

RESEARCH ARTICLE

# Functional trait differences between native bunchgrasses and the invasive grass *Bromus tectorum*

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**Abstract** We conducted 30- and 60-d greenhouse experiments to compare functional traits of *Bromus tectorum* (invasive annual grass) and four perennial bunchgrasses under well-watered or drought conditions. Even under drought, *B. tectorum* experienced significantly less stress (i.e., higher xylem pressure potential and greater shoot water content, water use per day and water-use efficiency) and biomass production than the perennial grasses after 30 d. However, after 60 d, its superiority was reduced under infrequent watering. Differences among perennial grasses were more pronounced for physiological traits under infrequent watering and for morphological traits under frequent watering. *Elymus multisetus* (fast-growing species) had a higher transpiration rate, lower leaf temperature, and lower water-use efficiency than the other grasses after 30 d. In contrast, *Pseudoroegneria spicata* (slow-growing) had lower xylem pressure potential and higher leaf temperature than all other grasses under infrequent watering. Under frequent watering, shoot dry mass and specific leaf area of *B. tectorum* was matched by *Elymus wawawaiensis* (moderate-growing species). Our results indicate that multiple-species plantings or seedings are necessary to foster greater weed resistance against *B. tectorum*. We also emphasize that when choosing plant material for restoration, performance during both pulse (resource-rich) and inter-pulse (resource-poor) periods should be considered.

**Keywords** annual grass, comparative growth, drought response, invasive plant, native grass, specific leaf area, soil-water use

## 1 Introduction

Native perennial bunchgrasses have long been recognized as an integral functional component of shrub-steppe ecosystems of western North America<sup>[1]</sup>. Dominance of these perennial grasses has steadily declined since European settlement due to inadequate grazing tolerance and widespread invasion by annual grass species, foremost among them *Bromus tectorum*<sup>[2,3]</sup>. Land managers quickly realized that native perennial grasses would not persist under heavy grazing, frequent wildfire regimes and intense *B. tectorum* competition<sup>[4,5]</sup>. While introduced forage grasses have historically been used to stabilize soils and support livestock grazing<sup>[6,7]</sup>, rehabilitation success has been considerably less with the reintroduction of native perennial grasses<sup>[8]</sup>.

Evidence indicates that the invasive annual grass, *B. tectorum*, is superior to native perennial grasses for shoot and root production, nitrogen utilization and water extraction when soil resources are abundant<sup>[9–11]</sup>. However, it remains unclear whether these advantages over perennial grasses are conserved when seedlings are exposed to drought conditions. For example, Mukherjee et al.<sup>[12]</sup> found that considerable variation exists between native populations of perennial grasses in response to drought and that certain populations may be better competitors with *B. tectorum*<sup>[13,14]</sup>. To clarify key functional differences between native grass species and *B. tectorum*, it is critical to compare morphological and physiological traits under conditions when resources are abundant and when they are limiting<sup>[15]</sup>.

Wild populations and improved cultivars of native grasses accommodate the growing demand for native species in ecosystem restoration<sup>[16]</sup>. Many native perennial grasses are available for shrub-steppe ecosystems of western North America, including fast-growing squirreltail (*Elymus multisetus*), moderate-growing Snake River wheatgrass (*Elymus wawawaiensis*) and slow-growing

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bluebunch wheatgrass (*Pseudoroegneria spicata*). However, comprehensive comparisons with *B. tectorum*, especially in response to drought stress, are needed to make sound decisions regarding their suitability for restoration. Consequently, in this study, our objective was to compare 10 functional traits of *B. tectorum* and these important perennial grasses under well-watered and drought conditions to (1) determine how drought differentially affects seedling functional traits and (2) elucidate how trait differences among perennial grasses can be used to improve seedling establishment success and competition with *B. tectorum*. Ultimately, these new insights may facilitate trait-based selection of perennial grasses for grassland and shrub-steppe restoration projects.

