

Short communication

The effects of precipitation and soil type on three invasive annual grasses in the western United States

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ABSTRACT

Multiple species of annual grasses are invading sagebrush-steppe communities throughout the western United States. Most research has focused on dominant species such as *Bromus tectorum* (cheatgrass), yet other, less studied annual grasses such as *Taeniatherum caput-medusae* (medusahead) and *Ventenata dubia* (ventenata) are spreading rapidly. Future precipitation regimes are expected to have less frequent but more intense rain events, which may affect soil moisture availability and favor these 'newer' invasives over cheatgrass. We conducted a full factorial, growth chamber study examining the effects of two watering regimes (small/frequent, large/infrequent rain pulses) across nine soil types on the growth of cheatgrass, medusahead and ventenata. We tested a hypothesis that medusahead or ventenata would have greater growth than cheatgrass with larger/infrequent rain events. The two watering regimes had relatively strong effects on soil water content, but generally did not impact plant growth. In contrast, variation in soil properties such as clay content, pH and soil N correlated with a two- to four-fold change in plant growth. The three invasive grass species generally respond similarly to changes in precipitation regimes and to edaphic factors. Nevertheless, medusahead had 30–40% overall greater root growth compared to the other species and a 15% increase in root growth in response to the large/infrequent watering treatment. Our findings reveal that 1) greater biomass allocation to roots and 2) greater responsiveness of root growth to differing precipitation regimes of medusahead may favor its ecological success over other invasive annuals under future climate scenarios.

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Sagebrush-steppe ecosystems in the Great Basin, western United States, are highly susceptible to annual grass invasion (Mack, 1981). Large regions have been overrun by *Bromus tectorum* (cheatgrass), which has been a dominant invasive for over a century (Knapp, 1996; Mack, 1981). In recent decades, there has been an upsurge in the abundance and distribution of additional invasive annual grass species, many of which may have substantially more detrimental impacts on native plant production and forage quality in sagebrush ecosystems (Monaco et al., 2005). *Taeniatherum caput-medusae* (medusahead) and *Ventenata dubia* (ventenata) are two annuals that are aggressively spreading into native sagebrush

communities and into areas previously dominated by cheatgrass alone (Northam and Callihan, 1994). Medusahead's success has been attributed to greater seed production, growth rates and competitive abilities (Monaco et al., 2005 and citations within). However, relatively little is known about their responses to the environment compared to cheatgrass. Despite the differences in ecological impacts among these three grass species, they are typically massed into a single functional group of 'invasive annual grasses'. In light of their unique impacts on the environment, it is increasingly important to improve our ecological understanding of each invasive annual grass.

In semi-arid ecosystems, invasive annual grasses have out-competed native vegetation through their rapid exploitation of soil moisture (Melgoza et al., 1990). Future climate models predict that precipitation events will generally occur with reduced frequency and greater intensity (IPCC, 2007), which will affect soil water availability and may favor some invasive species over others. Also, soil physical characteristics influence water infiltration and storage (McAuliffe, 1994), thus interacting with precipitation events in determining soil water availability for plants (Fravolini et al., 2005)

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(Fig. 1). Consequently, the spread of invasive grasses may depend on species-specific abilities to extract and use water following pulses of rain across a range of soil types (Huxman et al., 2004; Melgoza et al., 1990).

We performed a growth chamber study to test a hypothesis that medusahead or ventenata would have superior plant performance compared to cheatgrass under a less frequent/more intense precipitation regime that is expected in the future. Further, we used several soils that differed in physiochemical characteristics to understand how soil properties, such as soil nutrients, interact with precipitation to influence plant success. Based on the limited research and current distribution of medusahead in the study region, we expected medusahead to have greater performance on soils with higher clay content (Dahl and Tisdale, 1975). Given the distribution of ventenata in disturbed and dry habitats (Old and Callihan, 1987), we expected this species to be more successful under longer dry periods followed by large rain events. In accomplishing this study, we will demonstrate how three invasive species within a single functional group differ in their response to the environment and to environmental change.

