas exchange measurements were made on representative leaves of five arbitrarily selected individuals of each species starting at 0800 hours on days with clear skies. Different individuals were measured for each sampling. Carbon assimilation (A_{net}) and stomatal conductance to water vapor (g_{st}) were determined with a portable closed-flow gas exchange system (LI-6400, LI-COR, Lincoln, NE), equipped with a CO_2 controller, and an artificial red-blue light source. All measurements were made with CO_2 concentration at 370 ppm and under saturating light conditions (>1500 mmol m2s1, 400–700 nm). Transpiration (E) was calculated from the product of conductance and leaf-air vapor deficit (von Caemmerer and Farquhar 1981). Leaf-air vapor pressure deficit was determined from separate measurements of relative humidity and leaf and air temperatures taken before inserting leaf into measurement chamber (Hygro-Thermo-Anemometer, Extech, Waltham, MA; PM Plus infrared thermometer, Raytek, Santa Cruz, CA). Water use efficiency (WUE) was calculated as $A_{net} / E(\mu molCO_2/mmolH_2O)$. Gas exchange parameters were calculated on a projected leaf area basis, which was determined from digital photographs using the following procedure. After the measurement of photosynthesis, the measurement lid was opened without disturbing the arrangement of leaves resting on the chamber bottom. A spare chamber gasket was then pressed against the leaf, in alignment with the bottom gasket of the chamber. The leaf and spare gasket were then carefully removed as one unit and laid flat for photographing. The resulting image showed the display of leaves bound by the 2 3 3-cm gasket (which matched the chamber dimensions), and leaf area in the gasket area was determined to 0.05-cm^2 resolution using image-processing software (Scion, Frederick MD).

PLANT WATER STATUS

Plant water potential (Ψ_{plant}) was measured before dawn and between 1600 and 1700 hours using a Scholander-type pressure chamber (Plant Moisture Stress Instruments, Albany, OR) on several of the same days as plant gas exchange measurements. Five representative terminal shoots, ca. 4–8 cm long, were collected from the midcrown of different individuals of each species at each measurement period. Each sample was excised and immediately placed into the pressure chamber for measurement of Ψ_{plant} (MPa).

GREENHOUSE EXPERIMENT

Carbon assimilation and WUE were compared in *C. maculosa, P. spicata,* and *P. smithiiacross* three tightly controlled soil water regimes in the greenhouse during the summer of 2001, before the field observations. All species were grown from seed in a greenhouse with constant light and

temperature under three different soil water matric potentials: 1.0, 0.1, and 0.01 MPa (hereafter referred to as the dry, mesic, and wet levels, respectively). Seeds of each species were planted in 18 columns, each 0.1 m in diameter and 0.4 m tall, with six columns assigned to each of the three water treatments, for a total of 54 columns. These columns were randomly assigned to one of six blocks. Water treatments were maintained three times each week by adding enough water to attain target soil matric potentials that were previously determined from soil water retention curves of the columns (Or and Wraith 1999). Actual soil water potentials were somewhat less because of drying between water additions, though the tall, narrow column design minimized water loss. After 4 mo of growth during the summer under natural light, leaf-level gas exchange measurements were made for four consecutive days on three randomly chosen individuals of each species under each soil water treatment. Leaf-level gas exchange measurements were made to determine A_{net}, g_{st}, E, and WUE.

STATISTICS

The significance of differences in A_{net} and WUE throughout the study was determined with separate one-way ANOVAs using JMP software (SAS Institute, Cary, NC), with the years, sites, times of year, or species as factors. Gas exchange plant data were natural log–transformed when assumptions of normality were not met. A multifactor design was precluded because of differences in species composition among sites and the different phenology of the species. Least squares linear regression was used to determine the relationship between the natural logs of A_{net} and Ψ_{plant} of each species, and MANOVA was used to determine whether the slopes of A_{net} and Ψ_{plant} were significantly different among the species.