## 2 Materials and methods

Seed of *B. tectorum* was collected from a south-west-facing slope at 1450 m elevation in the north-eastern portion of the Great Basin, USA (41°46'07" N, 111°47'11" W). Seed of *E. multisetus* selection Sand Hollow, *E. wawawaiensis* cv. Secar and selection E-45, and *Pseudoroegneria spicata*. Goldar was obtained from the seed repository at the US Department of Agriculture, Agricultural Research Service, Forage and Range Research Laboratory in Logan, UT, USA. All seed had been stored at 4°C prior to these studies. E-45 had undergone two cycles of recurrent selection for general population improvement from cv. Discovery, a multiple-origin material from Whitman and Asotin Counties (WA, USA) and Idaho County (ID, USA).

Seed was germinated on moistened blotting paper in Petri dishes. Experimental units consisted of a germinated seedling transplanted into a 0.5-L plastic container filled with 525 g of Preston fine sand (mixed, mesic, Typic Xeropsamments) collected in Cache County (UT, USA). To compensate for different seedling growth rates, *B. tectorum* seeds were imbibed 7 d later than the perennial grasses, so seedlings would be of similar size at transplanting. Two independent randomized complete block experiments were established in a greenhouse at Utah State University, Logan. Experiments were located on different benches in the same greenhouse, and initiated on the same day in September. Both consisted of 14 blocks with randomly arranged combinations of the five grasses and two watering-frequency treatments, and they were terminated after 30 and 60 d, respectively. Mean hourly greenhouse net radiation during the 60 days peaked at hour 15:00, while air temperature and relative humidity remained relatively stable at 20°C and 35%, respectively.

Containers received 40 mL of water-soluble nutrient solution (24-8-16 NPK with micronutrients; Scotts Miracle-Gro Products Inc., Marysville, OH, USA) and were watered every other day to maintain field capacity, i.e., 11.5% soil-water content, for three weeks prior to

applying water treatments. Soil-water content was determined gravimetrically by weighing the containers on an electronic microbalance. We created watering-frequency treatments to evaluate functional traits under low (drought) and high resource availability<sup>[17]</sup>. Containers were either watered to field capacity every 2 d (frequent watering) or 4 d (infrequent watering). Extensive preliminary experiments were conducted with variable watering regimes to ensure frequent watering maintained soil-water content (SWC) between 8% and 11.5% and infrequent watering stressed plants by allowing SWC to drop to 4% before recharging to 11.5% without causing seedling mortality.

At the end of each experiment (i.e., 30 or 60 d), all plants were watered to field capacity in the early morning and physiological and morphological traits measured, one block at a time by randomly selecting plants. Transpiration rate and leaf temperature were measured for one leaf per seedling under ambient temperature and light conditions using a calibrated steady-state porometer (LI-1600, Li-Cor Corp., Lincoln, NE, USA.) affixed with a small aperture (0.60 cm<sup>2</sup>) between hour 11:00 and 13:00. Measurements were made on recently expanded leaves of similar size and hierarchical generation (third) from the seminal tiller. Leaves were immediately excised with a sharp razor, placed between a slit in a rubber gasket, and mounted in a Scholander-type pressure chamber (Model 1000, PMS Instrument Co., Corvallis, OR, USA.) to determine leaf water potential (xylem pressure potential) using standard procedures<sup>[18]</sup>. Shoots, including the subterranean crown portion and excised leaves, were then harvested and immediately weighed, dissected, and measured with a belt-driven leaf-area meter (LI-3000/3050A, Li-Cor Corp.). Root systems were gently rinsed with water to remove soil. Shoots and roots were dried in a convective oven at 60°C for 48 h and weighed to determine shoot and root dry mass. Shoot water content and specific leaf area (SLA) were calculated from the difference between fresh and dry shoot mass and the quotient of leaf area and shoot dry mass, respectively.

