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Effects of Elevated Temperature and CO_2 Concentration on Seedling Growth of *Ventenata dubia* (Leers) Coss. and *Bromus tectorum* L.

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Abstract: The impacts of climate change are expected to alter the abundance and distribution of invasive annual grasses, such as *Bromus tectorum* L. (cheatgrass) and *Ventenata dubia* (Leers) Coss. (ventenata). High temperature extremes will be more frequent and for longer periods, and increased atmospheric CO_2 is expected to double even with the most conservative estimates. Climate change draws concern for the potential success of winter annual grasses in arid and semi-arid plant communities. Information on *B. tectorum*'s growth response to climate change in laboratory and field experiments are available for monocultures; however, more knowledge is needed on the response when growing with other invasive grasses, such as *V. dubia*. We examined differences in seedling growth for *V. dubia* and *B. tectorum* growing alone and with each other under current (4 °C/23 °C at 400 ppm CO_2) and elevated (10.6 °C/29.6 °C at 800 ppm CO_2) climate conditions. There was one trial per climate scenario with 10 replications per competition type (inter-, intra-specific competition for each species). *Bromus tectorum* was larger than *V. dubia* across climate and competition treatments, but contrary to previous studies, both species were smaller in the elevated climate treatment. *Ventenata dubia* allocated more growth to its roots than *B. tectorum* across both climate treatments, indicating *V. dubia* may have a competitive advantage for soil resources now and in the future.

Keywords: annual grass; cheatgrass; climate change; downy brome; growth chamber; seedling competition; wiregrass

1. Introduction

Impacts of climate change are expected to alter the abundance and distribution of invasive annual grasses, such as *Bromus tectorum* L. (cheatgrass) and *Ventenata dubia* (Leers) Coss. (ventenata) [1,2]. *Bromus tectorum* was introduced to North America in the 1800s and is now the most widespread invasive plant in the western United States (US) [3]. *Ventenata dubia*, on the other hand, was documented in North America almost 100 years later, in the 1950s, and has rapidly expanded its distribution over the last several years [4,5]. Both species are winter annuals, and *B. tectorum* has generally demonstrated greater growth than *V. dubia* when compared in controlled growing conditions [6–8], and *B. tectorum* abundance is inversely related to *V. dubia* abundance in some areas where their distributions overlap [4].

Earth's surface temperature has warmed in each of the last three decades more so than any period before 1850 [2,9]. In the western US, high temperature extremes are projected to be more frequent and to last for longer periods, while low temperature extremes are projected to be less frequent; increased atmospheric CO_2 is expected to double across all ecosystems, even in the most conservative climate estimates [9,10]. Projected climate change draws concern for the potential success of winter annual grasses [1,2]. Information on *B. tectorum*'s potential biological response to climate change in laboratory and field experiments are available [11–18], but we are not aware of any literature on *V. dubia*'s response to a changing climate. Building on current knowledge regarding *B. tectorum* and expanding our knowledge of its competitive interactions with species such as *V. dubia* is necessary to understand the potential invasion risk of both species under a changing climate.

Increased temperatures, particularly the early onset of warming spring temperatures and elevated winter temperature, are expected in all climate change scenarios and are the most predictable explanatory condition for *B. tectorum* productivity [2]. Consistent findings of rapid maturation and an increase in *B. tectorum* biomass as a result of warming temperatures are well-known in both greenhouse and field experiments when grown in monocultures [1,16,18–22].