1. Study area, soils, watering treatments and plant propagation

The study was conducted the Eastern Oregon Agricultural Research Station located in the sagebrush-steppe ecosystem of the Northern Great Basin, western USA. The soils used for the study were collected from nine different sites within the region. The

coordinates for each site were determined in ArcMap using a random point generator within a pre-defined geographic area that covered approximately 2000 km². At each site, we bulked approximately 0.10 m³ of soil that was collected from the upper 10 cm of the soil surface. Soils were manually mixed and filled into plastic pots (10 × 10 × 22 cm). A subsample of each bulked soil was used for analyses of soil particle size (Gee and Bauder, 1986), ammonium (Foster, 1995), nitrate (Miranda et al., 2001), phosphorous (Bray and Kurtz, 1945), and pH. The soils of the nine sites had a gradient of clay content ranging from 13 to 29% (Table A.1). All three species are distributed in the study region, but only medusahead and cheatgrass were present at the soil collection sites.

We had a full factorial experimental design with each treatment combination of 3 species, 9 soils and 2 watering treatment with 4 replicates per treatment. The experiment was conducted over two trials in a growth chamber (Convion CNP6050) and was repeated identically for each trial. At the beginning of each trial, each pot was randomly assigned one of the treatment combinations and sown with 50 seeds (collected locally) of the assigned treatment species. The pots were placed in filtered water and allowed to reach saturation via capillary action and then randomly arranged within the growth chamber. There was >90% emergence for each species after approximately one week. We thinned plants to 13 per pot, which is a comparable density to sites that are invaded by annual grasses. The growth chamber was set to a diurnal schedule of 15 h light with 600 ppfd light intensity and 9 h of dark. During the first and second months of each trial, the daytime temperatures were set to 15.4 and 20.9 °C and the nighttime temperatures were set to 4.4 and 8.4 °C,