Given that each container was weighed and watered to maintain 11.5% soil-water content every two or four days, we were able to calculate water use per day (quotient of total water provided and days of experiment, i.e., 30 or 60 d) and shoot growth water-use efficiency (quotient of shoot dry mass and total water provided). When calculating water-use traits, we could not account for variation in container mass attributed to plant dry mass and/or plant-water mass; however, this variation was considered of minor significance because the greatest shoot fresh mass value determined after the 60-d experiment was only 4 g, an amount that corresponds to only 0.64% of total container mass at 11.5% soil-water content (624 g). Water loss from containers without plants was negligible.

All growth and water-use traits were analyzed with mixed-effect ANOVA models using JMP (ver. 11, SAS Institute Inc., Cary, NC, USA). Entries and treatment were

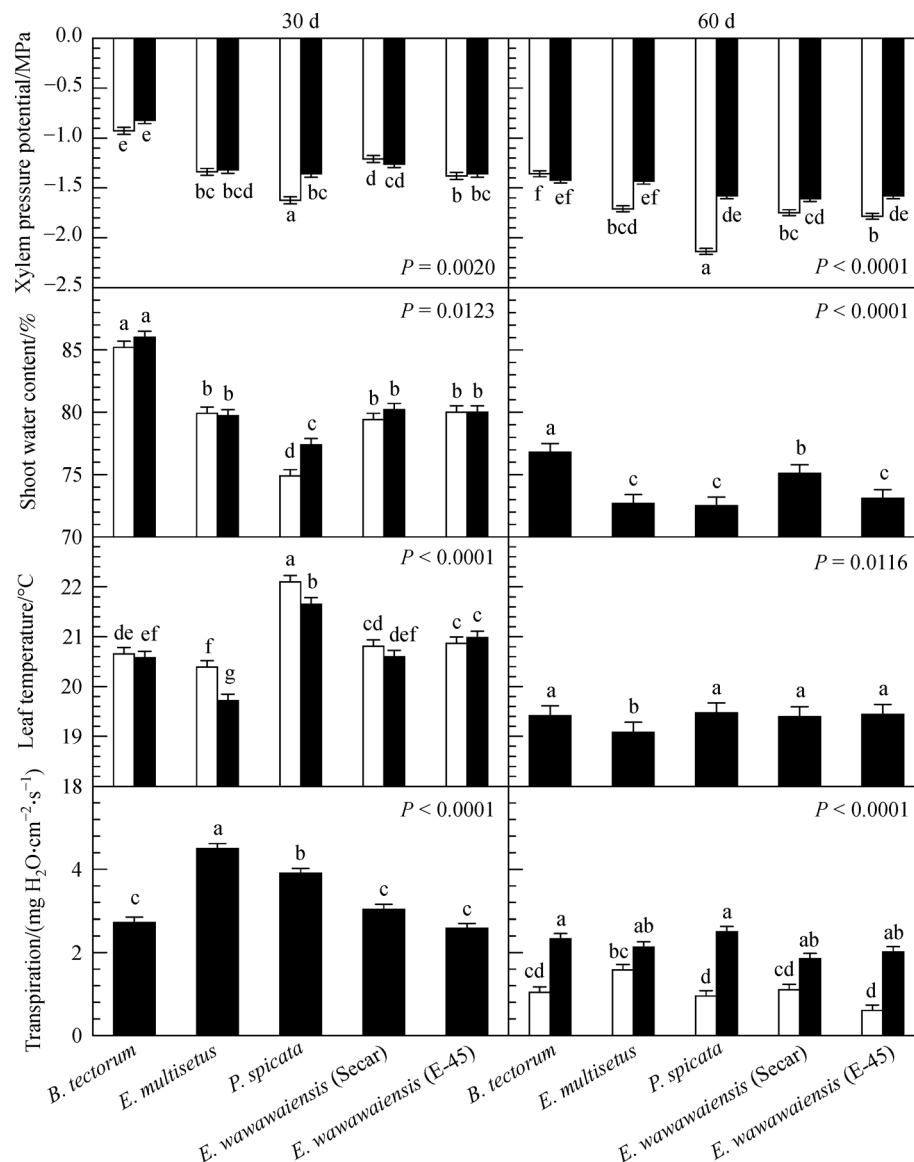
considered fixed effects and replicate (block) was considered a random effect. Means were compared with Fisher's Protected LSD test. Tests of significance for main- and interaction-effects are shown in figures, and significance for mean-separation tests was determined at  $\alpha = 0.05$ .

