Drought tolerance in two perennial bunchgrasses used for restoration in the Intermountain West, USA

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Abstract An ideal restoration species for the semi-arid Intermountain West, USA would be one that grows rapidly when resources are abundant in the spring, yet tolerates summer's drought. We compared two perennial C_3 Triticeae Intermountain-native bunchgrasses, the widely occurring *Pseudoroegneria spicata* and the much less widespread *Elymus wawawaiensis*, commonly used as a restoration surrogate for *P. spicata*. Specifically, we evaluated seedlings of multiple populations of each species for biomass production, water use, and morphological and physiological traits that might relate to drought tolerance under three watering frequencies (WFs) in a greenhouse. Shoot biomass of *E. wawawaiensis* exceeded that of *P. spicata* regardless of WF. At low WF, *E. wawawaiensis* displayed 38% greater shoot biomass, 80% greater specific leaf area (SLA), and 32% greater precipitation use efficiency (PUE). One *E. wawawaiensis* population, E-46, displayed particularly high root biomass and water consumption at high WF. We suggest that such a plant material could be especially effective for restoration of Intermountain rangelands by preempting early-season weeds for spring moisture and also achieving high PUE. Our data explain how *E. wawawaiensis* has been so successful as a restoration surrogate for *P. spicata* and highlight the importance of measuring functional traits such as PUE and SLA when characterizing restoration plant materials.

Keywords Bluebunch wheatgrass · Snake River wheatgrass · Specific leaf area · Specific root length · Precipitation use efficiency

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Introduction

Plant functional traits may play an important role in native-plant restoration planning by characterizing species' responses to environmental stress (Naeem 2006). For example, a suite of interrelated morpho-physiological traits may reveal the mechanisms underlying drought tolerance. Slow-growing species with low specific leaf area (SLA, leaf surface area per unit biomass) are known to be more stress tolerant (Lambers et al. 1998). SLA is considered to be the best single predictor of relative growth rate (Chapin et al.

1993; Hunt and Cornelissen 1997; Poorter and Van der Werf 1998; Westoby et al. 1998; Grime 2001; James and Drenovsky 2007; Poorter and Garnier 2007), and rapidly growing species with higher SLA are known to produce greater shoot biomass under high resource availability. Drought tolerance is also favored by a high specific root length (SRL, root length per unit biomass), indicating an increase in belowground absorptive surface area (Ryser 2006). However, rapidly growing species also feature traits that can be disadvantageous under drought conditions, such as low precipitation use efficiency (PUE), high stomatal conductance (g_s), and low root:shoot ratio (R:S) (Ryser and Lambers 1995; Fernández and Reynolds 2000; Poorter and Garnier 2007).

Frequent droughts and competition from invasive annual grasses constrain native-perennial seedling establishment in the arid and semi-arid rangelands of North America's Intermountain West (Daubenmire 1942; Harris 1967; Harris and Wilson 1970; Young and Allen 1997). *Pseudoroegneria spicata* (Pursh.) A. Löve (bluebunch wheatgrass) and *E. wawawaiensis* J. Carlson & Barkworth (Snake River wheatgrass) are perennial, C_3 Triticeae bunchgrasses native to Intermountain West rangeland ecosystems. *Pseudoroegneria spicata* generally occurs in medium- to coarse-textured soils from foothills to mid-montane habitats and is widespread in the region (Ogle 2002a). Due to annual grass invasion and resultant wildfires, restoration efforts have accelerated in the region (Monsen et al. 2004), and this species is prominent in seed mixes used for this purpose.

While *E. wawawaiensis* and *P. spicata* occur on similar soils, the former possesses a much more restricted distribution (Carlson and Barkworth 1997). Furthermore, due to a superficial morphological resemblance, *E. wawawaiensis* was taxonomically confused with *P. spicata* prior to being shown to be genomically distinct (Carlson and Barkworth 1997). In the meantime, 'Secar' *E. wawawaiensis* has become widely used a surrogate for *P. spicata* in restoration applications. Interestingly, the popularity of *E. wawawaiensis* in restoration seeding mixes has continued (Lambert 2006), despite its description as a new species. This is likely because in restoration practices, Secar establishes better and is generally considered to possess greater productivity and superior drought tolerance than commercially available *P. spicata* plant materials (Morrison and Kelley 1981;

Carlson and Barkworth 1997; Young and Allen 1997; Ogle 2002b; Monsen et al. 2004; Lambert 2006).