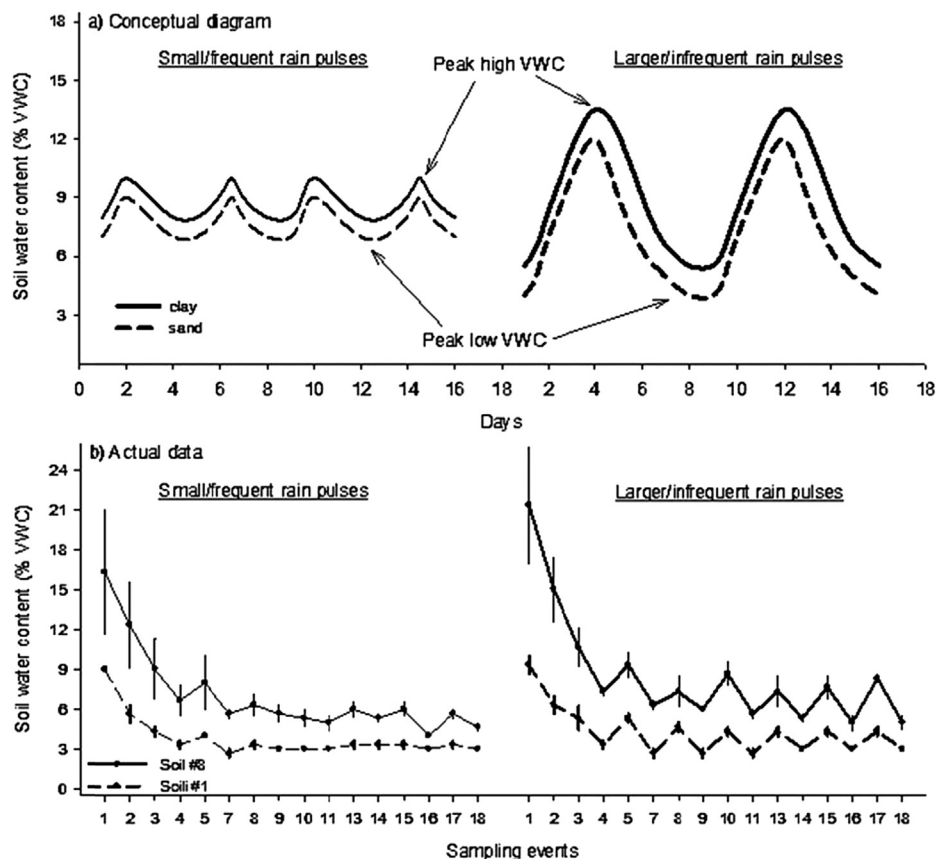


Fig. 1. Precipitation and soil effects on soil moisture. As global climate changes, precipitation regimes are shifting from small/frequent springtime rain pulses to relatively larger pulses followed by longer dry periods (large/infrequent). This leads to more extreme fluctuation in soil volumetric water content (VWC), which may favor some invasive species over others. Soil physical properties, such as clay (solid lines) and sand (dashed lines) content, may interact with precipitation to impact soil water availability. The upper panel (a) is a conceptual diagram of the potential difference in VWC in between two precipitation regimes in two soil types. The lower panel (b) is actual VWC data from repeated measurements in two representative soils that had higher sand content (Soil #1) or clay content (Soil #8) (see Table A.1 for soil information).

respectively. The temperatures were based on May and June averages over the last 15 years from a nearby climate station.

Watering treatments were initiated immediately after thinning and they continued for two months. Our watering treatments were based on the estimated springtime precipitation patterns in the study region over the previous 15 years (PRISM Climate Group, Oregon State University). Rain events between 0.1 and 5 mm and periods of 1–5 days without rain accounted for about 75% of precipitation sizes and frequencies, respectively (Fig. A.1). Rain events between 5.1 and 10 mm and periods of 6–10 days occurred much less frequently (16 and 18%, respectively), but would still be expected to occur approximately 3–5 times each spring. Using these data, we developed two distinct water regimes with either small/frequent or with large/infrequent simulated rain events (pulses), but with equivalent total water. The small/frequent regime consisted of 4 mm pulses occurring every 4 days; the large/infrequent regime consisted of 8 mm pulses that occurred every 8 days. A small area of each pot was kept free of plants to measure soil volumetric water content (VWC) using a 10 cm probe (Hydrosense, Campbell Scientific). Volumetric water content was repeatedly measured during the second trial in each pot immediately before the large/infrequent rain pulses and then again one day after, giving values of peak low and peak high VWC, respectively (Fig. 1). The rise in VWC from peak low to peak high values were used to determine the mean 'increase' in VWC, and the decline in VWC from peak high to the following peak low values were used to determine the mean 'drawdown' of VWC for each treatment combination.

The plants were harvested at the end of each trial by clipping shoots and gently washing roots in water. All plant materials were dried at 60 °C for 48 h and weighed (± 0.1 mg). Shoot and root masses per individual were calculated by dividing the total tissue mass by the number of individuals in each pot.

For soil moisture and plant growth data, we used three-factor, mixed-model ANOVAs (SAS v9.3) to determine the effect of species, soil, watering treatments and their interactions on VWC and plant biomass. Trial was considered a random factor. For VWC, repeated-measures analysis was additionally used in each ANOVA, with each individual pot as the subject that repeated measurements were conducted. Variables of VWC include overall VWC, peak high and peak low VWC, and the increase and drawdown of VWC; growth variables included whole plant, shoot and root biomass and the ratio of root to shoot biomass. Tukey's tests were used to compare means among species or between watering treatments within species. Values of VWC were natural log transformed to meet the assumptions of normality and homoscedasticity of error variance. We used Pearson's correlation coefficients

to determine which soil properties (based on bulked soils for each soil type) were most correlated with biomass response variables. Based on the correlations, we used the partial r^2 values from stepwise multiple regression analyses to determine the relative amount of variation that correlated soil properties explained.

2. The effects of species, soils and watering treatments on soil moisture

There were relatively modest (albeit significant) differences in overall soil VWC between watering treatments (based on F and P values from Table 1). Nevertheless, we found relatively large effects of the watering treatments during specific periods within the soil wetting/drying cycle. For example, the large/infrequent watering treatment had more than double the peak high VWC compared to the small/frequent water treatment, yet there were relatively small differences in peak low VWC (Table 1, Fig. 1). VWC following a precipitation pulses was also affected by species (greatest VWC for ventenata least for cheatgrass, $P < 0.001$), soils (greater overall, peak high and peak low VWC with increasing clay content, $r^2 = 0.63, 0.51$, and 0.52 , respectively; all $P < 0.001$) and their interactions ($P = 0.016$), indicating a complex relationship among species-specific plant water uptake, soil hydraulic properties, and precipitation size and frequency, as has been observed in other functional groups and ecosystems (Fravolini et al., 2013; Huxman et al., 2004).

