Rangeland Ecol Manage 64:358–365 | July 2011 | DOI: 10.2111/REM-D-10-00101.1

Immature Seedling Growth of Two North American Native Perennial Bunchgrasses and the Invasive Grass *Bromus tectorum*

Jayanti Ray-Mukherjee,[1] Thomas A. Jones,[2] Peter B. Adler,[3] and Thomas A. Monaco[4]

Authors are [1]Postdoctoral Fellow, Florida International University, Miami, FL 33199, USA; [2]Research Ecologist, USDA-ARS Forage and Range Research Laboratory, Utah State University, Logan, UT 84322-4820, USA; [3]Assistant Professor, Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322-4820, USA; and [4]Research Ecologist, USDA-ARS Forage and Range Research Laboratory, Utah State University, Logan, UT 84322-6300, USA.

Abstract

Pseudoroegneria spicata (Pursh) A. Löve and *Elymus wawawaiensis* J. Carlson & Barkworth are two native perennial grasses widely used for restoration in the Intermountain West. However, the rapid establishment and spread of *Bromus tectorum* L., an invasive annual grass, has led to a decline in the abundance of native perennial grasses. Proliferation of *B. tectorum* has been attributed to its early germination, superior cold-temperature growth, profuse root production, and high specific leaf area (SLA). To enhance restoration success, we compared *B. tectorum* to commercially available plant materials of two perennial rangeland bunchgrasses, *P. spicata* (cv. Whitmar, cv. Goldar, and Anatone Germplasm) and *E. wawawaiensis* (cv. Secar), for germination, seedling morphological traits, and growth rates at the immature seedling stage. We monitored germination and immature seedling growth in a growth chamber in two separate experiments, one under low (5/10°C) and the other under high (15/20°C) day/night temperatures. Compared to the average of the two perennials, *B. tectorum* was 93% (77%) greater at high (and low) temperature for root:shoot length ratio, but only 14% (14%) greater for root:shoot biomass ratio and 12% (19%) lower for SLA. This suggests that *B. tectorum*'s substantial investment in surface area of roots, rather than in shoot length, root biomass, or leaf area, may be responsible for the annual's success at the early seedling stage. Compared to *E. wawawaiensis*, *P. spicata* averaged 65% (41%) higher shoot biomass, 39% (88%) higher root biomass, and 70% (10%) higher absolute growth rate, but 25% (15%) lower SLA and 15% (36%) lower specific root length (SRL) at high (and low) temperatures, respectively. Although *P. spicata*'s greater productivity may initially make for better seedling establishment than *E. wawawaiensis*, it may also prove disadvantageous in competitive or highly resource-limited environments where high SLA or SRL could be an advantage.

Resumen

Pseudoroegneria spicata (Pursh) A. Löve y *Elymus wawawaiensis* J. Carlson & Barkworth son dos pastos perennes nativos ampliamente utilizados para la restauración de pastizales naturales de la región comprendida entre las Rocallosas y las Sierras Nevadas del Oeste de los Estados Unidos (Intermountain West). Sin embargo, el rápido establecimiento y dispersión de *Bromus tectorum* L., una planta invasora anual, ha ocasionado una disminución en la abundancia de pastos perennes nativos. La proliferación de *B. tectorum* ha sido atribuida a su germinación temprana, su habilidad superior de crecer en condiciones de bajas temperaturas, su elevada producción radicular, y una elevada área foliar específica (AFE). Con la finalidad de mejorar el éxito de los proyectos de restauración, comparamos la germinación, los atributos morfológicos de las plántulas, y las tasas de crecimiento en los estadios previos a la madurez de las plántulas de *B. tectorum* y germoplasma disponible comercialmente de dos pastos cespitosos perennes, *P. spicata* (cv. Whitmar, cv. Goldar, y Anatone Germplasm) y *E. wawawaiensis* (cv. Secar). Monitoreamos la germinación y el crecimiento de plántulas durante los estadios previos a la madurez en una cámara de crecimiento en dos experimentos diferentes, uno en condiciones de baja (5/10°C) y otro en condiciones de alta (15/20°C) temperatura diurna/nocturna. Comparado con el promedio de ambas especies perennes, *B. tectorum* fue 93% (77%) superior en condiciones de alta (y baja) temperatura en la proporción del largo de raíz:tallo, pero solamente 14% (14%) mayor en la proporción de biomasa raíz:tallo y 12% (19%) más bajo en AFE. Esto sugiere que el éxito de esta especie anual durante los estadios tempranos de la plántula podría deberse a la inversión sustantiva en el área de superficie de raíces, en vez de invertir en largo de tallos, biomasa radicular, o área foliar. Comparado con *E. wawawaiensis*, *P. spicata* tuvo una biomasa de tallos 65% (41%) más elevada, una biomasa radicular 39% (88%) más elevada y una tasa absoluta de crecimiento 70% (10%) más elevada, pero un AFE 25% (15%) inferior y una longitud específica de raíces (LER) 15% (36%) inferior bajo temperaturas altas (y bajas), respectivamente. Si bien la productividad superior de *P. spicata* podría inicialmente producir mejor establecimiento de

---

This research has been partially funded by the Great Basin Native Plant Selection and Increase Project, and we gratefully acknowledge this contribution by the Bureau of Land Management and the U.S. Forest Service Rocky Mountain Research Station.

At the time of research, Ray-Mukherjee was a research assistant, Department of Wildland Resources and the Ecology Center, and research geneticist, USDA-ARS Forage and Range Research Laboratory, both at Utah State University, Logan, UT 84322, USA.

Correspondence: Jayanti Ray-Mukherjee, Dept of Wildland Resources, Utah State University, Logan, UT 84321, USA. Email: plants@scientist.com

Manuscript received 26 June 2010; manuscript accepted 22 March 2011.

plántulas comparado con *E. wawawaiensis*, podría también estar en desventaja en situaciones de alta competencia o en ambientes con alta limitación de recursos en los que un elevado AFE o LER podrían ser ventajosos.