While drought tolerance of *E. wawawaiensis* is reputed to be greater than *P. spicata* (Ogle 2002b), the relative effect of drought on growth and physiological response of the two species has not been characterized. We investigated the effect of experimental drought on functional traits associated with drought tolerance in four populations of *P. spicata* and two populations of *E. wawawaiensis* in a greenhouse. Along with biomass production and total water use by the species, we examined six additional plant traits: SLA, SRL, PUE, R:S, mid-day leaf water potential (Ψ), and g_s. Our objective was to compare multiple populations of the two species for productivity at three water levels and to identify traits that might be responsible for drought tolerance in these grasses. In addition, we wished to test the validity of the reputation of *E. wawawaiensis* as the more drought tolerant of the two species, which would justify its use as a surrogate for *P. spicata* in restoration practice. We hypothesized that *E. wawawaiensis* would display greater drought tolerance and levels of traits associated with drought tolerance, such as lower SLA, higher R:S, higher SRL, less negative Ψ, lower g_s, and higher PUE.

Materials and methods

Materials for this study included four *P. spicata* populations and two *E. wawawaiensis* populations. The *P. spicata* populations were 'Goldar' (originally from the Umatilla National Forest, WA, 1000–1200 mm average annual precipitation), Anatone germplasm (Anatone Valley, WA, 250–500 mm), P-22 (developed from the P-1 population, origin unknown), and P-26 (developed from P-7 germplasm, a commercially released multiple-origin polycross). The *E. wawawaiensis* populations were 'Secar' (Lewiston, ID, 200–300 mm) and E-46 (developed from populations originating at 10 different locations in ID and WA). Of these six populations, Goldar, Anatone, P-7 (all *P. spicata*), and Secar (*E. wawawaiensis*) are commercially released populations used in contemporary restoration, while the remainder are experimental populations.

Plastic pots (23 cm in height and 8 cm in diameter) were filled with 2,450 g of a 3:1 mix of Kidman

fine sandy loam (coarse-loamy, mixed, mesic Calcic Haploxerolls) and Ricks gravelly loam (coarse-loamy, mesic Calcic Haploxerolls). Water-holding capacity of pots of similar size and equal amount of soil mix was standardized using the gravimetric method (Israelson and West 1922), in which five pots with four drainage outlets apiece were watered to saturation. These pots were covered with paper sheets to preclude evaporation, drained, and weighed every 5 min. Once drainage ceased, final weights averaging 3,010 g were recorded. Percentage relative water content was calculated as: $(Wt_{wet}/Wt_{Dry}) \times 100$, where Wt_{wet} is the weight of wet soil and Wt_{Dry} is the weight of dry soil.

The experiment was conducted at the USDA-ARS Forage and Range Research Laboratory greenhouse at Utah State University, Logan, Utah. Fifty seeds of each population were germinated on blotter paper 1 week before initiation of the experiment. After 1 week, on 13 June 2006, 21 seedlings of similar size of each population were transplanted to pots. The pots had been filled with steam-sterilized soil mixed as described above, except they had no drainage holes in order to maintain them at water-holding capacity for each treatment.

We imposed three levels of drought stress by manipulating watering frequency (WF) based on a preliminary experiment modified from the protocol of Sack and Grubb (2002). Tap water was used for all watering treatments, which were imposed within a week of initiation of the study. The high WF treatment was watered every 4–7 days (18 times in 12 weeks), moderate WF every 10–12 days (8 times), and low WF every 17–21 days (5 times). The low WF treatment was designed to reduce growth without resulting in plant mortality.

The greenhouse temperature ranged from 18 to 31°C, slightly lower than natural summer temperatures in Logan. Immediately following transplanting, pots were watered to 3,010 g, which was previously determined to be field capacity. Pots were rewatered to reach 3,010 g when the total pot mass fell to 2,840 g for the high WF treatment, 2,640 g for the moderate WF treatment, and 2,510 g for the low WF treatment (Fig. 1). At the beginning of the experiment, the high, moderate, and low WF treatments corresponded to 15.9, 7.8, and 2.4% water contents, respectively. The experiment was conducted for 12 weeks under natural day-length conditions under a shadecloth. Pots were fertilized with Miracle-Gro ($20N–20P_2O_5–20K_2O$ with all micronutrients) along with watering (560 ml for each pot, 4.2 g/l) at the initiation of the experiment.