RESULTS

FIELD MICROCLIMATE

Mean growing season temperatures were 1°–2°C higher in 2003 than in 2002, and Helena was generally warmer than the Bozeman site in both summers (table 1). The maximum air temperature at 5 cm, the height of rosettes, was up to 7°C warmer at the drier Helena site than at the Bozeman site, as in 2003. Mean temperatures at 1 m of both sites were similar, 1° and 2°C higher than the long-term averages in 2002 and 2003, respectively. Maximum temperatures at 1 m were 2°–3°C higher in both summers, compared to long-term averages.

Table1. Average Daily Mean and Maximum Air Temperature (°C; ±1SE) at the Bozeman and Helena Field Sites during June, July, and August of 2002 and 2003.

Temperature, height	2002		2003		Long-term average	
	Bozeman	Helena	Bozeman	Helena	Bozeman	Helena
Mean:						
1 m	17.7 ±0.4	18.6 ± 0.4	18.6 ± 0.5	20.2 ± 0.5	17.4	18.5
5 cm	18.1 ± 0.4	19.7 ± 0.4	19.4 ±0.5	21.8 ± 0.5		
Maximum:						
1 m	27.9 ± 0.6	29.4 ± 0.6	29.1 ± 0.7	30.7 ± 0.6	26.1	26.6
5 cm	34.2 ± 0.6	37.4 ± 0.6	34.8 ± 0.7	42.0 ± 0.8		

Note. Temperatures were determined with shaded fine-wire thermocouples at 1 m (n= 2) and 5 cm (n= 4) above soil surface. Long-term (40–60-yr) averages were obtained from three climate monitoring stations closest to each site (from WRCC).

Mean annual precipitation since ca. 1950 was 452 ± 45 and 276 ± 13 mm yr1 at weather stations closest to the Bozeman and Helena sites, respectively, with long-term precipitation totals of 255 ±

20 and 181 ± 6 mm for the respective sites from May through September. During the May–September growing season, Bozeman received 362 and 161.5 mm and Helena received 263.4 and 120.4 mm precipitation in 2002 and 2003, respectively (WRCC). During 2002, both sites received almost double the long-term average precipitation for the month of June.

Soil water potential (Ψ_{soil}), determined from volumetric water content (VWC) in the top 30 cm of soil, decreased twofold from June to August at the Helena site, and more than threefold from June to August at the Bozeman site (fig. 1). The Ψ_{soil} was greater (by 32% initially) at the Bozeman compared to the Helena site earlier in the 2003 season and remained greater throughout August (fig. 1). Soil water potentials that are less than or equal to 1.5 MPa are generally considered to be difficult for plants to extract water from, although species can differ in this respect. Water was more readily available to plants when Ψ_{soil} was greater, particularly above ca. 1.5 MPa (fig. 2). At both sites, VWCs under *Centaurea* maculosa and the grasses were in the typical range of plant-available water at all of the measured depths during the early part of the season, but during later months of summer, only soils deeper than ca. 40–50 cm had Csoil greater than 1.5 MPa (fig. 2). Mean VWC in 60–120-cm soil depths decreased significantly more under *C. maculosa* (43%), compared to soils under grasses (27%), from June to August for both years, at the Bozeman site ($F_{1, 15} = 7:64$, P = 0.015). At the Helena site, there was less statistical support for greater decreases in mean VWC of soils between 60 and 100 cm under *C. maculosa* (21%), compared to soils under grasses (9%), from June to August ($F_{1, 11} = 1:28$, P = 0.28). No differences in VWC were evident in soils shallower than 40 cm under the different species.
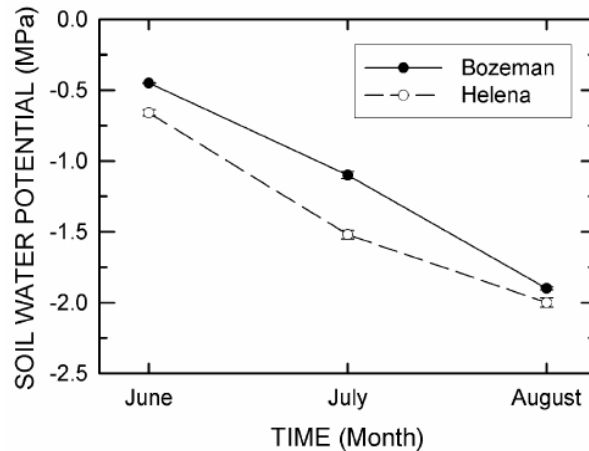

Figure 1. Monthly average (±1 SE; error bars are smaller than symbols) of soil water potential for the top 30 cm of soil under all vegetation types at Bozeman (filled circles) and Helena (open circles) field sites, as determined from soil water content measurements made with time domain reflectometry probes during the 2003 season (n = 24) and converted to MPa with soil water retention curves.