Key Words: absolute growth rate, bluebunch wheatgrass, relative growth rate, Snake River wheatgrass, specific leaf area, specific root length

INTRODUCTION

Past grazing practices, invasion by flammable weeds, and resultant increased fire frequency have contributed to declines in the abundance of perennial bunchgrasses, such as *Pseudoroegneria spicata* (Pursh.) A. Löve, on the rangelands of North America's Intermountain West (Daubenmire 1942; Young and Allen 1997; Whisenant 1999). Consequently, this C_3 species is widely used for restoration applications in the region (Monsen et al. 2004). Prior to 1986, another C_3 perennial Triticeae bunchgrass, *Elymus wawawaiensis* J. Carlson & Barkworth, was taxonomically confused with *P. spicata*, owing to their superficial morphological resemblance (Carlson and Barkworth 1997). Since the commercial release of "Secar" *E. wawawaiensis* in 1980, this cultivar has become widely and successfully used as a restoration surrogate for *P. spicata* (Jones 2003). However, the realization that Secar is not *P. spicata* has made its use somewhat controversial. In addition, the natural distribution of *E. wawawaiensis* is mostly limited to eastern Oregon, eastern Washington, and northern and central Idaho (Carlson and Barkworth 1997), while most restoration sites where *E. wawawaiensis* is used fall outside of this area. Nevertheless, Secar *E. wawawaiensis* continues to be widely used in the Intermountain West (Young and Allen 1997; Monsen et al. 2004).

When present, invasive annual grasses, particularly *Bromus tectorum* L., threaten the integrity of sagebrush steppe rangelands (Jones and Monaco 2009) by limiting native grass seedling establishment (Harris and Wilson 1970; Young and Allen 1997) and replacing native vegetation (Sperry et al. 2006). Invasion by *B. tectorum* greatly increases fire frequency (Brooks et al. 2004), consequently damaging native vegetation (Whisenant 1990) and possibly modifying the soil environment in a way that reinforces its dominance (Saetre and Stark 2005; Norton et al. 2007). *B. tectorum* currently dominates large areas in western North America, and additional areas are at risk of invasion (Bradley and Mustard 2006; Jones and Monaco 2009).

The rapid establishment and spread of *B. tectorum* have been attributed to its superior germination, growth, and fitness. For example, it has the ability to germinate in fall, putting spring-germinating perennial seedlings at a competitive disadvantage (Hardegree et al. 2010), and to germinate earlier in the spring than perennial grasses (Harris 1967; Harris and Wilson 1970; Harris 1977; Hardegree et al. 2010). In addition, *B. tectorum* grows vigorously above (Svejcar 1990) and below ground (Harris and Wilson 1970; Harris 1977; Young and Allen 1997; Arredondo et al. 1998) when temperatures are cold and soil moisture is least limiting (Bradford and Lauenroth 2006). This annual grass also produces large quantities of seeds in summer (Svejcar 1990; Young and Allen 1997; Sperry et al. 2006).

The competitive ability of *B. tectorum* has been attributed to functional traits such as high relative growth rate (RGR) (Arredondo et al. 1998), high specific leaf area (SLA) (Svejcar 1990), and high specific root length (SRL) (Svejcar 1990). The high RGR of invasive species is thought to be a major factor contributing to their invasive ability (Grotkopp et al. 2002; James and Drenovsky 2007). Annuals are known to have higher RGR than perennials (Poorter and Garnier 2007), and high RGR often reflects high resource-uptake rates exhibited by invasive species (Grotkopp et al. 2002). Specific leaf area is generally considered to be the best predictor for RGR (Poorter and Garnier 2007), and high SRL is often associated with rapid extraction of water and nutrients (Eissenstat 1991; Ryser 2006), as well as high SLA and RGR (Poorter and Garnier 2007). Studies have shown that *B. tectorum*'s high SRL enables acquisition and utilization of early-season resources that typically diminish over the course of the season (Svejcar 1990; Ryser 2006). However, these studies compare established seedlings or mature plants, and functional-trait expression of germinating seedlings remains mostly unexplored (Jones et al. 2010).

Successful establishment of native grasses is often the limiting factor in sagebrush steppe restoration (Whisenant 1999; Monsen et al. 2004). A better understanding of growth and development of germinating perennial grass seedlings may lead to restoration plant materials with more successful establishment, particularly under cold-temperature conditions. Germination attributes, morphological traits, and growth rates are important factors that contribute to plant establishment (Monsen et al. 2004), especially under low spring temperatures. In this study our objectives were the following: 1) to identify immature seedling traits that may explain *B. tectorum*'s early life-stage advantage relative to two perennial grasses (*P. spicata*, *E. wawawaiensis*) native to the sagebrush steppe; 2) to determine which commercially available native plant materials of these two native bunchgrasses display the best immature seedling-growth characteristics; and 3) to identify perennial-grass seedling traits associated with high productivity and superior growth rate. To this end we compared three commercially available *P. spicata* populations ["Whitmar" (released in 1946), "Goldar" (1989), and Anatone Germplasm (2003)], "Secar" (1980) *E. wawawaiensis*, and *B. tectorum* for germination, seedling morphological traits, and seedling growth under favorable (high temperature) and unfavorable (low temperature) conditions. In addition to days to germination, days to shoot initiation, shoot and root biomass, absolute growth rate (AGR), and RGR, we examined seedling morphological growth traits such as shoot and root length, SLA, SRL, root-to-shoot (R:S) biomass ratio, and R:S length ratio.

We predicted that *B. tectorum* would germinate sooner, produce greater shoot and root biomass, and produce greater shoot and root length, as well as display higher R:S biomass ratio, R:S length ratio, SLA, and SRL than *P. spicata* and *E. wawawaiensis*, particularly at low temperature. We also predicted that *B. tectorum* would have the highest seedling RGR and that perennial plant materials with levels of trait expression most similar to *B. tectorum* would also have high seedling RGR. Based on previous findings (Gibbs et al. 1991; Kitchen and Monsen 1994), we also anticipated that the two native perennial grasses, once erroneously regarded as the same species, would display similar seedling biomass and growth characteristics. Finally, we predicted that the more recently released *P. spicata* plant materials, Goldar and particularly Anatone Germplasm, would display superior seedling growth characteristics relative to Whitmar, the first released *P. spicata* plant material.