In determining the pot mass for rewatering each treatment, as described above, we did not adjust for increasing fresh weight of the seedlings as the experiment proceeded. As a result, water contents at rewatering declined relative to initial water content (field capacity) as the experiment proceeded and the plants grew. However, based on calculations we made with biomass measured at the end of the experiment when this effect would be the largest, this bias appears to be small. The difference in water content between pots of high- and low-biomass accessions was 0.2%

Fig. 1 Soil-water content at three watering frequencies (WFs) through a 12-week greenhouse experiment (2006). *Points* denote dates that pots were watered to water-holding capacity
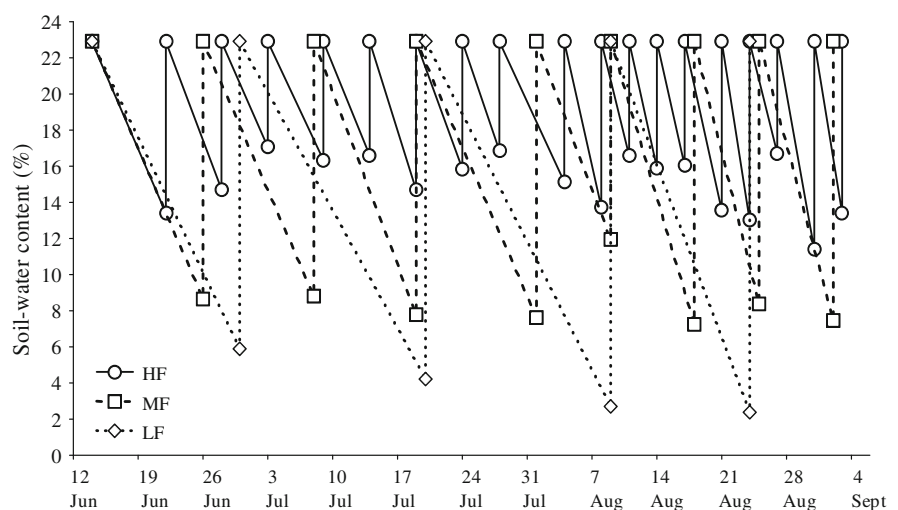
for the low WF treatment and 1.3% for the high WF treatment. Furthermore, this small amount of bias was on the conservative side, making differences we report smaller than they actually were.

A total of 378 pots were arranged in a randomized complete block design with three WF treatments, six populations, and 21 replications as blocks, plus nine control pots. Watering frequencies, species, and population within species were considered to be fixed effects, and replications were considered to be random. Data were analyzed using PROC MIXED in SAS (2003). We used CONTRAST statements to calculate significant difference among populations within the two species and we employed ESTIMATE statements to calculate the interaction of WF and populations within species.

Stomatal conductance was measured at 11.00 to 13.00 h during the last week before harvest on two leaves per plant using a steady-state leaf porometer (SC-1, Decagon Devices, Inc., Pullman, WA). In the same week, mid-day leaf water potential was measured using a Scholander pressure chamber (PMS Instruments Co., Corvallis, OR, USA). Leaf water potential was measured on a single fully green leaf, not more than 1 min following leaf excision. We used a sharp razor blade to incise fully green leaves across the midrib, and 95% of the leaf surface was then inserted it into the slit-seal rubber stub. Pressure was then applied to the stub until the appearance of xylem solution through the cut end of the leaf, and this pressure was recorded (Boyer 1995). Stomatal conductance and Ψ were measured on 15 of 21 replicates, just before rewatering was required for each treatment. Aboveground and below-ground biomass were subsequently harvested and dried (60°C for 3 days), R:S was calculated, and the experiment was terminated on 2 September 2006. To calculate SLA, a sub-sample of five fresh leaves was fed through a LI-3100C leaf-area meter (LI-COR leaf-area meter, Lincoln, NE), after which the leaves were dried (60°C for 3 days) and weighed. We subsampled six replicates to determine SRL. Roots were extracted, cleaned thoroughly under flowing water, scanned using WinRHIZO Pro Version 2005b (Reagent Instrument Inc., Québec City, Canada), and analyzed for total root length. SRL was calculated as total root length divided by root biomass. Total water used by an individual plant was calculated as water added across all watering dates minus water lost through evaporation over the same

dates, as determined by the control pots. PUE of productivity was calculated by dividing total biomass (g) by total water added (kg) for each individual (Kramer and Boyer 1995; Huxman et al. 2004).