Carbon dioxide (CO_2) enrichment studies on *B. tectorum* monocultures in the greenhouse have found generally positive growth responses to elevated CO_2 concentrations [11,14,17,18]. For example, CO_2 conditions were recreated for the early 19th century (270 µmol mol^{-1} CO_2), 1960s (320 µmol mol^{-1} CO_2), 2005 (370 µmol mol^{-1} CO_2), and "future" 2020 conditions (420 µmol mol^{-1} CO_2), and *B. tectorum* biomass increased with increasing CO_2 concentrations, supporting the enduring historical success of this species in the western US over the last century [14]. Despite such findings in monoculture studies, there are only a few studies that have addressed competitive interactions between *B. tectorum* and other species, and the findings have been less clear. For instance, in a free-air CO_2 enrichment (FACE) study in the Mohave Desert, Smith et al. [12] determined that seed production and above-ground biomass of *Bromus* species increased at elevated CO_2 concentrations as compared to native annual grasses. Larson et al. [18] found *B. tectorum* monocultures responded positively to increased CO_2, but in competition with native perennial grasses, *B. tectorum* was suppressed at ambient CO_2, and the magnitude of suppression increased with CO_2 levels.

Competition studies are important when addressing changing climates, as species are not singularly affected by changing conditions, but rather the whole community will respond. For example, water and nutrient uptake are species-specific [1,23,24], and water and nutrient availability are affected by precipitation and soil moisture [19,20], adding to the complexity of how communities will respond to climate change.

Our current understanding of *V. dubia* and other non-native annual grasses (e.g., *Taeniatherum caput-medusae* (L.) Nevski; medusahead) is limited, and the information we do have suggests they may not respond like *B. tectorum* [6,25]. Generally, invasive annual grasses are found in a wide range of habitats (i.e., grass-shrublands, open forests, and mountain habitats), furthering the complexity of understanding their species-specific responses to climate change [26–28]. An exploration of potential climate scenarios for *V. dubia* growth in the Northern Rockies Ecoregion is needed to determine this species' range and potential infestation severity compared to *B. tectorum*. Thus, the goal of this study was to evaluate the effects of elevated temperatures and CO_2 concentrations on the growth of *V. dubia* and *B. tectorum* using current (year 2018) and predicted regional end-of-century (year 2100) conditions.

The objectives of this study were to determine differences in growth (shoot and root biomass, shoot length, and number of leaves) under current and elevated climate treatments, (1) in monoculture, and (2) with inter-specific competition. Based on previous research on *B. tectorum* and *V. dubia* [1,2,6–8,11,12,14], we hypothesized that *B. tectorum* and *V. dubia* shoot and root biomass would be higher when growing under elevated temperature and CO_2 concentrations compared to current climate levels, but the magnitude of the difference would be greater for *B. tectorum* than *V. dubia*. We also expected *B. tectorum* to have higher shoot and root biomass than *V. dubia* under either climate condition and to, therefore, exert a greater competitive effect on *V. dubia* than *V. dubia* would exert on *B. tectorum*. Our results showed that *Bromus tectorum* outgrew *V. dubia* across all treatments, but neither species grew larger in elevated climate conditions. *Ventenata dubia* allocated more growth to its roots than *B. tectorum*, suggesting it may be competitive for soil resources in the future.

2. Materials and Methods

Estimated changes in elevated temperature (°C) and CO_2 concentration (ppm) for southwestern Montana [9] were used to determine seedling growth responses for two different competition scenarios. For the current climate treatment, we used the 30-year (1985–2015) historical average maximum and minimum temperatures in September for southwestern Montana, 23 °C and 4 °C, respectively (Table 1) [29], because winter annual grasses start to germinate at this time. The current CO_2 concentration was set as 400 ppm. For the elevated climate treatment, we used end-of-century predicted values of 29.6 °C and 10.6 °C for average maximum and minimum temperatures and 800 ppm CO_2 (Table 1) [9,10]. These treatments were established within a Conviron® BDR-16 CO_2-regulated growth chamber equipped with a Vaisala CO_2 sensor (Conviron®, Winipeg, MB, Canada) where light emission was 0 and 800 μmol m^{-2} s^{-1} to reflect 12-h diurnal fluctuations for each treatment, which was also matched by diurnal day–night changes in temperature (Table 1). Pots were watered equally with approximately 30 mm per day once seedlings emerged and throughout the experiment.

Table 1. Climate treatments, including time (24 h clock) during which temperature and carbon dioxide (CO_2) conditions were administered, temperature (°C), and CO_2 (parts per million, ppm).