GAS EXCHANGE MEASUREMENTS
Leaf-level carbon assimilation (A_{net}) of all of the species was twofold greater in 2002 than in the drier summer of 2003 at both the Helena ($F_{1, 51} = 32:98$, P< 0.0001) and Bozeman sites ($F_{1, 44} = 7:01$, P= 0.012). Mean A_{net} of all species combined at Bozeman was 48% greater than at the Helena site in both years ($F_{1, 96} = 11.97$, P= 0.0008). *Centaurea maculosa* had greater A_{net} than the co-occurring dominant rangeland grasses during both seasons at the Helena site ($F_{2, 51} = 3.60$, P= 0.035) and the Bozeman site ($F_{1, 44} = 19:0$, P< 0:0001; fig. 3). In addition, A_{net} was measured later into the growth season for *C.maculosa* during the wetter 2002 season. Rosette leaves of *C.maculosa* senesced earlier (by mid-August) in 2003 than in 2002 at both sites (fig. 3). Mean E for both sites throughout both growth seasons was more than twofold greater for *C.maculosa*(5.4

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± 1.3 mmol H_2O m^{-2}s^{-1}) than for any of the grasses (2.5 ±0.4 mmol H_2O m^{-2}s^{-1}; $F_{2, 95}$ = 6.32, P= 0.03; fig. 3).
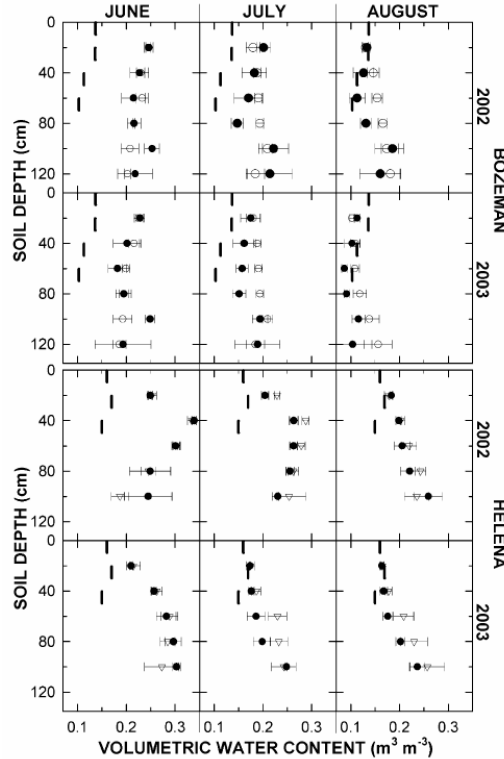

Figure 2. Mean volumetric soil water content (VWC; ±1 SE), as determined with neutron probe, at multiple depths under monospecific stands of *Centaurea maculosa* (filled circles) at both field sites, as well as *Bromus inermis* (open circles) at the Bozeman site and *Pseudoregneria spicata* (triangles) at the Helena site (*n*=4). Solid vertical bars show the VWC values for 10-cm soil depth intervals that correspond to the approximate soil water potential of _1.5 MPa (*n*=3 water retention curves). Soil water would typically be scarce for most plants at VWCs less than the VWC values shown by the bars.