Results

Plant mortality was similar for high [7.1 ± 3.1 (SE) %], moderate (4.8 ± 3.0%) and low (7.1 ± 3.5%) WFs. Reduced WF made mid-day leaf water potential (Ψ) more negative (Table 1; Fig. 2a), indicating our treatments were effective in generating variation for drought stress. However, Ψ did not differ among species or populations within species, and neither interacted with WF (Table 1; Fig. 2b). Compared to high WF, moderate and low WFs reduced g_s by 47 and 63%, respectively (Table 1; Fig. 2c). Among all populations, g_s of P-26 *P. spicata* was considerably higher than the other five populations (Fig. 2d), and the WF × population interaction was not significant.

Averaged over WFs and populations, *E. wawawaiensis* produced 22% greater shoot biomass than *P. spicata* (Table 1). *Pseudoroegneria spicata* populations differed in shoot biomass, with Goldar being highest, but *E. wawawaiensis* populations did not (Table 1). When averaged over WFs and populations, *E. wawawaiensis* also produced 35% greater root biomass than *P. spicata* (Table 1). Averaged over WFs, *P. spicata* populations differed in root biomass, while *E. wawawaiensis* populations did not (Table 1). Despite this trend, we found a significant interaction between populations of both species and WF for root biomass (Table 1). Specifically, this resulted because P-26 (78%) and Goldar (76%) *P. spicata* showed greater reduction in root biomass from high WF to low WF than P-22 (66%) and Anatone (68%), as did E-46 *E. wawawaiensis* (81%) relative to Secar (61%). This suggests that P-26, Goldar, and E-46 displayed more phenotypic plasticity for the response of root biomass to soil moisture.

Across species, moderate drought (from high to moderate WF) reduced total biomass by 30%, while severe drought (high to low WF) caused 64% reduction of total biomass. Across WFs and populations, *E. wawawaiensis* produced 24% greater total biomass than *P. spicata* (Table 1; Fig. 3a). The *P. spicata* populations did not interact with WF for total biomass (Table 1), but an interaction of

Table 1 Analysis of variance (F values) for six morphological and four physiological traits of four *P. spicata* (PSSP) and two *E. wawawaiensis* (ELWA) populations at three watering frequencies (WFs)

Traits/effects	WF	Species	PSSP populations	ELWA populations	WF × species	WF × PSSP populations	WF × ELWA populations
df	2	1	3	1	2	6	2
Morphological traits							
Shoot biomass (g)	113.57***	16.71***	5.69**	0.23	2.42	2.00	0.64
Root biomass (g)	109.70***	19.46***	8.93***	1.62	0.45	2.24*	6.13**
Total biomass (g)	65.20***	12.67**	4.32**	1.09	0.40	1.86	4.48*
Root : shoot	76.36***	7.17**	12.00**	16.62*	6.48**	0.94	16.41***
SLA (m^2 kg^{-1})	5.86**	170.58***	2.22	4.65*	5.47**	0.71	2.19
SRL (mm mg^{-1})	0.96	4.95*	7.16**	0.08	2.42	1.45	1.05
Physiological traits							
Ψ (MPa)	22.80***	0.01	0.72	0.66	0.03	1.90	0.94
Total water use (l)	553.66***	15.60***	6.02**	2.03	2.79	2.96**	6.83**
g_s (mmole m^2 s^{-1})	38.93***	15.91***	3.93**	0.27	0.50	1.01	1.89
PUE (g kg^{-1})	33.41***	25.70***	4.82**	0.00	1.66	1.31	0.00