Time	Temperature (°C)	CO_2 (ppm)
Current conditions		
07:00–19:00	23	400
19:00–07:00	4	400
Elevated conditions		
07:00–19:00	29.6	800
19:00–07:00	10.6	800

Seeds of *B. tectorum* and *V. dubia* were collected near Bozeman, Montana (45°40′13.47″ N, 111°1′33.40″ W), during summer 2017. All seeds were stored at room temperature until the start of the experiment in February 2018. Twenty seeds per pot were sown just before placing pots in the growth chamber. After 14 days, seedlings were thinned to 4 total individuals per pot (10 cm × 10 cm × 12.5 cm) for the intra-specific competition treatment or 2 individuals per species per pot for the inter-specific treatment, reflecting a replacement series design [30]. The following proportions were used: *V. dubia* alone, 4:0; *B. tectorum* alone, 0:4; and *V. dubia* with *B. tectorum*, 2:2, with 10 replications per competition type. Seedlings chosen to continue growing were of similar size and chosen to create a consistent spatial arrangement (i.e., crowded seedlings were removed). Montana State University Plant Growth Center (PGC) "MSU Mix" (1:1:1 by volume mineral soil, Canadian Sphagnum Peat Moss, and washed concrete sand) was used, and Aqua-Gro 2000G, a wetting agent, was added at the rate of 0.59 kg per cubic meter; the mix was aerated and steam pasteurized for one hour at 70 °C. All pots were rotated weekly to account for variation within the chamber.

Plants grew for 22 days under the current climate treatment and 19 days under the elevated climate treatment. Shoot length was measured (to nearest 0.1 cm) from the base to the end of the longest leaf tip, and all leaves were counted for all plants in each pot before biomass processing. The total plant material in each pot was collected all at once. After shoot biomass was harvested by clipping green foliage from the top of the plant, root biomass was carefully rinsed for 10 min in cold water using 1- and 2-mm sieves. All biomass, separated by shoot and root portions, were placed into coin envelopes, dried at 37 °C for 72 h, and weighed to the nearest 0.0001 g. All measurements were performed on individual species.

We investigated differences in shoot and root biomass (g per individual), root–shoot ratios, and maximum shoot length (cm) in response to species differences and climate and competition treatments. To account for the difference in growth periods between current (22 days) and elevated (19 days) climate treatments, adjusted shoot and root biomass reflecting 22 growing days for the elevated treatment were calculated by dividing final shoot and root biomass by the number of growing days (19) to arrive at biomass per day. Then, biomass per day was multiplied by three to account for the three additional growing days between elevated and current treatments, and this value was added to measured shoot and root biomass. We assumed linear growth and that growth per day was consistent for both species. Adjusted shoot and root biomass were analyzed in addition to measured biomass for the actual growth period. Results were similar between adjusted and measured biomass models; therefore, measured shoot and root biomass were used for clarity of presentation. All response variables were analyzed using an analysis of variance (ANOVA) on a log-transformed linear model to meet normalization assumptions. Data were not back-transformed raw values are reported. The most parsimonious model was used for all responses, and all models were evaluated for independence and constant variance. Independent factors were the species *B. tectorum* and *V. dubia*, climate treatment (current and elevated), and competition treatments (inter-specific and intra-specific). A Tukey Honest Significant Difference (HSD) pairwise comparison was conducted for significant factors. Graphical interpretations and analyses were conducted using R Software 3.5.1 [31], and specifically, emmeans, dplyr, and ggplot2 packages [32–34].

3. Results

Differences in seedling shoot and root biomass were evident across species, competition, and climate, and there was an interaction between competition and climate treatments ($p < 0.01$) (Table 2). For root–shoot ratios, differences were evident across species ($p < 0.01$), competition ($p = 0.02$) and climate ($p = 0.05$). Shoot length varied by species ($p < 0.01$) and climate treatment ($p < 0.01$) and was affected by the interaction between competition and climate treatments ($p = 0.02$) (Table 2).