MATERIALS AND METHODS

We employed three released populations of *P. spicata* (Goldar, Whitmar, and Anatone Germplasm), Secar *E. wawawaiensis*, and *B. tectorum* in this study. Seeds of all four perennial populations were produced in a common environment at Utah State University's Evans Farm at Millville, Utah, to avoid bias from confounded maternal effects resulting from multiple seed-production environments. While all seeds were produced in the same field, individual seed-production plots were established perpendicular to the prevailing wind and isolated by distance to minimize cross-pollination between plots. Seeds were harvested in 2007, cleaned, and refrigerated (5°C) until experimental use. *Bromus tectorum* seeds were harvested in 2005 from multiple locations in Idaho, USA, bulked, cleaned, and refrigerated until experimental use. Simultaneously, we conducted a laboratory germination trial with seeds collected from these sources with approximately 90–94% germination success of all seed sources.

We conducted two separate growth-chamber (Percival Scientific, Perry, IA) experiments under two contrasting temperature regimes. Both temperature regimes featured 12-h days and nights, and temperatures were recorded using data loggers (Watchdog, Spectrum Technologies, Plainfield, IL). Actual day/night temperatures were $20 \pm 1.25^\circ\mathrm{C}/15 \pm 2.16^\circ\mathrm{C}$ for the high-temperature regime and $10 \pm 0.33^\circ\mathrm{C}/5 \pm 0.28^\circ\mathrm{C}$ for the low-temperature regime. Light intensity was calculated (average $191.4 \pm 9\ \mu\mathrm{moles} \cdot \mathrm{m}^2 \cdot \mathrm{s}^{-1}$ across temperatures) using a LI COR Model LI-185B photometer with a LI-190SB quantum sensor (LI-COR Biosciences, Lincoln, NE).

A total of 1 000 seeds across two temperature regimes and three species, including the three *P. spicata* populations, were arranged in a completely randomized design. Four seeds (subsamples) were placed in a single germination pouch (CYG seed germination pouch, Mega International, St. Paul, MN), which is a folded plastic sheet enclosing a blotter paper. Twenty-five pouches (replicates) of each population were used in each growth chamber, which were nested within populations. Thus, we evaluated a total of 100 seeds of each population at each temperature.

We sprayed blotter papers to saturation with distilled water, and pouches were rewatered as necessary throughout the experiment to maintain desirable moisture conditions. The study was initiated on 12 August 2008. Each seed was monitored daily, and the dates of first appearance of radicle (approximately 1 mm) and coleoptile (1 mm) were recorded as germination and shoot initiation, respectively. Germination pouches were randomly rotated each week within the growth chambers.

Seedlings from 12 replicates were destructively harvested 8 d following initial watering for the high-temperature experiment and 16 d for the low-temperature experiment. The remaining 13 replicates were harvested 7 d following the first harvest for both temperatures. The low-temperature harvest was delayed relative to high temperature to allow seedlings to be sufficiently sizeable for measuring seedling traits. At harvest, a digital image of each seedling was obtained with a flatbed scanner (300 dpi). Images were analyzed with WinRHIZO Pro Version 2005b (Reagent Instrument, Québec City, Canada) to determine leaf area, leaf length, and root length. Subsequently, shoots and roots were separated and oven dried (60°C for 48 h) to determine dry mass. For each temperature, scanned images were analyzed for shoot and root length, leaf area, SLA ($\mathrm{cm}^2 \cdot \mathrm{mg}^{-1}$), and SRL ($\mathrm{cm} \cdot \mathrm{mg}^{-1}$). Absolute growth rate (AGR) was calculated as $\mathrm{AGR} = [\mu(W_2) - \mu(W_1)]/(t_2 - t_1)$, and relative growth rate was calculated as $\mathrm{RGR} = [\mu(\ln W_2) - \mu(\ln W_1)]/(t_2 - t_1)$, where and W_1 and W_2 were the dry masses (shoot + root) from the first and second harvests, respectively, and μ was the mean biomass for the indicated harvest.

Data were analyzed using SAS 9.1.3 (SAS 2003), and data were transformed as necessary to meet normality assumptions (Table 1). Data were analyzed separately for each temperature, and nontransformed means were used for graphical presentation. Using the formulas mentioned above and the data collected at the two harvests, we used ESTIMATE statements in PROC MIXED in SAS to calculate means and standard errors for AGR and RGR for species and populations. From these values, confidence intervals were calculated to separate individual means.

We used data from all replicates to calculate days to germination and days to shoot initiation, while the remaining traits were determined only from replicates assigned to the second harvest. For mean comparisons, one-way analysis of variance (ANOVA) was performed for each variable separately with PROC MIXED. We used a comparison-wise error term rather than an experiment-wise error term because we wished to perform separate examinations for each of the functional traits. We set the minimum critical alpha value for tests of significance at 0.05.

RESULTS

Bromus tectorum germinated (initiated roots) approximately 1.5 d earlier than *P. spicata* and Secar *E. wawawaiensis* at high temperature ($P < 0.0001$), and approximately 3 d earlier at low temperature ($P < 0.0001$) (Table 1; Fig. 1a). The two native perennial species did not differ for days to germination at either temperature ($P > 0.05$) (Table 1). *Bromus tectorum* initiated shoots (coleoptiles) approximately 0.9 d earlier than *P. spicata* and 1.1 d earlier than Secar *E. wawawaiensis* at high temperature ($P < 0.0001$), while *B. tectorum* initiated shoots 1.0, 1.3, 2.6, and 1.9 d earlier than Whitmar, Anatone, Goldar, and *E. wawawaiensis*, respectively, at low temperature ($P < 0.0001$) (Table 1; Fig. 1b).