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$
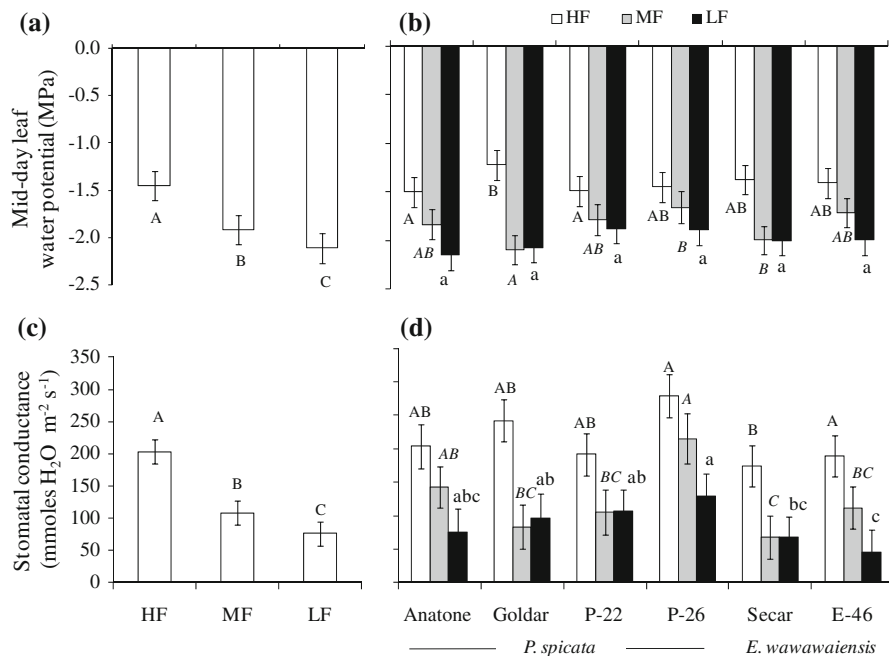
Fig. 2 Means and standard errors for **a** mid-day leaf water potential at three watering frequencies averaged across six populations; **b** mid-day leaf water potential at high (*HF*), moderate (*MF*), and low (*LF*) watering frequencies for four *P. spicata* (PSSP) and two *E. wawawaiensis* (ELWA) populations; **c** stomatal conductance at three WFs averaged across six populations; and **d** stomatal conductance of six populations at HF, MF, and LF. **a**, **c** *Different letters* represent significant ($P < 0.05$) differences among means, and in **b**, **d** *different letters* represent significant ($P < 0.05$) differences among populations within HF (*upper case*), MF (*upper case italics*), and LF (*lower case*). The two-way watering frequency × population interaction was not significant for either mid-day leaf water potential or stomatal conductance

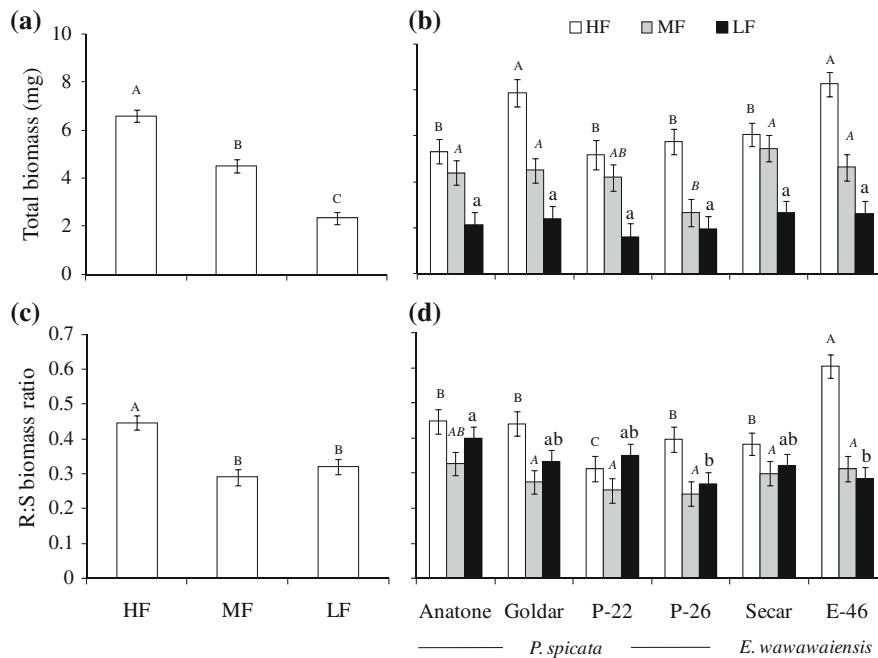**Fig. 3** Means and standard errors for **a** total biomass at high (*HF*), moderate (*MF*), and low (*LF*) watering frequencies averaged across four *P. spicata* and two *E. wawawaiensis* populations; **b** total biomass of the six populations at HF, MF, and LF; **c** root:shoot (R:S) biomass ratio at HF, MF, and LF averaged across six populations *P. spicata* and *E.* *wawawaiensis* populations; and **d** R:S biomass ratio of six populations at HF, MF, and LF. **a**, **c** *Different letters* represent significant ($P < 0.05$) differences among means, and in **b**, **d** *different letters* represent significant ($P < 0.05$) differences among populations within HF (*upper case*), MF (*upper case italics*), and LF (*lower case*)