Table 2. Analysis of variance (ANOVA) table for average shoot biomass, root biomass, root–shoot ratio, and shoot length of *Bromus tectorum* and *Ventenata dubia*. Comp = Competition treatment and Clim = Climate treatment. Df = degrees of freedom. F = F-value; *p* = *p*-value.

		Shoot Biomass		**Root Biomass**		**Root–Shoot Ratio**		**Shoot Length**	
Source	**Df**	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
Species	173	2064	<0.01	769	<0.01	50.2	<0.01	1305	<0.01
Comp	273	15.3	<0.01	20.1	<0.01	4.2	0.02	0.83	0.44
Clim	173	267	<0.01	184	<0.01	3.82	0.05	107	<0.01
Comp × Clim	273	24	<0.01	11.6	<0.01	1.92	0.15	4.13	0.02

Bromus tectorum growing in the current climate treatment had the largest shoot biomass and responded similarly across intra- and inter-specific competition treatments at 0.050 g per individual (Figure 1a). Shoot biomass of *B. tectorum* was lower when grown in the elevated climate treatment, and the intra-specific competition treatment resulted in higher shoot biomass than the inter-specific treatment, at 0.025 and 0.013 g per individual, respectively. Shoot biomass of *V. dubia* in the current climate treatment was similar across competition treatments at 0.003 g per individual for inter-specific and intra-specific competition. The elevated climate treatment resulted in lower *V. dubia* shoot biomass, and shoot biomass was greater in the intra-specific competition treatment at 0.0014 g per individual than the inter-specific competition treatment at 0.0005 g per individual.

Like shoot biomass, root biomass of *B. tectorum* was highest when grown in the current climate treatment in either intra- or inter-specific competition treatments (Figure 1b). The second highest *B. tectorum* root biomass was found in the elevated climate, intra-specific competition treatment at 0.018 g per individual, followed by the inter-specific competition treatment at 0.009 g per individual. Root biomass of *V. dubia* was lowest in the elevated, inter-specific competition treatment (0.001 g per individual) but similar in the other treatments (0.003 g per individual).