At high temperature, *P. spicata* and *B. tectorum* produced 65% and 29% greater shoot biomass than *E. wawawaiensis*, respectively ($P < 0.0001$) (Table 1; Fig. 2a). Meanwhile, at low

Table 1. Analysis of variance (*F* values) for 10 seedling traits of three populations of *Pseudoroegneria spicata*, Secar *Elymus wawawaiensis*, and *Bromus tectorum* at high temperature and low temperature.

Traits	df	Transformations	Species[1]	Among *P. spicata* populations[1]
		High-temperature experiment		
Days to root initiation	2,120	Fourth root	270.64***	2.30
Days to shoot initiation	2,120	Log	66.45***	0.89
Shoot (S) biomass (mg)	2,60	Cube root	37.82***	6.27**
Root (R) biomass (mg)	2,60	—	7.57*	2.82
R:S biomass ratio	2,60	—	7.45**	4.47*
Shoot length (mm)	2,60	—	85.22***	12.49***
Root length (mm)	2,60	—	14.27***	4.11*
R:S length ratio	2,60	Square root	95.10***	3.74
SLA ($cm^2 \cdot mg^{-1}$)	2,60	Log	20.69***	2.31
SRL ($cm \cdot mg^{-1}$)	2,60	Log	3.19*	0.62
		Low-temperature experiment		
Days to root initiation	2,120	Reciprocal square root	135.26***	1.83
Days to shoot initiation	2,120	Cube root	61.51***	31.37***
Shoot (S) biomass (mg)	2,55	Cube root	7.50**	0.05
Root (R) biomass (mg)	2,55	Square root	13.89***	1.38
R:S biomass ratio	2,55	Square root	9.24**	5.28**
Shoot length (mm)	2,55	—	39.97***	0.43
Root length (mm)	2,55	—	7.97**	5.83**
R:S length ratio	2,55	Cube root	62.71***	2.83
SLA ($cm^2 \cdot mg^{-1}$)	2,55	Log	14.99***	0.26
SRL ($cm \cdot mg^{-1}$)	2,55	Log	8.94***	1.10

[1] $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.0001$.

temperature, *P. spicata* and *B. tectorum* produced 41% and 30% greater shoot biomass than *E. wawawaiensis*, respectively ($P < 0.05$) (Table 1; Fig. 2a). Among *P. spicata* populations, shoot biomass of Goldar and Anatone was 24% and 16% greater, respectively, than Whitmar at high temperature ($P < 0.05$), while at low temperature the populations displayed similar shoot biomass ($P > 0.05$) (Table 1; Fig. 2a).

Under both temperatures, species differed for root biomass, while *P. spicata* populations did not ($P > 0.05$) (Table 1; Fig. 2b). At high temperature, root biomass of *E. wawawaiensis* was 28% and 26% lower than *P. spicata* and *B. tectorum*, respectively ($P < 0.05$), while at low temperature, these differences, 46% and 40%, were much greater ($P < 0.0001$) (Table 1; Fig. 2b). *Bromus tectorum* and Whitmar displayed

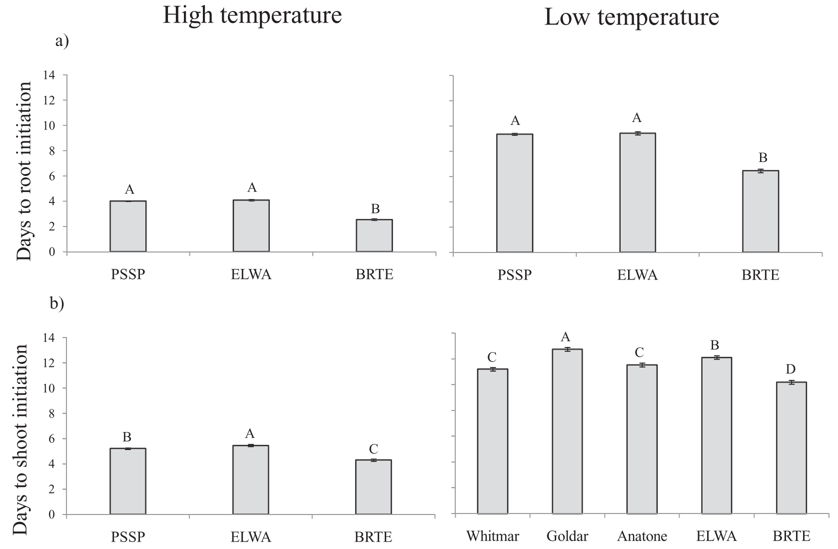

Figure 1. Means and standard errors at high (left panels) and low (right panels) temperatures for (**a**) days to root initiation and (**b**) days to shoot initiation for three *Pseudoroegneria spicata* (PSSP) populations, or their mean when they were not significantly different ($P > 0.05$), Secar *Elymus wawawaiensis* (ELWA), and *Bromus tectorum* (BRTE). Different letters represent significant ($P < 0.05$) differences among populations or species within each temperature.