WUE of *C. maculosa* was similar to that of the grasses during June and July 2002 at both sites but greater than that of the grasses for all 2003 sampling dates at Helena and during late summer of 2003 at Bozeman (fig. 3). WUE of *C. maculosa* was 102% greater than that of *Pseudoregneria spicata* ($F_{1, 19}$ = 29.63, P< 0:0001) and 32% greater than that of *Bromus inermis* ($F_{1, 17}$ = 3.07, P= 0.099) at the Helena site during 2003. At the Bozeman site during July 2003, WUE of *C. maculosa* was 75% greater than WUE of *B. inermis* ($F_{1, 9}$ = 5.97, P= 0.040; fig. 3). WUE also varied considerably more among sampling dates in *C. maculosa* than in the grasses. WUE in C. maculosa in 2002 was 93%–252% greater in August than in July at the Bozeman ($F_{2, 14}$ = 6.80, P= 0.011) and Helena ($F_{2, 13}$ = 38.80, P< 0:0001) sites, respectively (fig. 3). WUE in *C. maculosa* was 82% greater in 2003 than in 2002 at Helena during June and July ($F_{1, 19}$ = 22.80, P=0.0002). Seasonal variations in WUE for grasses were relatively smaller, and the greatest changes were decreases in WUE of 42% for *B. inermis* and 21% for *P. spicata* as soils dried during 2003 (fig. 3).
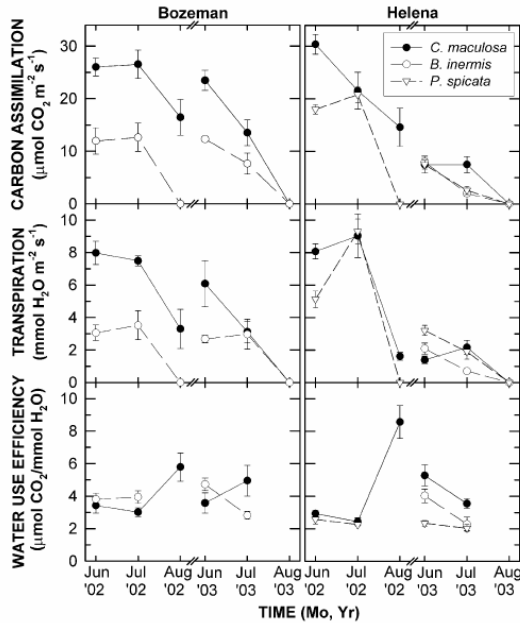
Figure 3. Daily maximum carbon assimilation rate, transpiration, and corresponding water use efficiency (A_{net}=E) of rosette leaves of *Centaurea maculosa* (filled circles), *Bromus inermis* (open circles), and *Pseudoregneria spicata* (triangles) in natural communities across 2002 and 2003 at two field sites in SW Montana (±1 SE); *n* = 5 plants.

PLANT WATER STATUS

Centaurea maculosa did not always have the greatest predawn Ψ_{plant}, but midday Ψ_{plant} measurements of C. maculosa were relatively higher and closer to predawn observations, compared to the other species ($F_{2, 14}$ = 8.46, P= 0.004; fig. 4). For example, at the Helena site in June 2003, mean Ψ_{plant} of *C. maculosa* decreased only 18% from predawn to midday measurements in June (-0.94 ± 0.09 to -1.12 ± 0.1 MPa) and only 19% in late July (-3.32 ± 0.27 to -3.95 ±0.17 MPa). At the Bozeman site during the same two months, Ψ_{plant} of *C. maculosa* decreased only 58% from predawn to midday in June (-0.58 ±0.02 to -0.92 ±0:.0 MPa) and decreased 194% in July (-0.78 ±0:08-2.28 ±0.09 MPa at midday). In comparison, Ψ_{plant} of *P.spicata* at the Helena site decreased 108%, from -1.69 ±0.9 MPa at predawn to -3.45 ±0.12 MPa at midday, in June and well over 100%, from -3.97 ±0.6 MPa at predawn to <-8 MPa at midday, in July (beyond the maximum scale of the pressure chamber). In 2003, diurnal decreases in Ψ_{plant} of *B.inermis* at the Bozeman site were 292% in June (-0.40 ±0.03 to -1.55 ±0:11 MPa) and 207% in July (-0.93 ±0:09 to -2.88 ±0:20 MPa). Over the course of the study, Ψ_{plant} of *C. maculosa* decreased an average 77% ±23% from predawn to midday, compared with decreases of 104% ±2% and 408% ±84% in *P. spicata* and *B. inermis*, respectively (fig. 4). Accordingly, throughout the study, *C.maculosa* also had midday water potentials that were 183% and 110% greater than those of *P. spicata* and *B .inermis*, respectively.