### 3 Results

The main-effect of watering frequency significantly impacted all functional traits in the two experiments, with the exception of root dry mass at 30 d and water-use

efficiency at 60 d ( $P < 0.05$ ). Watering frequency rarely had the same effect on the five grasses. Instead, we found a significant interaction between watering frequency and grasses ( $P < 0.05$ ) for all 10 traits in at least one of the experiments (30 or 60 d). Results indicate that the grasses differentially responded to drought conditions and reveal key traits that must be considered in order to improve seedling establishment of perennial grasses and increase their ability to compete with *B. tectorum*.

Xylem pressure potential and shoot water content were highest for *B. tectorum* and lowest for the slow-growing *P. spicata* under infrequent watering at 30 d (Fig. 1). In addition, *P. spicata* showed relatively greater reductions in



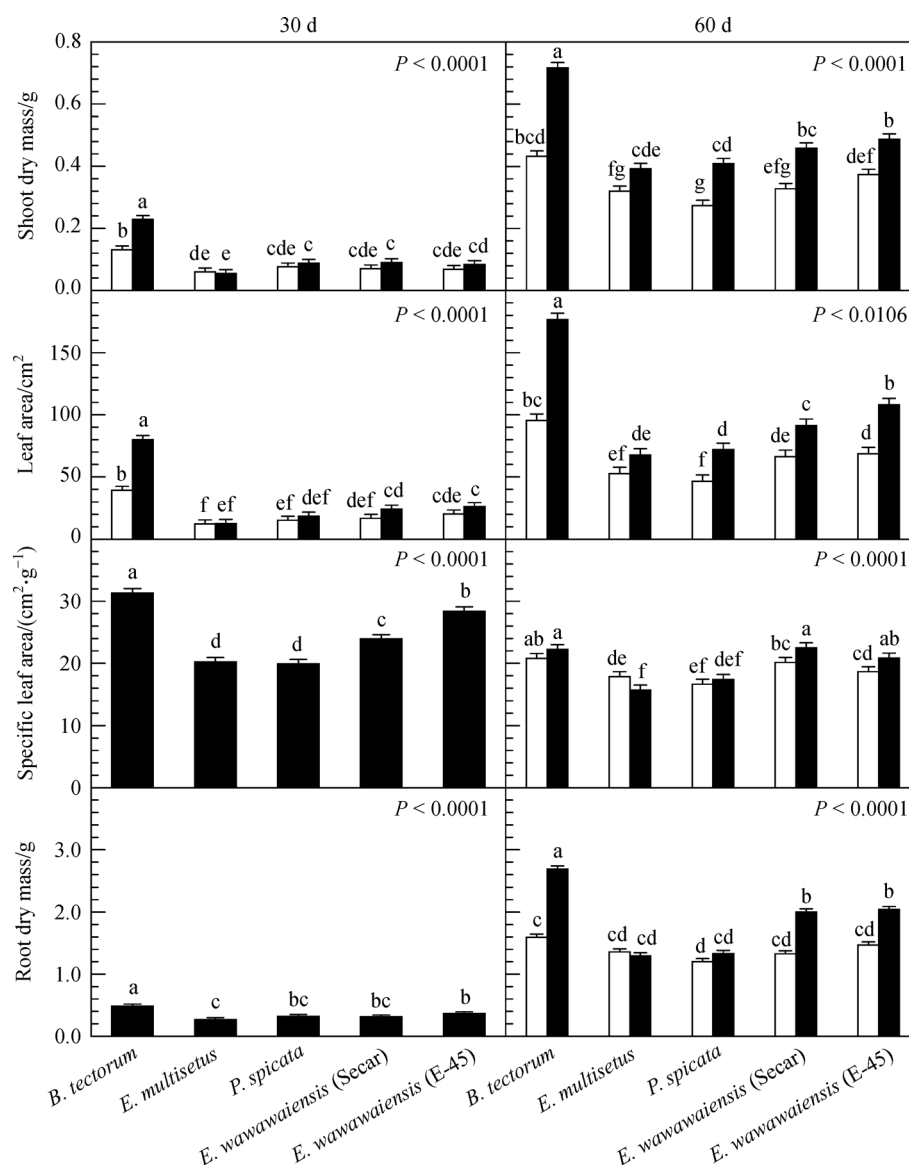
**Fig. 1** Mean (± 1 SE) xylem pressure potential, shoot water content, leaf temperature and transpiration rate of five grasses (*Bromus tectorum*, *Elymus multisetus*, *Pseudoeegneria spicata*, *Elymus wawawaiensis* cv. Secar and *Elymus wawawaiensis* selection E-45) grown with infrequent (open bars) and frequent watering (closed bars) in 30- and 60-d greenhouse experiments. Means for entries ( $n = 28$ ) or entry by treatment ( $n = 14$ ) with the same lowercase letter are not significantly different ( $P > 0.05$ ). ANOVA significance for entry main-effect or entry by treatment interaction is indicated.