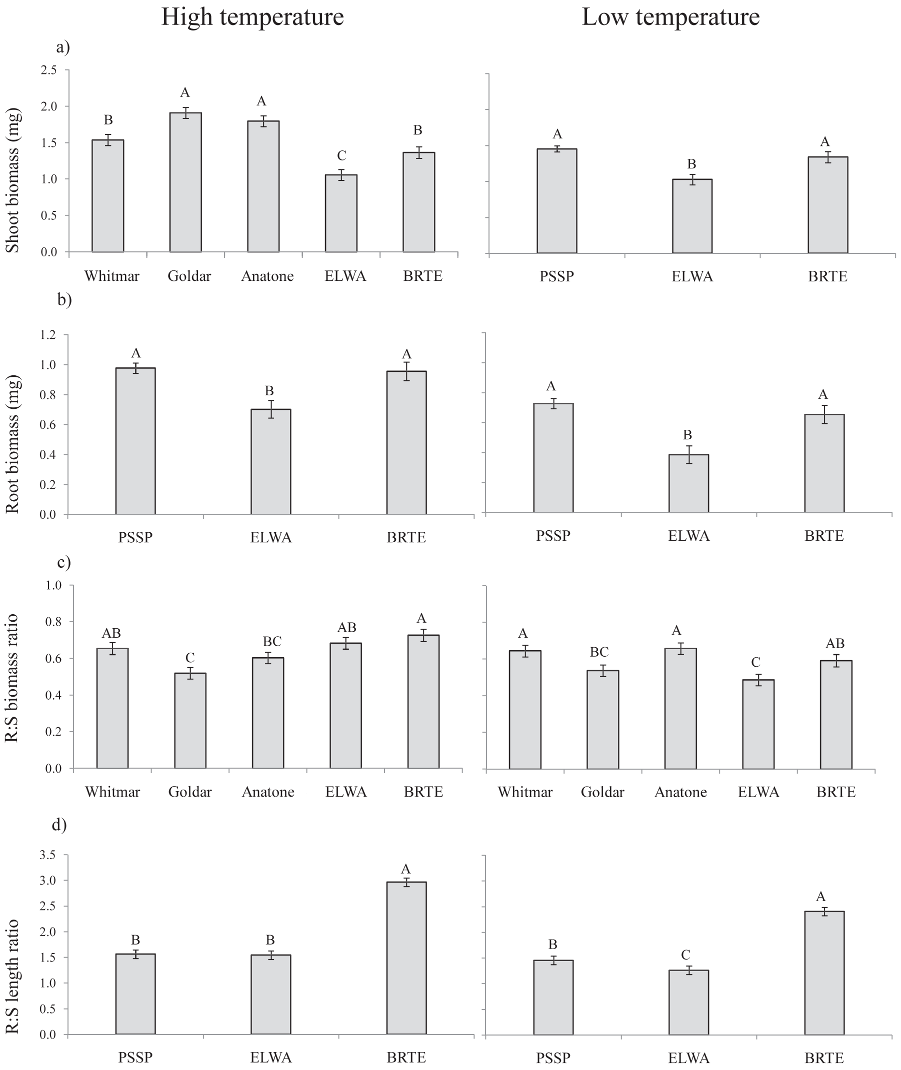

Figure 2. Means and standard errors at high (left panels) and low (right panels) temperatures for (**a**) shoot biomass, (**b**) root biomass, (**c**) root:shoot biomass ratio (R:S biomass ratio, and (**d**) root:shoot length ratio (R:S length ratio) for three *Pseudoroegneria spicata* (PSSP) populations, or their mean when they were not significantly different ($P > 0.05$), Secar *Elymus wawawaiensis* (ELWA), and *Bromus tectorum* (BRTE). Different letters represent significant ($P < 0.05$) differences between populations or species within each temperature.

high R:S biomass ratios at both temperatures, while Goldar was low at both temperatures (Fig. 2c). Anatone exhibited a high R:S biomass ratio at low temperature and a low ratio at high temperature, while Secar *E. wawawaiensis* displayed the reverse (Fig. 2c). Great differences among species were found for R:S length ratio at both temperatures (Table 1). At high temperature, the invasive *B. tectorum* displayed 91% greater R:S length ratio ($P < 0.0001$) than *P. spicata* and *E. wawawaiensis*, which were similar ($P > 0.05$) (Fig. 2d). At low temperature, R:S length ratio of *Bromus tectorum* was 65% greater than *P. spicata* and 90% greater than *E. wawawaiensis*, and *P. spicata*'s R:S length ratio was 15% greater than that of *E. wawawaiensis* ($P < 0.0001$) (Fig. 2d). The three *P. spicata* populations were similar for R:S length ratio under both temperature regimes ($P > 0.05$) (Table 1).

No differences were found among *P. spicata* populations for SLA or SRL at either temperature (Table 1). At high temperature, *E. wawawaiensis* produced 31% more SLA than the mean *P. spicata* and *B. tectorum* ($P < 0.0001$), which were similar ($P > 0.05$) (Table 1; Fig. 3a). At low temperature, SLA of *E. wawawaiensis* was 18% greater than *P. spicata* and 34% greater than *B. tectorum* ($P < 0.0001$) (Fig. 3a). At high temperature, *Elymus wawawaiensis* produced the highest SRL, with *P. spicata* being lowest ($P < 0.05$) and *B. tectorum* being intermediate and not different from the other species ($P > 0.05$) (Table 1; Fig. 3b). At low temperature, *E. wawawaiensis* was again highest for SRL, this time being 53% greater than the mean of *P. spicata* and *B. tectorum*, which were similar ($P > 0.05$) (Fig. 3b).

On average, *P. spicata* had the highest AGR under both temperature regimes (Fig. 4a), 45% (71%) and 66% (35%) greater than *E. wawawaiensis* and *B. tectorum*, respectively, at high (and low) temperature. *Elymus wawawaiensis* and *B. tectorum* were similar ($P > 0.05$) for AGR at high temperature, but *B. tectorum* was higher than *E. wawawaiensis* at low temperature. Among *P. spicata* populations, Anatone and Goldar exceeded Whitmar for AGR at high temperature ($P < 0.05$), while at low temperature, the *P. spicata* populations