All three species exhibited a decrease in photosynthesis at lower Ψ_{plant} (fig. 5). A positive correlation was observed between ln A_{net} and Ψ_{plant} for *C. maculosa* (slope = 0.41 [μmol CO_2 m^{-2} s^{-1} Ψ^{-1}], $F_{1, 17}$ = 5.59, P= 0.030, r^2 = 0.25), *B. inermis* (slope = 0.24, $F_{1, 9}$ = 10:50, P= 0.010, r^2 = 0.54), and *P. spicata* (slope = 0.55, $F_{1, 4}$ = 16.16, P= 0.057, r^2 =0:89), and there was marginal statistical support for differences in slopes among the species (MANOVA: $F_{2, 32}$ = 2:98, P= 0.07). The most notable difference among species was greater photosynthesis in *C.maculosa* than in the grasses at water potentials above ca. -1 MPa..
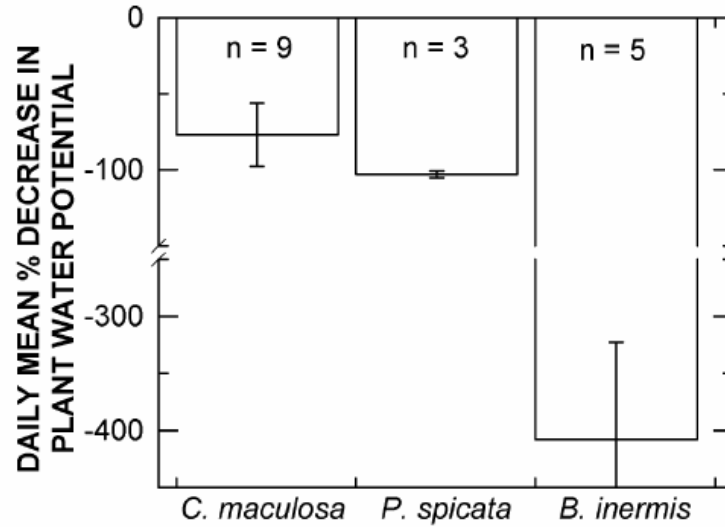
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Figure 4. Mean percent change in plant water potential between predawn and midday measurements (±1 SE) at two field sites in southwestern Montana during the 2002 and 2003 growth seasons for *Centaurea maculosa, Pseudoregneria spicata*, and *Bromus inermis*. Number of replicates (daily means) is shown in each bar.
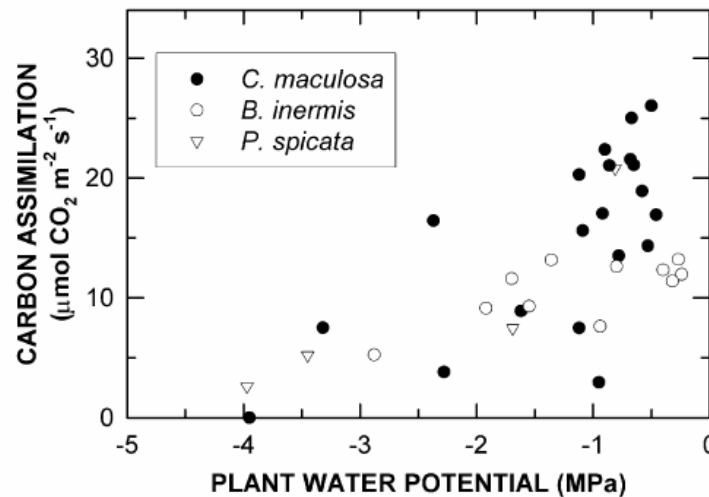

Figure 5. Relationship between photosynthesis and plant water potential for *Centaurea maculosa* (filled circles), *Bromus inermis* (open circles), and *Pseudoregneria spicata* (triangles) at two field sites in southwestern Montana during the 2002 and 2003 growth seasons.