xylem pressure potential than the other perennial grasses under infrequent watering at both 30 and 60 d. Leaf temperatures were consistently lowest for fast-growing *E. multisetus* and greatest for *P. spicata* at 30 d, and were greater under infrequent than frequent watering for both species. Transpiration rates of *E. multisetus* and *P. spicata* were also greater than the other grasses at 30 d. However, at 60 d, transpiration rate of *E. multisetus* was greater than that of only two perennial grasses under infrequent watering (i.e., *P. spicata* and *E. wawawaiensis* E-45).

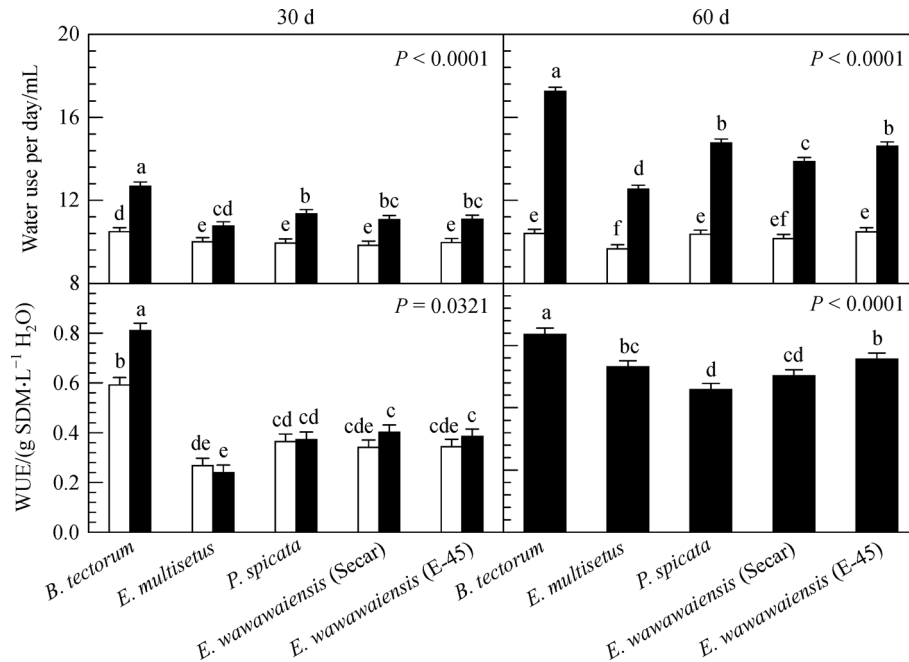
Shoot and root dry masses, leaf areas, and specific leaf areas were consistently greater for *B. tectorum* than for the