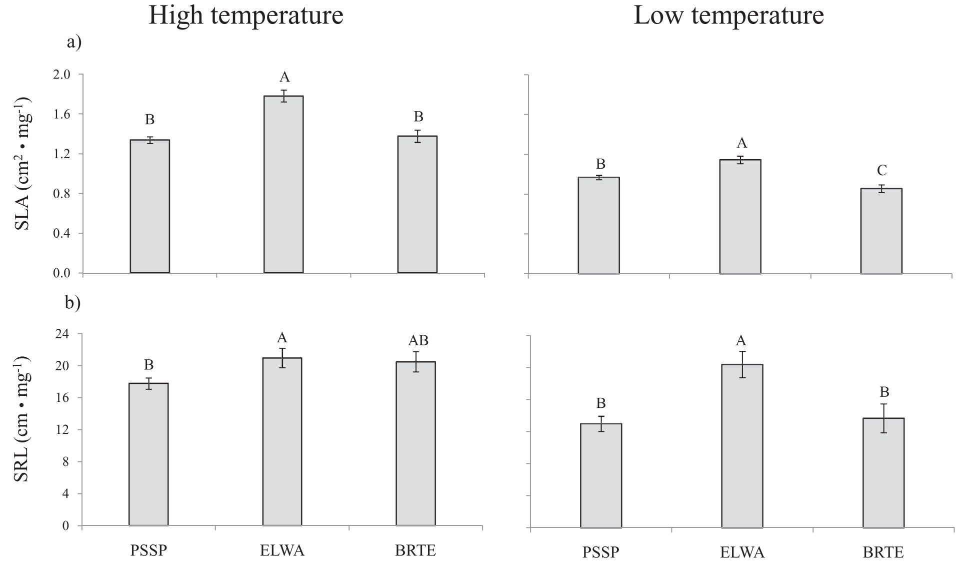

Figure 3. Means and standard errors at high (left panels) and low (right panels) temperatures for (**a**) specific leaf area (SLA) and (**b**) specific root length (SRL) for the mean of three not significantly different ($P > 0.05$) *Pseudoroegneria spicata* (PSSP) populations, Secar *Elymus wawawaiensis* (ELWA), and *Bromus tectorum* (BRTE). Different letters represent significant ($P < 0.05$) differences between species within each temperature.

were similar ($P > 0.05$). At high and low temperature, *B. tectorum* displayed 40% and 27% lower RGR ($P < 0.0001$), respectively, than the mean of the perennial species, which were similar ($P > 0.05$) (Fig. 4c). The three *P. spicata* populations did not differ ($P > 0.05$) in RGR for either temperature regime.

DISCUSSION

Our first objective was to identify seedling traits that are likely to contribute to *B. tectorum*'s rapid establishment. Overall, the most striking difference displayed by *B. tectorum* compared to the native perennials was the former's exceptionally high R:S length ratio, which was evident at both temperatures. In addition, in accordance with our prediction, *B. tectorum* also produced high R:S biomass ratio under both temperature regimes. These data suggest that *B. tectorum* displays a strategy of emphasizing root biomass, and particularly root surface area, in young seedlings at the expense of photosynthetic shoot biomass and leaf area. In semiarid environments, this strategy may pay dividends as the season progresses and plant competition increases for declining soil moisture.

Consistent with our prediction, *B. tectorum* germinated and initiated shoots earlier than the perennials under both temperature regimes, and these differences were greater at cold temperature. Mean germination time is considered to be a

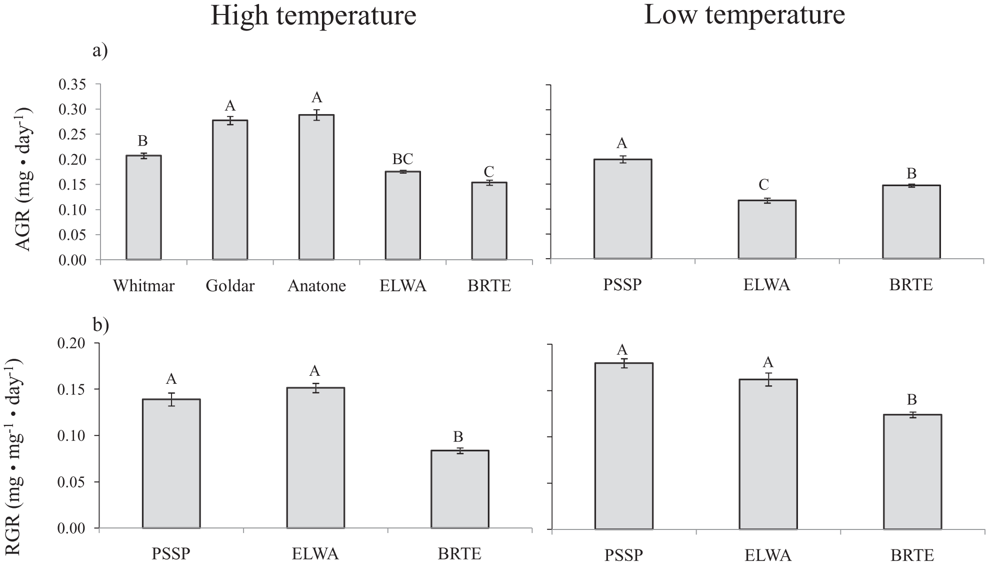

Figure 4. Means and standard errors at high (left panels) and low (right panels) temperatures for (**a**) absolute growth rate (AGR) and (**b**) relative growth rate (RGR) for three *Pseudoroegneria spicata* (PSSP) populations, or their mean when they were not significantly different ($P > 0.05$), Secar *Elymus wawawaiensis* (ELWA), and *Bromus tectorum* (BRTE). Different letters represent significant ($P < 0.05$) differences between populations or species within each temperature.

highly phylogenetically conserved trait (Norden et al. 2009), and early germination may be associated with a species's invasive ability (Grotkopp et al. 2002). However, early germination of *B. tectorum* was not associated with high AGR or RGR at the early seedling stage, contrary to our expectation based on the literature (Aguirre and Johnson 1991; Grotkopp et al. 2002). This disparity in AGR may be attributed to the small seed mass (2.63 ± 0.05 $\text{mg} \cdot \text{seed}^{-1}$) of the annual compared to the perennials (3.76 ± 0.20 mg seed^{-1}). The substantially lower RGR of *B. tectorum* compared to that of both perennials is more surprising and was associated with its low SLA. Relative growth rate may change over time in a plant's life cycle (Hunt 1982), and typically RGR is highest (RGR_{max}) during the first few days postgermination and then declines over time. A low RGR for *B. tectorum* and a high RGR for *P. spicata* could thus result from temporal differences in RGR_{max} between species (Hunt 1982; Grotkopp et al. 2002). Because *B. tectorum* germinates in the fall, it may require seedling tissues that are well constructed (low SLA and SRL) to overwinter. At the same time, it is conceivable that *B. tectorum* may shift its growth strategy in spring to favor greater surface area that may fuel faster growth.