GREEN HOUSE EXPERIMENT

Mean A_{net} in the greenhouse increased among all species with greater water availability ($F_{2, 99} =$ 17.08, P< 0.0001). Mean A_{net} was not greater at any water level in *C. maculosa*, and there was no statistical support for differences in A_{net} between any of the species ($F_{2, 99} = 1.96$, P= 0.147; fig. 6). WUE decreased with increasing water levels for all of the species ($F_{2, 99} = 8.35$, P= 0.0005; fig. 6), but no differences were observed between the species ($F_{2, 99} = 0.21$, P= 0.810).
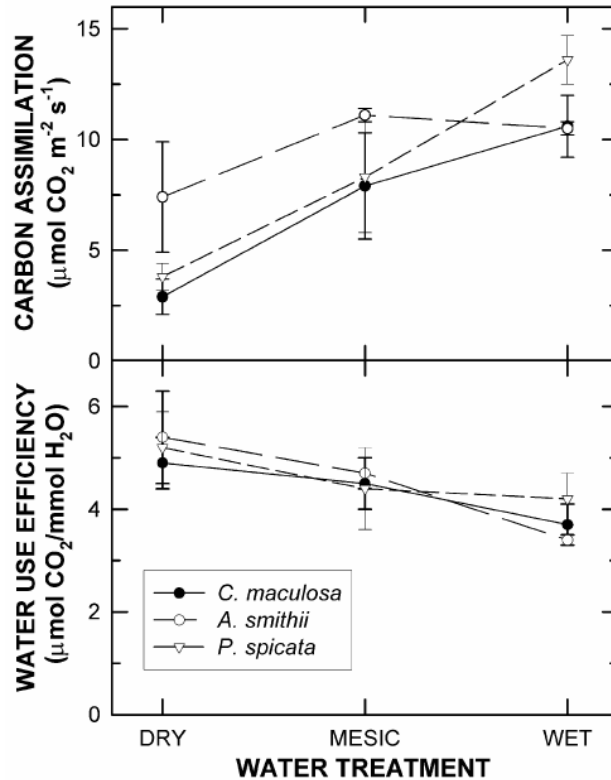
Figure 6. Mean carbon assimilation rate (±1 SE) and water use efficiency (Anet=E; 61 SE) of *Centaurea maculosa* (filled circles), *Pascopyron smithii* (open circles), and *Pseudoregneria spicata* (triangles) in a greenhouse under three target soil water matric potentials: dry (-1.0 MPa), mesic (-0.1 MPa), and wet (-0.01 MPa); *n*=4 daily means.

DISCUSSION

Centaurea maculosa had greater carbon assimilation (A_{net}) and Ψ_{plant} at midday than established grasses during two years that were considerably drier than average. Photosynthetic WUE was greater in *C. maculosa* than in grasses only under the most unusually dry conditions. Greater A_{net} of *C.maculosa*, combined with several-fold greater leaf area per individual and a longer season for carbon assimilation, likely led to much greater annual carbon assimilation for individuals of *C. maculosa* than for established grasses. Active photosynthetic tissue in the form of green stems and cauline leaves persisted later in the season than the rosette leaves of *C. maculosa* we measured (Hill and Germino, forthcoming). Our emphasis on rosette leaves therefore potentially underestimates the amount of carbon gain for *C. maculosa* relative to grasses during dry periods but does not alter our general findings of superior net carbon gain in *C. maculosa*. Therefore, greater yearly carbon assimilation could potentially contribute to greater growth and reproductive output in *C. maculosa* than in the perennial grasses.

RELATIONSHIPS OF WATER RELATIONS AND PHOTOSYNTHESIS AMONG SPECIES
Correspondence between greater A_{net} and higher Ψ_{plant} in *C. maculosa* compared to established grasses indicated that greater A_{net} was related to traits that enhance water relations in these water-limited communities. Photosynthetic advantages for *C. maculosa*, compared to the grasses, were most evident at high Ψ_{plant} (fig. 5). *Centaurea maculosa* also had lower diurnal variation in Ψ_{plant} than established species (fig. 4), despite greater transpiration per unit leaf area (fig. 3), especially per whole plant (based on relatively greater leaf area in *C. maculosa* compared to grasses; data not shown). Maintenance of higher Ψ_{plant} during days, despite greater transpiratory water efflux,

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was most likely to result from greater supply of water from roots to foliage. The lack of differences in A_{net} and $A_{net} = \Psi_{soil}$ relationships among the species under greenhouse conditions (fig. 6), where *C. maculosa* was rooted in soil with VWC levels similar to those for the grasses, suggests that photosynthetic advantages in *C. maculosa* in the field depend on *C. maculosa* having greater water availability than neighboring grasses. The greater water supply to foliage for *C. maculosa* than for grasses could result from a number of factors, including greater access to soil water sources, a greater ability to extract water from dry soils, and water storage in *C. maculosa*.