3. The effects of species, soils and watering treatments on plant growth

Unlike most studies on precipitation regimes, we used a unique experimental design that manipulated the frequency and pulse size of simulated precipitation, but kept the total amount of water addition equivalent across treatments. Cheatgrass and ventenata were unresponsive to the different watering regimes (Fig. 2a,b), which suggest that total cumulative soil moisture may be relatively important compared to the frequency and pulse size for these two annual grass species. In contrast, medusahead was the only species to respond (positively) to long dry periods followed by large precipitation events (Table 1, Fig. 2a,b). In addition, medusahead had the greatest overall root growth across all soils and watering treatments compared to cheatgrass and ventenata. These fundamental differences in root growth of medusahead likely contribute to its rapid spread and ecological success in the western USA over recent decades.

Table 1

Results from a three-factor ANOVA testing for the effects of species, soil type and watering treatments on soil moisture content (a) and plant growth (b). We used nine soils and two watering regimes that were characterized by small/frequent or large/infrequent rain pulses. Volumetric water content (VWC) variables include overall VWC, peak high values following large pulses, peak low values following long dry periods, relative increase (Increase) in VWC one day after large pulses, and relative drawdown (Drawdown) of VWC after long dry periods. Plant growth was measured as whole plant, shoot, and root biomass and the ratio of root to shoot biomass.

	Species (Spec)		Soil		Water		Spec $\times$ soil		Spec $\times$ water		Soil $\times$ water		Spec $\times$ soil $\times$ water	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
a) Soil moisture content														
Overall VWC	12.71	<0.001	85.66	<0.001	12.48	<0.001	1.90	0.017	7.61	<0.001	1.85	0.065	3.80	<0.001
Peak high VWC	10.58	<0.001	88.09	<0.001	151.28	<0.001	1.95	0.016	5.62	0.004	1.26	0.262	5.04	<0.001
Peak low VWC	8.00	<0.001	83.45	<0.001	14.48	<0.001	2.32	0.003	9.80	<0.001	2.73	0.006	2.83	<0.001
Increase	1.68	0.189	5.17	<0.001	214.69	<0.001	0.082	0.665	1.08	0.341	0.91	0.507	1.59	0.072
Drawdown	1.88	0.155	5.54	<0.001	170.77	<0.001	0.77	0.720	0.13	0.877	0.70	0.695	1.71	0.044
b) Plant growth														
Whole plant biomass	16.76	<0.001	17.81	<0.001	4.91	0.031	1.33	0.218	3.25	0.047	1.94	0.074	1.56	0.118
Shoot biomass	2.91	0.063	13.74	<0.001	1.46	0.232	0.89	0.589	1.73	0.187	1.26	0.284	0.54	0.907
Root biomass	64.69	<0.001	28.46	<0.001	7.81	0.007	1.49	0.138	3.17	0.050	1.23	0.300	1.61	0.102
Root to shoot Biomass	67.95	<0.001	26.05	<0.001	1.15	0.289	1.52	0.129	0.31	0.734	0.31	0.960	1.12	0.361

Significant effects are in bold.