Our second objective was to compare the four commercially available perennial populations for immature seedling characteristics that may contribute to enhanced seedling growth. In contrast to our prediction, we found that *P. spicata* produced greater shoot biomass, root biomass, and shoot length than Secar *E. wawawaiensis* under both temperature regimes. On the other hand, SLA for Secar was consistently greater than that for *P. spicata* at both temperatures. In addition, Secar had 50% greater SRL than *P. spicata* at low temperature. As shown in previous studies, high SLA, SRL, and RGR are properties of fast-growing species (Poorter and Garnier 2007). This suggests that, of the two native perennials, *E. wawawaiensis* may be better equipped, by virtue of its high SLA and SRL, to compensate for its low initial biomass as the growing season progresses (Zhang and Maun 1990). Consistent with our final prediction, the most recently released *P. spicata* population, Anatone, displayed superior seedling growth characteristics compared to the earliest-released Whitmar, particularly at high temperature.

Overall, our results suggest that *E. wawawaiensis* is more conservative in shoot and root biomass investment relative to surface-area investment (SLA and SRL) at the immature-seedling stage at both temperatures, while *P. spicata* exhibits the opposite trend. Differences in immature-seedling traits could be crucial for seedling establishment, particularly under the low temperatures of early spring, the time of year when soil moisture is most favorable for seedling growth on Intermountain rangelands. For example, low temperature reduced root biomass more for Secar *E. wawawaiensis* (45%) than *P. spicata* (26%), while low temperature reduced shoot biomass more for *P. spicata* (33%) than for *E. wawawaiensis* (22%). Together, these numbers resulted in a 28% reduction in R:S biomass ratio by low temperature for *E. wawawaiensis*, compared to only a 6% reduction for *P. spicata*. In contrast to root biomass, reductions in root length due to low temperature were similar in *P. spicata* (54%) and *E. wawawaiensis* (58%). This resulted in a 27% reduction in SRL from high to low temperature for *P. spicata*, compared to a 3% decline for *E. wawawaiensis*. On the other hand, SLA of *P. spicata* was reduced 28% from high to low temperature, while the reduction was 36% for *E. wawawaiensis*.

Our final objective was to identify traits associated with superior seedling growth. Our prediction that perennials most similar to *B. tectorum* would display the greatest RGR was based on the assumption that *B. tectorum* would feature the greatest RGR. However, our data did not support this assumption. Nevertheless, we were able to identify traits in the perennial species that are likely to contribute to superior seedling growth rate.

For AGR, *P. spicata* was clearly superior to *E. wawawaiensis,* which we attribute to its larger seed mass (3.76 $\text{mg} \cdot \text{seed}^{-1}$) relative to *E. wawawaiensis* (2.88 $\text{mg} \cdot \text{seed}^{-1}$). On the other hand, the two perennials were similar for RGR. Traits associated with high AGR in *P. spicata* were high length and biomass of shoots and roots, while traits that likely contributed to high RGR in *E. wawawaiensis* were high SLA and SRL. Specific leaf area and SRL are two traits closely associated with plant life history, and species with high SLA and SRL are associated with high competitive and invasive ability (Grotkopp et al. 2002) and resource-rich environments (Reich et al. 1998; Ryser 2006). Nevertheless, despite originating from a more arid locale than any of the three *P. spicata* populations, Secar *E. wawawaiensis* displayed very high SLA and SRL (Monsen et al. 2004). We believe that high SLA and SRL are two traits that may be crucial for future selection of perennial plant materials for restoration. High SLA may confer high growth rate, and high SRL may enable greater resource extraction (Svejcar 1990; Arredondo et al. 1998).

IMPLICATIONS

Our comparison at the immature seedling stage reveals two traits that may contribute to *B. tectorum*'s successful establishment and great competitive ability: 1) rapid germination and 2) a high investment in root length relative to shoot length. While we predicted that perennial species that displayed trait levels most similar to *B. tectorum* would display greatest seedling growth, we found that *P. spicata* and *E. wawawaiensis* were quite similar for the two above-mentioned traits, particularly when compared to *B. tectorum*. In spite of this, inspection of other traits revealed fundamental differences that elucidate contrasting seedling-growth strategies for these two perennial grasses. While *P. spicata*'s high AGR provides an advantage for initial seedling establishment, its relatively low SLA and its greater investments in biomass, despite a greater RGR (RGR_{max}), may eventually limit its growth rate (Harris 1977; Reich et al. 1994) as resource availability declines. Secar *E. wawawaiensis*, on the other hand, displays greater above- and below-ground surface area per unit biomass that likely contributes to biomass accumulation and competitive ability once established.

Bromus tectorum is an extremely effective competitor with perennial grasses, particularly under cold temperatures. Establishment of seeded perennial grasses could be improved if seedlings displayed improved cold-temperature growth in spring, making them more competitive with spring-germinating *B. tectorum*. Perennial grass materials that germinate earlier and display higher R:S length ratios, particularly under cold temperatures, are potentially more effective competitors with *B. tectorum*. While this research was conducted on bluebunch wheatgrass (*P. spicata*) and Snake River wheatgrass (*E. wawawaiensis*), the results may provide clues for selecting for improved cold-temperature growth potential in other perennial grass species, such as sandberg bluegrass (*Poa secunda* J. Presl), big squirreltail (*Elymus multisetus* [J. G. Sm.] Burtt Davy), and bottlebrush squirreltail (*E. elymoides* [Raf.] Swezey).

ACKNOWLEDGMENTS

We thank Ronald J. Ryel and Christopher A. Call for their fruitful comments and intriguing discussions. We also thank Dale Nielson, Jenny Christiansen, Tren Hagman, and Phil Harrison for their technical help throughout the project and Susan Durham for her help with statistical analysis. We thank Josh Leffler for his useful comments prior to journal submission. We also thank the two anonymous reviewers, whose contributions improved our manuscript to a great extent.

LITERATURE CITED

Aguirre, L., and D. A. Johnson. 1991. Root morphological development in relation to shoot growth in seedlings of four range grasses. *Journal of Range Management* 44:341–346.