Roots of mature *C. maculosa* and other forbs are commonly observed growing more than 1 m deep, which may allow access to more abundant, less variable water supplies below typical rooting zones of grasses, which are from less than 25 to 40 cm deep (Jackson et al. 1996; Swan 2004). Similarities in seasonal trends of VWC at 20–40-cm depths under *C. maculosa* and grasses, where we ascertained roots of both species, did not support (or rule out) a greater ability of *C. maculosa* to extract water from dry soils. However, greater depletion of water from soils deeper than 40–60 cm under *C. maculosa* than under the grasses but similar soil water depletion patterns between the species at 20–40-cm depths (fig. 2) indicated greater uptake of deeper water in *C. maculosa*. California rangelands dominated by *Centaurea solstitialis* also had lower soil water contents in deep soils than nearby rangelands that did not have *C. solstitialis* (Gerlach 2004).

Site differences in photosynthesis and water relations further point to the potential significance of deeper soil water uptake in *C. maculosa* than in grasses. Water availability appeared to be scarce in soils above the 80-cm depth at Bozeman and the 40-cm depth at Helena in August 2002, when photosynthesis persisted in *C. maculosa* but not in the grasses. By August 2003, as gas exchange decreased below detection limits in all species, water decreased to (or below) -1.5 MPa at all depths at Bozeman and down to the 60-cm depth at Helena. Our estimates of water potential in deep soils rely on the assumption that water retention characteristics measured for soils from 50–70-cm depths were also representative of deeper depths. Soils also had more clay at Helena than at Bozeman, which may reduce root penetration to deeper soils, in addition to possibly enhancing water availability, water relations, and photosynthesis at Bozeman (see Rosenthal et al. 2005 for a similar scenario in *Helianthus*).

Although *C. maculosa* does not have the ability to store large amounts of water like some succulent arid plants, its large taproot may act in a limited capacity to store water taken up overnight for use during dry days. Taproots are commonly perceived as organs specialized more for storage than for assimilation, but our crude calculations (data not shown) suggest that taproots with a typical volume of 30 cm^3 could provide a few hours of water required for late-season transpiration, at best. These estimates are based on total leaf area, whole-plant sunlight interception, transpiration, tissue water contents, and pressure-volume curves (fig. 3; P. Schwarz, K. Harbuck, and M. J. Germino, unpublished data).

Thus, the greater persistence of photosynthesis in *C. maculosa*, compared to grasses, in mid-late summer appeared to be dependent on the availability of water from depths greater than typical rooting zones of grasses but apparently within the rooting depth of *C. maculosa*. Annual herbs with a greater ability to persist through seasonal drought had relatively deeper roots and deeper soil water uptake than less persistent herbs in California grasslands (Gulmon et al. 1983). Reliance of *C. maculosa* on soil water deeper than that available to grasses could be verified directly using stable-isotope tracers of water source.

PHYSIOLOGICAL ADJUSTMENT TO WATER AVAILABILITY

Plant species that persist under low soil water availability often have adaptations for greater WUE than species from mesic environments (e.g., Anderson et al. 1997). *Centaurea maculosa* did not use water more efficiently than other species in the greenhouse or in the field under relatively wet or average conditions. Similarly, *C.maculosa* did not use water more efficiently than *Pseudoregneria spicata* and *Festuca idahoensis*, based on carbon isotope discrimination (Blicker et al. 2003). Carbon isotopes of plant biomass provide a time-integrative measure of WUE that is unable to detect fine-scale fluctuations that may include potentially critical events. Indeed, the few cases where WUE was greater in *C. maculosa* than in established flora happened under the driest conditions of the study period, such as the unusually warm and dry days in the drought of 2003 (fig. 3).