bunchgrasses at 30 d (Fig. 2). However, at 60 d, *B. tectorum* was matched under infrequent watering by at least one of the *E. wawawaiensis* populations for shoot dry mass and specific leaf area, and by all grasses except *P. spicata* for root dry mass. Specific leaf area of both *E. wawawaiensis* entries exceeded the other perennial grasses at 30 d, and values matched *B. tectorum* under frequent watering at 60 d. Likewise, root dry mass of both *E. wawawaiensis* entries exceeded the other perennial grasses at 60 d and showed marked increases under frequent watering (e.g., similar to *B. tectorum*).

Water use and water-use efficiency of *B. tectorum* were



**Fig. 2** Mean ( $\pm$  1 SE) shoot dry mass, leaf area, specific leaf area, and root dry mass of five grasses (*Bromus tectorum*, *Elymus multisetus*, *Pseudoglyceria spicata*, *Elymus wawawaiensis* cv. Secar and *Elymus wawawaiensis* selection E-45) grown with infrequent (open bars) and frequent watering (closed bars) in 30- and 60-d greenhouse experiments. Means for entries ( $n = 28$ ) or entry by treatment ( $n = 14$ ) with the same lowercase letter are not significantly different ( $P > 0.05$ ). ANOVA significance for entry main-effect or entry by treatment interaction is indicated.



**Fig. 3** Mean ( $\pm$  1 SE) water use per day and shoot growth water-use efficiency (WUE) of five grasses (*Bromus tectorum*, *Elymus multisetus*, *Pseudogegneria spicata*, *Elymus wawawaiensis* cv. Secar and *Elymus wawawaiensis* selection E-45) grown with infrequent (open bars) and frequent watering (closed bars) in 30- and 60-d greenhouse experiments. Means for entries ( $n = 28$ ) or entry by treatment ( $n = 14$ ) with the same lowercase letter are not significantly different ( $P > 0.05$ ). ANOVA significance for entry main-effect or entry by treatment interaction is indicated

significantly greater than the perennial grasses at 30 d (Fig. 3). *Elymus multisetus* also showed less divergence between watering treatments and had lower water use than the other perennial grasses under frequent watering at 60 d. Only *B. tectorum* had greater water-use efficiency under frequent compared to infrequent watering. Water-use efficiency was lowest for *E. multisetus* and *P. spicata* at 30 and 60 d, respectively.

## 4 Discussion

Interpreting differential drought responses of perennial grasses is challenging because *plant effects* on soil-water availability are difficult to distinguish from *plant responses* to soil-water availability<sup>[19]</sup>. Furthermore, differential water use is ecologically important because it provides additional awareness of how a species may directly influence its own growth and indirectly affect growth of neighboring species in field settings. Our results clearly indicate that physiological and morphological traits were consistently hindered by low watering frequency, yet reductions were differentially expressed among species. These drought responses provide new insights into functional-trait differences between perennial grasses and identify a number of traits that may limit successful seedling establishment and competition with *B. tectorum*.

### 4.1 Differential physiological traits

Low soil-water availability arguably poses one of the greatest threats to the survival of perennial grass seedlings<sup>[20]</sup>. During this sensitive developmental stage, seedlings must exhibit physiological traits to successfully persist under the biotic, atmospheric and edaphic stresses associated with variable and/or diminishing soil-water content<sup>[21]</sup>. Our results indicate that slow-growing *P. spicata* has lower capacity to avoid drought stress relative to the other perennial grasses based on it exhibiting lower xylem pressure potential, low shoot water content, and elevated leaf temperature at this critical seedling stage, i.e., 30 d.