E. wawawaiensis populations with WF (Table 1) resulted because E-46 was able to produce higher root biomass at high WF relative to Secar (Fig. 3b), rather than to any differences in shoot-biomass production. Moderate to low WF reduced R:S ratio by 35 and 28%, respectively (Table 1; Fig. 3c). *E. wawawaiensis* exhibited 24% greater R:S than *P. spicata* at high WF (Table 1), while under moderate and low WFs both species were similar for this trait (Fig. 3d). Among *P. spicata* populations, Anatone and Goldar displayed greater R:S ratio than P-22 and P-26 when averaged across WFs (Fig. 3d). A significant WF × *E. wawawaiensis* population interaction for R:S ratio (Table 1) resulted from an exceptionally high R:S ratio of E-46 at high WF (Fig. 4c), which resulted from this population's exceptionally plastic root-biomass production (Fig. 3d).

Elymus wawawaiensis produced 37% greater SLA than *P. spicata* under high WF, while this difference grew to 54 and 80% under moderate WF and low WF, respectively, generating a WF × species interaction (Table 1). However, populations within each

of these species responded similarly to WF for SLA (Table 1; Fig. 4a). While SLA of all *P. spicata* populations was quite similar averaged across WFs, E-46 *E. wawawaiensis* displayed 12% greater SLA than Secar (Table 1; Fig. 4a). SRL was not affected by WF (Table 1), although *E. wawawaiensis* displayed 15% greater SRL than *P. spicata*. P-22 had the lowest SRL of the *P. spicata* populations (Table 1; Fig. 4b), while the *E. wawawaiensis* populations were similar for this trait.

Averaged across WFs and populations, *P. spicata* used 5.8% less water than *E. wawawaiensis* (Table 1). The *P. spicata* populations varied in their water use, and they also interacted with WF for this trait (Table 1; Fig. 5a). At high WF, P-22 used less water than the other *P. spicata* populations, while *P. spicata* populations were similar for water use at moderate and low WFs (Fig. 5a). Between *E. wawawaiensis* populations, Secar used 10% less water than E-46 at high WF, while like *P. spicata* populations, their water use was similar at moderate and low WFs (Fig. 5a). PUE was highest for high WF, followed by moderate and low
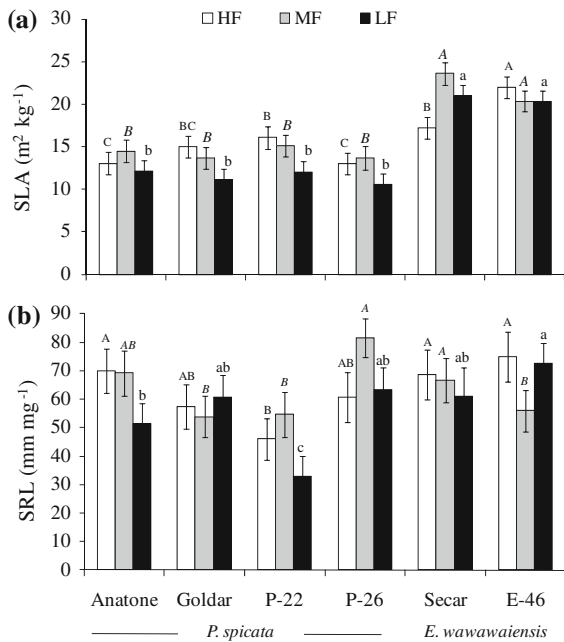
Fig. 4 Comparison of means and standard errors for **a** specific leaf area (SLA) and **b** specific root length (SRL) for four *P. spicata* and two *E. wawawaiensis* populations at high (*HF*), moderate (*MF*), and low (*LF*) watering frequencies. *Different letters* represent significant (*P* < 0.05) differences **a** between the six populations within each WF and **b** between means. The two-way watering frequency × population interaction was not significant for either SLA or SRL
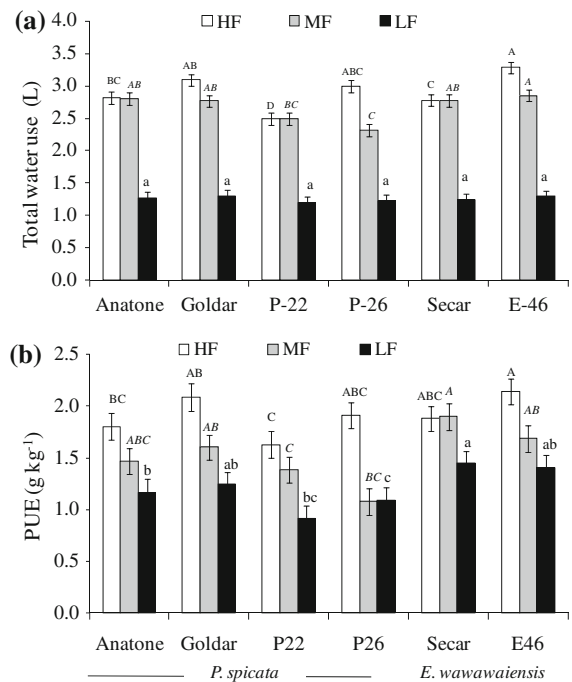
Fig. 5 Means and standard errors for **a** total water use and **b** precipitation use efficiency (PUE) for four *P. spicata* and two *E. wawawaiensis* populations at high (*HF*), moderate (*MF*), and low (*LF*) watering frequencies. *Different letters* represent significant (*P* < 0.05) differences **a** between species and **b** among populations at HF (*upper case*), MF (*upper case italics*), and LF (*lower case*). The two-way watering frequency × population interaction was not significant for PUE