Arredondo, J. T., T. A. Jones, and D. A. Johnson. 1998. Seedling growth of Intermountain perennial and woody annual grasses. *Journal of Range Management* 54:584–589.

Bradford, J. B., and W. K. Lauenroth. 2006. Controls over invasion of *Bromus tectorum*: the importance of climate, disturbance, soil and seed availability. *Journal of Vegetation Science* 17:693–704.

Bradley, B. A., and J. F. Mustard. 2006. Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications* 16:1132–1147.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. Ditomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effect of invasive alien plants on fire regimes. *Bioscience* 54:677–688.

Carlson, J. R., and M. E. Barkworth. 1997. *Elymus wawawaiensis*: a species hitherto confused with *Pseudoroegneria spicata* (Triticeae, Poaceae). *Phytologia* 83:312–330.

Daubenmire, R. F. 1942. An ecological study of the vegetation of southeastern Washington and adjacent Idaho. *Ecological Monographs* 12:53–79.

Eissenstat, D. M. 1991. On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. *New Phytologist* 118:63–68.

Gibbs, J. L., G. Young, and J. R. Carlson. 1991. Registration of 'Goldar' bluebunch wheatgrass. *Crop Science* 31:1708.

Grotkopp, E., M. Rejmánek, and T. L. Rost. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life history strategies of 29 pine (*Pinus*) species. *American Naturalist* 159:396–419.

Hardegree, S. P., C. A. Moffet, B. A. Roundy, T. A. Jones, S. J. Novak, P. E. Clark, F. B. Pierson, and G. N. Flerchinger. 2010. A comparison of cumulative-germination response of cheatgrass (Bromus tectorum L.) and five perennial bunchgrass species to simulated field-temperature regimes. *Environmental and Experimental Botany* 69:320–327.

Harris, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89–111.

Harris, G. A. 1977. Root phenology as a factor of competition among grass seedlings. *Journal of Range Management* 30:172–177.

Harris, G. A., and A. M. Wilson. 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology* 51:530–534.

Hunt, R. 1982. Plant growth curves: the functional approach to plant growth analysis. London, UK: Edward Arnold. 248 p.

James, J. J., and R. E. Drenovsky. 2007. A basis of relative growth rate differences between native and invasive forb seedlings. *Rangeland Ecology & Management* 60:395–400.

Jones, T. A. 2003. The Restoration Gene Pool concept: beyond the native vs. non-native debate. *Restoration Ecology* 11:281–290.

Jones, T. A., and T. A. Monaco. 2009. A role for assisted evolution in designing native plant materials for domesticated landscapes. *Frontiers of Ecology and the Environment* 10:541–547.

Jones, T. A., T. A. Monaco, and J. J. James. 2010. Launching the counterattack: interdisciplinary deployment of functional traits to repair Intermountain rangelands damaged by annual grass invasion. *Rangelands* 32:38–42.

Kitchen, S. G., and S. B. Monsen. 1994. Germination rate and emergence success in bluebunch wheatgrass. *Journal of Range Management* 47:145–150.

Monsen, S. B., R. Stevens, and N. L. Shaw. 2004. Grasses. *In:* S. B. Monsen, R. Stevens, and N. L. Shaw [eds.]. Restoring western ranges and wildlands. Vol. 2. Fort Collins, CO, USA: U.S. Forest Service, General Technical Report RMRS-GTR 136. 698 p.

Norden, N., M. I. Daws, C. Antoine, M. A. Gonzalez, N. C. Garwood, and J. Chave. 2009. The relationship between seed mass and mean time to germination for 1037 tree species across five tropical forests. *Functional Ecology* 23:203–210.

Norton, J. B., T. A. Monaco, and U. Norton. 2007. Mediterranean annual grasses in western North America: kids in a candy store. *Plant and Soil* 298:1–5.

Poorter, H., and E. Garnier. 2007. Ecological significance of inherent variation in relative growth rate and its components. *In:* F. I. Pugnaire and F. Valladares [eds.]. Functional Plant Ecology. Boca Raton, FL, USA: CRC Press. p. 67–100.

Reich, P. B., J. Oleksyn, and M. J. Tjoelker. 1994. Seed mass effects on germination and growth of diverse European Scots pine populations. *Canadian Journal of Forest Research* 24:306–320.

Reich, P. B., M. G. Tjoelker, M. B. Walters, D. W. Vanderklein, and C. Buschena. 1998. Close association of RGR, leaf and root morphology, seed mass, and shade tolerance in seedlings of nice boreal tree species grown in high and low light. *Functional Ecology* 12:327–338.

Ryser, P. 2006. The mysterious root length. *Plant and Soil* 286:1–6.

Saetre, P., and J. M. Stark. 2005. Microbial dynamics and carbon and nitrogen cycling following re-wetting of soils beneath two semi-arid plant species. *Oecologia* 142:247–260.

SAS [computer program]. 2003. Version 9.1.3. Cary, NC, USA: SAS Institute. 707 p.

Sperry, L. J., J. Belnap, and R. D. Evans. 2006. *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed grassland ecosystem. *Ecology* 87:603–615.

Svejcar, T. J. 1990. Root length, leaf area, and biomass of crested wheatgrass and cheatgrass seedlings. *Journal of Range Management* 43:446–448.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. *In:* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller [eds.]. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. 5–7 April 1989; Las Vegas, NV; General Technical Report INT-276. Ogden, UT, USA: USDA Forest Service, Intermountain Research Station. p. 4–10.

Whisenant, S. G. 1999. Repairing damaged wildlands: a process-oriented, landscape-scale approach. Cambridge, UK: Cambridge University Press. 312 p.

Young, J. A., and Allen, F. L. 1997. Cheatgrass and range science: 1930–50. *Journal of Range Management* 50:530–535.

Zhang, J., and M. A. Maun. 1990. Effects of sand burial on seed germination, seedling emergence, survival, and growth of *Agropyron psammophilum*. *Canadian Journal of Botany* 68:304–310.