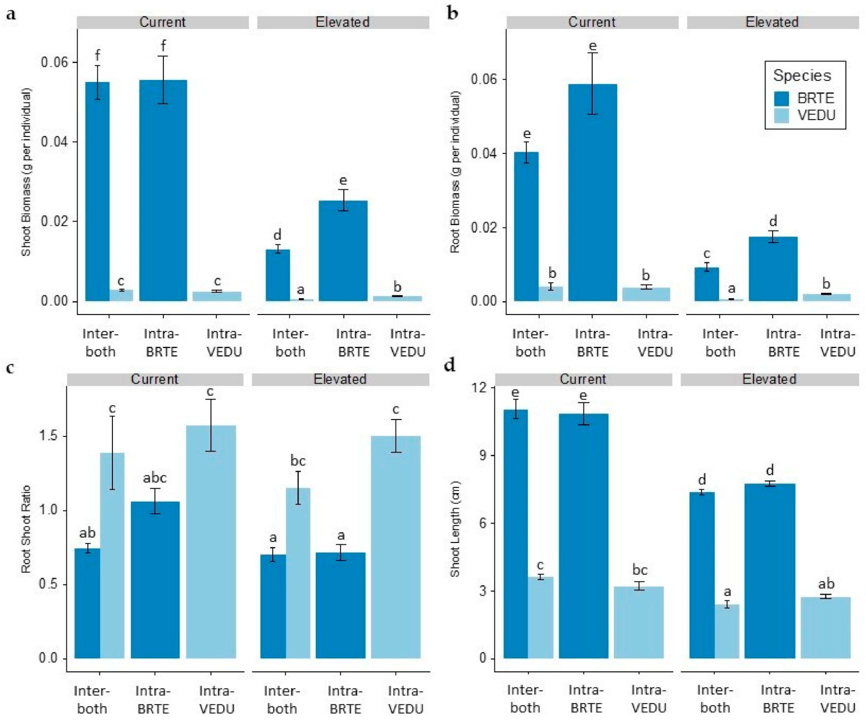

Figure 1. (**a**) Mean shoot biomass (g per individual), (**b**) mean root biomass (g per individual), (**c**) root–shoot ratio, and (**d**) mean shoot length (cm) for each species in competition and climate treatments. Competition treatments are indicated by Inter-both = *Bromus tectorum* + *Ventenata dubia*, Intra-BRTE = *B. tectorum* only, Intra-VEDU = *V. dubia* only. Climate treatments are Current (4 °C/23 °C at 400 ppm CO_2) and Elevated (10.6 °C/29.6 °C at 800 ppm CO_2) conditions. Error bars represent ± 1 standard deviation. Means with the same letter are similar to each other across all climate and competition treatments at $\alpha = 0.05$.

Root–shoot ratios differed between species ($p < 0.01$) and competition treatments ($p < 0.01$) (Table 2). *Bromus tectorum* root–shoot ratios ranged from 0.701 to 1.06, with an average of 0.80 across climate and competition treatments (Figure 1c). *Ventenata dubia* root–shoot ratios were higher than *B. tectorum* and ranged from 1.15 to 1.57, with an average of 1.40 across climate and competition treatments. There was a trend ($p = 0.05$) indicating the current climate treatment had higher root–shoot ratios than the elevated climate treatment.

Shoot length differed by species ($p < 0.01$), climate treatments ($p < 0.01$), and the interaction of competition and climate treatments ($p = 0.02$) (Table 2). *Bromus tectorum* had the longest shoot length in the current climate treatment in both inter- and intra-specific competition treatments at 11.1 cm and 10.9 cm, respectively, followed by *B. tectorum* growing in the elevated climate treatment in either competition treatment at about 7.6 cm (Figure 1d). Shoot length of *V. dubia* was lower than *B. tectorum* shoot length across all treatments. *Ventenata dubia* shoot length differed between the inter-specific, current, and inter-specific, elevated at 3.6 cm and 2.4 cm, respectively. All other *V. dubia* shoot length responses were similar at about 3.0 cm. There was a general trend ($p < 0.001$) for shorter shoot length by both species in the elevated climate treatment when contrasted to the current climate treatment.

4. Discussion

Overall, *B. tectorum* grew larger than *V. dubia* across all climate and competition treatments, consistent with our hypotheses and previous research where *B. tectorum* and *V. dubia* biomass were compared under varying growing conditions [6–8]. Even though *B. tectorum* always grew larger than *V. dubia*, root–shoot ratios were higher for *V. dubia*, particularly in the elevated climate treatment. Greater allocation of resources to root growth instead of shoot growth is seen as an adaptive growth strategy for invasive annual grasses in dry climates [34]. Previous research has shown *V. dubia* to have overall lower biomass and root length than *B. tectorum* and another invasive winter annual grass, *T. caput-medusae* [6], and although *V. dubia* was also smaller than *B. tectorum* in this study, there was evidence for more root allocation by this species when growing in elevated temperature and CO_2 conditions, which could enable it to become more competitive with *B. tectorum* in the future.

In the elevated climate treatment, *B. tectorum* decreased in size in both competition treatments, consistent with Larson et al. [18], where *B. tectorum* growth was reduced in the presence of competition when grown in a growth chamber at elevated CO_2 (800 ppm) and increased watering. We acknowledge that the growing period was three days shorter in the elevated climate treatment and could have affected our results concerning *B. tectorum.* At the same time and in contrast to *B. tectorum*'s decreasing growth under elevated temperature and CO_2, *V. dubia*'s root biomass and shoot length were mostly similar for both climate treatments. Maintaining shoot length and root biomass at elevated temperature and CO_2 could increase the abundance and distribution of *V. dubia* in the future as these traits can translate to reproductive success (i.e., seed production) in annual grasses [35,36]. Furthermore, the optimal temperature range for *V. dubia* seed germination is 23.3 °C to 29.2 °C [4], higher than the optimal range of 10 °C to 20 °C for *B. tectorum* [37]. Current and elevated temperatures used in this study were within the optimal range for *V. dubia* seed germination, and this, coupled with our results, suggests both temperature scenarios may be more favorable for *V. dubia* than *B. tectorum* from seed through seedling growth stages. However, additional studies investigating growth beyond the seedling stage, e.g., flowering and seed production, are required to elucidate future interactions between these two species.