WFs (Table 1), and across WFs, *E. wawawaiensis* was 20% greater for PUE than *P. spicata* (Table 1; Fig. 5b). Across WFs, Goldar exhibited significantly higher PUE than P-22 and P-26, with Anatone being intermediate, while the two *E. wawawaiensis* populations were similar to Goldar (Fig. 5b).

Discussion

In our study, *E. wawawaiensis* produced greater shoot biomass than *P. spicata* under both drought and non-drought conditions. Therefore, based on the plant materials we evaluated, we consider *E. wawawaiensis* to be the more drought tolerant of the two species. If a species is more productive regardless of the level of drought stress, it will likely be more successful in difficult Intermountain West environments. In spite of its greater drought tolerance, *E. wawawaiensis* displayed greater SLA, a trait associated with high

growth rate under favorable conditions and drought susceptibility. In fact, SLA of *E. wawawaiensis* increased relative to *P. spicata* at reduced WFs.

For these species, then, there appears to be no trade-off between growth potential and drought tolerance (Fernández and Reynolds 2000; Grime 2001), although it is possible that inclusion of a more stressful "killing treatment" would have permitted the detection of such a trade-off. The lack of trade-off does not deny the validity of the classical trade-off hypothesis. Rather, a trade-off may lie within some other trait combination, for example, between drought tolerance and defense or survival or between mechanisms of drought tolerance and those of drought resistance (Chapin et al. 1993; Haugen et al. 2008).

While we expected that *E. wawawaiensis*, due to its high SLA, would display lower PUE under drought, we found the opposite to be the case at moderate and low WFs. Although several studies have shown that drought increases PUE and decreases SLA (Wright

et al. 1994; Craufurd et al. 1999; Xu and Zhou 2008; Songsri et al. 2009), in our study, drought reduced both PUE and SLA in *P. spicata* and reduced PUE, but not SLA, in *E. wawawaiensis*. Although there was a positive trend, SLA and PUE were not significantly correlated across WFs. A classical hypothesis in plant ecophysiology would be that PUE increases with drought, but studies showing a higher PUE with increasing drought stress are generally a consequence of mild experimental stress (Ramirez et al. 2008). In our study, PUE decreased with increased experimental drought, which is more likely to be the typical ecological response under severe drought conditions (Songsri et al. 2009). Similar to Songsri et al. (2009), we measured PUE of productivity, a measurement integrated over the duration of the experiment, as opposed to instantaneous PUE. The former measurement is preferable for rangeland plants, as optimal use of water over time involves optimal distribution of stomatal opening along the gradient of aridity (Jones 1992).