Given that leaf area and root biomass of bunchgrasses were relatively similar during early developmental stages (i.e., 30 d), lower xylem pressure potential and lower shoot water content of *P. spicata* were likely driven by its higher transpiration rates<sup>[17]</sup>. In addition, high leaf temperature of *P. spicata* was possibly an indirect consequence of the lack of leaf pubescence in this species<sup>[22]</sup>. Leaf pubescence is a distinguishing trait present on seedlings of the other perennial grasses<sup>[23]</sup> and is known to reduce absorbance, heat loading and transpiration rates in semiarid plants<sup>[24]</sup>. However, high transpiration rates at midday had less-negative impacts on leaf water status of *E. multisetus*. High transpiration and its contribution to latent heat exchange<sup>[25]</sup> may be a drought-avoidance mechanism by which



*E. multisetus* experiences lower leaf temperature than the other perennial grasses, even when they have more favorable (i.e., less negative) leaf xylem pressure potentials.

Our results offer two insights into competition with *B. tectorum* and relative establishment potential of perennial grasses. First, previous research suggests that high growth rate, short lifespan and vigorous root growth of *E. multisetus*<sup>[26–28]</sup> enable it to successfully compete with annual grasses<sup>[5,29]</sup>. Our results indicate that its ability to compete with annual grasses may also be associated with high rates of transpiration to maintain low leaf temperature during young seedling growth (i.e., 30 d); traits necessary to exhaust soil resources before they can be acquired by annual grasses. Indeed, field experiments similarly illustrate that successful competitors must rapidly deplete early spring and localized soil water, while avoiding drought stress associated with coexistence with annual grasses<sup>[30]</sup>. Second, differential physiological and water-use patterns among perennial grasses help explain previous observations of lower summer survival of *P. spicata* cv. Goldar than *E. wawawaiensis* cv. Secar when drought conditions persist<sup>[12,31]</sup>. For example, under infrequent watering, our observation of lower leaf water stress, higher shoot water content, lower leaf temperature and lower leaf transpiration in young seedlings of *E. wawawaiensis* cv. Secar (i.e., 30 d) indicate a clear drought-avoidance advantage relative to *P. spicata* cv. Goldar during the critical establishment phase. Although the strategies employed by the perennial grasses to cope with drought conditions were very different, additional research is needed to explore potential trade-offs encountered when species exhibit higher resource acquisition (i.e., *E. multisetus*) vs higher drought avoidance (i.e., *E. wawawaiensis*).

#### 4.2 Differential morphological traits

Synchronizing morphological traits of perennial grasses with *B. tectorum* when soil resources are abundant may also enhance establishment of restoration species. While, this approach is common in crop breeding to improve the competitive ability of crops when competing with undesirable weeds<sup>[32]</sup>, it has received less emphasis for native perennial grasses<sup>[33,34]</sup>. As a result of the necessary trade-offs, however, the traits that confer competitiveness may be entirely different than the traits that confer physiological stress avoidance or tolerance<sup>[35,36]</sup>. In addition, the likelihood of a single species expressing (1) physiological traits important to stress avoidance when resources are limiting as well as (2) morphological traits important to competitive ability when resources are plentiful is constrained because of the unavoidable trade-offs between traits that confer stress tolerance and competitive ability<sup>[37,38]</sup>.