There was no effect of competition on each species' biomass when growing under current temperature and CO_2 conditions. This was somewhat surprising to us, and we suspect that seeding the two species at higher densities, using small pots, or allowing them to grow longer and presumably bigger would have resulted in more pronounced competitive effects [38,39]. Under elevated temperature and CO_2 conditions, however, inter-specific competition resulted in a decrease in both species' biomass compared to intra-specific treatments. The effect of inter-specific competition was most evident with *B. tectorum,* whose shoots and roots were smaller when grown with *V. dubia* compared to growing alone. Even though densities of each species were the same between the two climate treatments, higher temperatures in the elevated treatment may have led to higher transpiration rates [40] and decreased soil water availability, and a stronger effect of competition, especially since watering was similar across the two different climate treatments. While elevated temperature and CO_2 conditions are predicted to perpetuate the distribution of invasive annual grasses in the western US [41], it is possible that species-specific responses may change competition dynamics between co-dominant annual grasses, such as *B. tectorum* and *V. dubia*. More research into these dynamics is necessary to predict which invasive annual grass may be most problematic moving forward.

Ventenata dubia generally exhibited a higher root–shoot ratio than *B. tectorum*. Allocation of resources to roots versus shoots is one mechanism by which plants increase water use efficiency (WUE), the ability to gain carbon while minimizing water loss during photosynthesis [42]. Higher CO_2 concentrations and temperatures typically enhance water use efficiency of C3 plants, such as *B. tectorum* [43] and *V. dubia*. We are not aware of any research into *V. dubia*'s WUE, but a field study in California found *Avena barbata* Pott ex Link (slender oat), which is a non-native annual grass in the same taxonomical tribe as *V. dubia*, doubled its WUE when grown in enhanced (723 μmol mol^{-1}) compared to ambient (+350 μmol mol^{-1}) CO_2 levels [44]. Evidence has indicated *V. dubia* may be displacing *B. tectorum* in some parts of the western US, especially where the initial establishment of *V. dubia* is known to be favored by moist conditions. Our study raises the question of whether *V. dubia* has a greater WUE than *B. tectorum*, and more research is warranted. If future investigations show a difference in WUE between *V. dubia* and *B. tectorum*, the difference could favor *V. dubia* and contribute to it displacing *B. tectorum* under a warming climate.

5. Conclusions

Characterizing species-specific responses of invasive annual grasses to climate change is important for invasions across the western US. Understanding the extent of the newest annual grass invader in the Intermountain West, *V. dubia*, is critical to determining its potential distribution. Management should consider the effects of shifting competitive relationships between invasive annual grasses, as well as native species, due to increasing temperatures and CO_2. These impending changes in climate are cause for concern due to intensifying catalyst events, such as wildfire, that encourage invasive annual grass expansion [2,14]. At the seedling stage, when establishment and survival are most important, we speculate that *V. dubia* may have a greater ability to access soil resources than *B. tectorum* due to its higher root–shoot ratio and maintenance of root biomass in changing conditions. Our study focused on the early growth of seedlings, but the growth of these species to reproductive adults could have resulted in different conclusions. Lastly, our study suggests annual grasses may have lower growth at elevated conditions compared to current conditions, which has implications for future species' distribution. Evaluating the response of these annual grasses along with the native community, should be the next step. Characterizing species-specific and inter-specific responses to climate change will be important for guiding management and future research to understand better annual grass invasions across the western US, where competition with other invasive species and native species is likely.

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