The trait combination of high water use under non-limiting conditions and high PUE under limiting conditions may be favored in pulse-regulated arid and semi-arid ecosystems (Goldberg and Novoplansky 1997). In light of this principle, a desirable plant material would have greater water use at high WF and high PUE at low WF, which provides balance between productivity and water conservation (Jones 1992). In our study, E-46 *E. wawawaiensis* used the greatest amount of water at high WF and, along with Secar *E. wawawaiensis*, also had the highest PUE at low WF. Among the *P. spicata* populations, Goldar best displayed this trait combination.

Of the two *E. wawawaiensis* populations, E-46 displayed higher root biomass at high WF, which may have been facilitated by its high SLA relative to Secar. At high WF, E-46 also exhibited higher R:S and water use, yet at low WF, E-46 was similar to Secar for these traits. These data suggest that E-46 is better suited to take advantage of resource pulses than Secar, yet just as well suited to the drought conditions of the inter-pulse period. The superior growth of E-46 plants under non-limiting conditions may allow it to capitalize on and competitively preempt soil resources when they are most abundant in the spring, thereby enhancing its prospects for survival through the difficult first summer of establishment (Goldberg and Novoplansky 1997).

We also found that *E. wawawaiensis*, the species with higher SLA and greater shoot biomass, tended to have lower g_s regardless of WF. Although the difference in g_s between the two species was primarily due to one population, P-26 *P. spicata*, this high-g_s population also exhibited low SLA, indicating a negative association between these traits. High g_s could be a strategy that *P. spicata* employs to lower its leaf temperature to avoid heat stress and photoinhibition (Kappen and Valladares 2007; Pereira and Chaves 1993), as *P. spicata* has fewer seedling leaf hairs compared to *E. wawawaiensis* (Jones et al. 1991). More recent studies focusing on plant architecture show that crown architecture might play an important role conserving water by influencing microclimatic conditions (Ryel et al. 1993, Ramirez et al. 2008). Species with greater SLA, such as *E. wawawaiensis*, may be able to maintain cool temperatures by self-shading, effecting reduced transpiration water loss and increased PUE (Ramirez et al. 2008).

We believe that plant materials like E-46 *E. wawawaiensis*, which express high water use in the pulse period and high PUE in the interpulse period, are more likely to be successful for restoration applications in water-limited pulse-regulated environments, particularly in the face of competition from invasive plants. In our study, Secar *E. wawawaiensis* sustained the smallest reduction of mean root biomass with infrequent watering, followed by P-22 and Anatone *P. spicata*, while Goldar and P-26 *P. spicata* and E-46 *E. wawawaiensis* showed greater reductions in mean root biomass, reflecting greater phenotypic plasticity. Species with greater phenotypic plasticity are generally considered to be less drought tolerant (Fernández and Reynolds 2000, Grime 2001), but E-46 produced as much shoot and root biomass as Secar at moderate and low WFs. High SRL confers greater root absorptive surface area under drought (Ryser 2006), but in our study reduced watering reduced root biomass without reducing SRL. Maintenance of SRL in response to drought, despite a decrease in root biomass, could be a successful strategy for survival in water-limited pulse-regulated environments.

In summary, two species once thought to be taxonomically synonymous, showed significant differences for functional traits and growth rates. If we define a highly productive genotype as one that maintains high productivity under both drought and

non-drought conditions, then *E. wawawaiensis* is the more productive of the two species. Although claims have previously been made that Secar *E. wawawaiensis* is relatively more drought resistant in comparison to *P. spicata* (Morrison and Kelley 1981; Asay et al. 2001), this study is the first to provide an explanation of its drought tolerance based on functional traits. While we correctly hypothesized that *E. wawawaiensis* would be the more drought tolerant of the two species, our predictions regarding associated functional traits were only partially correct. While *E. wawawaiensis* tended to be favored with high SRL, low g_s, and high PUE, it still displayed high SLA. The finding that *E. wawawaiensis* has greater SLA than *P. spicata* helps to explain the former's higher shoot biomass.

This study forms a baseline for understanding drought-tolerance mechanisms in native perennial Triticeae bunchgrasses. Together, these results help to explain how *E. wawawaiensis* has come to be a widely and successfully used restoration surrogate for *P. spicata* in restoration plantings since Secar's release in 1980. Water use, PUE, SLA, and SRL are functional traits that deserve to be emphasized when evaluating species and developing new plant materials for the purpose of rangeland restoration. Quantitative studies conducted under field conditions that examine relative growth rates with respect to functional traits are needed to verify our findings.

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