Flexible WUE could allow plants to exploit favorable conditions while maintaining growth during drier conditions (Williams et al. 1995; Silim et al. 2001). Greater flexibility of WUE probably contributed to effects of deep-water uptake in extending *C. maculosa's* growing season beyond that of grasses, whose primary strategy for avoiding drought is dormancy. Flexibility in WUE may enable high A_{net} when water is abundant while possibly conserving soil water as it becomes scarce and consequently increasing the duration of *C. maculosa's* seasonal carbon assimilation as soils dry. Water conservation may not be advantageous to a species when competitors consume the otherwise conserved soil water. However, *C. maculosa's* greater WUE corresponded in time to an apparent reliance on deep moisture (or water stored in taproots), which grasses presumably could not access. Moreover, grasses appeared to enter dormancy as WUE increased in *C. maculosa* (fig. 3).

CONCLUSIONS

Most research on *C. maculosa* has emphasized escape from natural enemies (e.g., herbivores or pathogens) or novel weapons, such as soil allelopathogens, as factors contributing to its ecological success (Ridenour and Callaway 2001; Bais et al. 2003). Whether interspecific differences in soil resource use also contribute to the vulnerability of steppe to exotic forbs is a key issue, because such differences could point to the availability of niches open to invasive species. Availability of soil resource niches, in turn, is likely affected by land uses or disturbances that alter relative abundances of species or functional groups (e.g., Seefeldt and McCoy 2003). While our results indicate that several interspecific differences in resource use likely contribute to the success of *C. maculosa*, previous research shows that *C. maculosa* is unlikely to benefit from relatively greater acquisition or efficient use of nitrogen (Olson and Blicker 2003) or alteration of soil physical properties (Sperber et al. 2003). The ability to sustain high transpiration without significant lowering of Ψ_{plant} and the ability to adjust WUE to variation in water availability are potentially key factors that enable *C. maculosa* to have relatively greater and more persistent A_{net} than neighboring grasses. Superior water status, despite high transpiration in *C. maculosa*, appears to result from greater access to consistently available water in deep soils, which appears to represent an available niche within the steppe we examined (fig.2). Use of deeper soil water also contributed to the success of invasive shrubs and forbs, compared to native grasses, in other semiarid rangelands (Harrington 1991; Yoder et al. 1998). These findings illustrate how invasions in semiarid lands are affected by site conditions resulting from community resource use as they compare with resource requirements of invasive compared to established species.

Sixty percent of the 46 exotic plants considered to be invasive problems on rangelands are deep-rooted forbs in the Asteraceae like *C. maculosa* (Taylor 1992; Pyke 1999), whose phenology, rapid growth patterns, growth form, and other traits seem to contrast with growth strategies of established grasses that dominate rangelands (Whitson 2000). The rapid growth and extended phenology into seasonally dry periods commonly observed in these other exotic forbs might

result from ecophysiological mechanisms similar to those reported here for *C. maculosa*. Our findings provide empirical support for theoretical predictions that fluctuations in resource availability can contribute to the success of exotic invaders in grasslands (Tilman 1997; Davis et al. 2000). Whereas relatively undisturbed communities in sagebrush steppe use soil water relatively completely (Anderson et al. 1987), many rangelands experience disturbances (e.g., fire) that temporarily exclude deep-rooted native species that reestablish slowly by seed and thereby lead to corresponding increases in deep soil water (Harniss and Murray 1973; Link et al. 1990; Sturges 1993). *Centaurea maculosa* and other exotic forbs are particularly problematic in disturbed areas such as burns and roadsides. On the basis of relatively high water demands required for photosynthetic advantages of *C. maculosa*, we speculate that increases in deep soil water may be a key way that disturbances that select against deep-rooted species encourage site persistence by *C. maculosa* and possibly other deep-rooted exotic forbs. Variation in ecophysiological traits between native and invasive species may lead to better generalizations on factors contributing to invasiveness or invasibility, if ecophysiological advantages can be related to specific changes in resource availability and resource utilization by the native community.

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