*Bromus tectorum* exhibits traits common among highly

competitive species—namely high growth rate, rapid leaf-area development, prolific root production, and rapid capture and depletion of soil resources<sup>[27,39,40]</sup>. In a temporal context, *B. tectorum* also appears to outperform native bunchgrasses in late autumn and early spring during periods of high resource availability<sup>[41,42]</sup>. Similarly, our results confirm that native perennial grasses are unable to match the overall productivity of *B. tectorum*, regardless of watering frequency. However, variation in morphological traits indicate that *E. wawawaiensis* is more similar to *B. tectorum* compared to the other perennial grasses, especially under frequent watering at 60 d. For example, *E. wawawaiensis* plants consistently had higher SLA (at both 30 and 60 d) and root dry mass at 60 d than the other perennial grasses under frequent watering. High SLA facilitates rapid early-season growth by maximizing carbon gain per unit leaf mass, and confers competitive and fitness advantages when soil resources are plentiful<sup>[43,44]</sup>. Conversely, low SLA (as shown by *E. multisetus* and *P. spicata*) is typically correlated with greater leaf longevity and is a common trait for species from nutrient-poor habitats<sup>[45,46]</sup>. Invasive annual grasses with high growth rates also show greater plasticity to soil resources through prolific root production and nutrient acquisition in nutrient-rich microsites than slower-growing perennial grasses<sup>[47,48]</sup>. Viewing the morphological responses of *E. wawawaiensis* in this ecological context suggests that its plasticity for SLA and root growth is greater than the *E. multisetus* and *P. spicata* entries evaluated here. Further research is needed to explore whether these key functional-trait differences enhance early-season growth and establishment when soil resources are abundant.

In shrub-steppe ecosystems of western North America, where soil resources are temporally available and supplied in seasonal pulses<sup>[41,49]</sup>, it is imperative to determine the processes occurring during pulse- and inter-pulse periods that influence individual plant or population persistence<sup>[15]</sup>. Therefore, when choosing suitable perennial grasses for restoration projects, expression of physiological and morphological traits during these two critical periods is essential. The functional traits expressed by seedlings of the grasses in this study indicate that relative to the other grasses, *P. spicata* cv. Goldar is relatively less suited to persist in resource-limited inter-pulse periods. In contrast, the conservative water-use and drought avoidance of *E. multisetus* selection Sand Hollow may confer greater survival through inevitably stressful inter-pulse periods, especially when soil water has been depleted. The high SLA and root growth of *E. wawawaiensis* suggests that, of the perennial grasses studied here, it may possess the most rapid growth during pulse periods when invasive annual grasses are most prolific. However, the responses we observed for these particular perennial grasses should not be used to characterize entire species, since we used specific genetic material in our studies. In addition, our studies were conducted under controlled conditions, thus

they do not take into account potential growth differences under variable and/or cooler temperatures common in field settings where *B. tectorum* is most successful<sup>[50,51]</sup>. Species differences in drought avoidance or competitive ability under lower temperatures that coincide with greater resource availability in shrub-steppe ecosystems are poorly understood<sup>[13,49]</sup>. More research is needed to understand the temperature dependence of key growth processes, including root growth and resource acquisition of perennial grass species used for restoration in shrub-steppe ecosystems.

## 5 Conclusions

Physiological and morphological trait variation not only provide criteria for selecting plant material for restoration projects, but also indicate the necessity for utilizing multiple species to grow and utilize resources during pulse- and inter-pulse periods. Experimental and theoretical studies support the concept that functional diversity of multiple-species plantings or seedings foster more complete nutrient acquisition and improve resistance to weed invasion<sup>[52,53]</sup>. In addition, restoration-seeding efforts indicate that early- and later-establishing mixtures differ greatly in their ability to suppress annual species<sup>[54,55]</sup>. Multiple-species plantings are also hypothesized to provide greater spatial acquisition of resources<sup>[56,57]</sup>. A promising future linkage between screening functional traits and assessing restoration success may include determining whether multiple-species mixtures, that contain a broad range of functional traits, improve temporal and spatial resource-use such that mixtures effectively coexist and resist annual grass invasion.

## 6 Implications

- When choosing plant material for restoration, performance during both pulse (resource-rich) and inter-pulse (resource-poor) periods should be considered.
- Established plants from plant material that best match performance of critical invasive species are most likely to be able to compete effectively.
- Physiological and morphological traits within a species suggest which plant materials are most likely to be successful competitors of *B. tectorum*.
- When assembling a seeding mix, aiming for high functional diversity, both among species and among selections within a species, may enhance the resistance for the plant community to weed invasion.

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