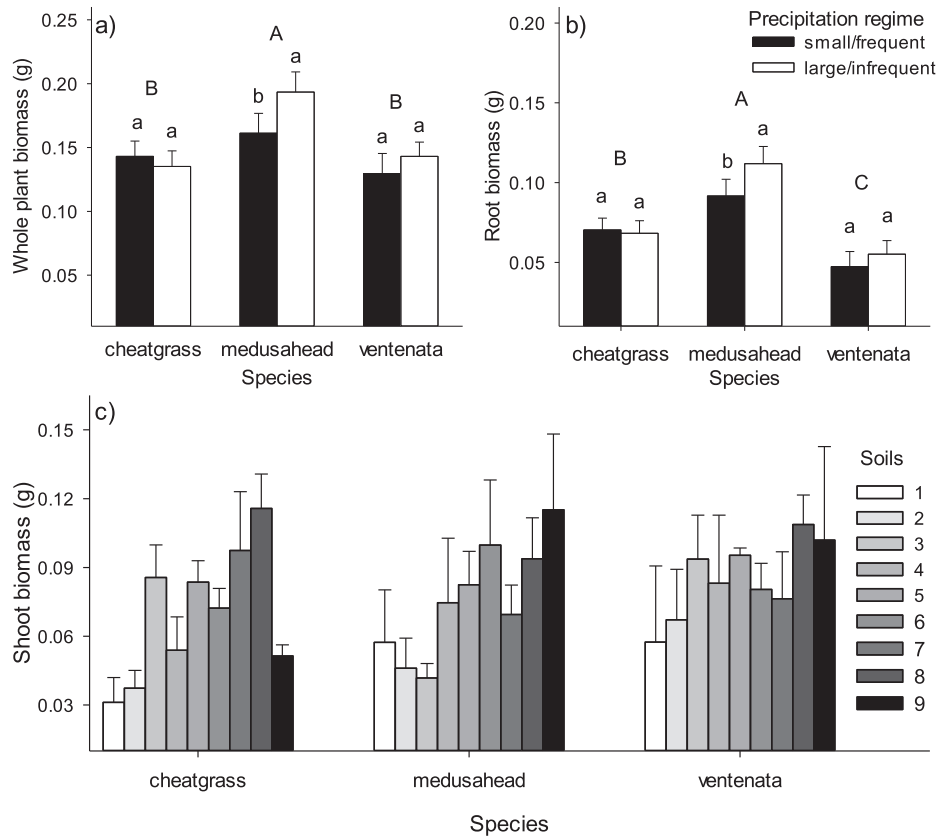


Fig. 2. Precipitation and soil effects on plant growth. Top two panels show a comparison of whole plant (a) and root (b) biomass of cheatgrass (*Bromus tectorum*), medusahead (*Taeniatherum caput-medusae*) and ventenata (*Ventenata dubia*) in response to two simulated precipitation regimes across nine soil types. The precipitation regimes of the two water treatments were characterized smaller/frequent (black bars) or larger/infrequent (white bars) rain pulses. Within each group of two bars, different lower case letters indicate significant differences between watering treatments, and within each panel different capitalized letters indicate significant overall differences between the three species following ANOVA (ANOVA results in Table 1). The bottom panel (c) shows the effect of soils on shoot biomass of the three invasive annual grass species. The nine soils were collected around a local study region and varied in physiochemical properties (see Table A.1 for soil information). The nine soils are in rank order of clay content from lowest (1) to highest (9).

The effects of soil properties (e.g., texture, nutrients, pH) were greater on whole plant, shoot and root biomass compared to the water treatments, but were relatively consistent among species (Table 1). We expected medusahead to have superior performance on soils with higher clay content compared to the other two species (Dahl and Tisdale, 1975), but instead, there were no species $\times$ soil interactions (Table 1, Fig. 2c). Similarly, cheatgrass is known to have a high degree of responsiveness to soil properties (Miller et al., 2006), although it did not perform differently than medusahead or ventenata across soil types. These results contrasted other studies on closely related, even congeneric species, that often shown unique responses to soil variability (Hacker et al., 2012). Evidently, our three study species of invasive annual grasses have seemingly evolved similar response patterns to soil physiochemical properties.

Across species, shoot growth was more affected by soil properties compared to root growth. Specifically, shoot biomass correlated positively to clay content ($r = 0.44$), but was also positively related to soil N ($r = 0.42$) and negatively to pH ($r = -0.53$) (Table A.2). Partial r^2 from stepwise regressions revealed that pH and clay explained 39 and 23%, respectively, of variation in shoot growth. Given that soil nutrient dynamics are largely influenced by soil moisture, pH and clay content, the interacting effects of precipitation and soil properties may play an important role in determining plant growth patterns and should be further investigated. In general, our results suggest that soil chemical properties, such as pH, may be equally or more important to plant performance than soil

physical properties, such as texture, despite the strong effects of texture on soil water availability (Fig. 1).

Studies on invasive annual grasses in sagebrush-steppe are abundant, yet the majority of research has focus on the most dominant species, cheatgrass. The traits that confer invasion success of cheatgrass are well documented (Fenesi et al., 2011), but there are limited studies to develop robust hypotheses for other species such as medusahead and especially ventenata. We expected ventenata to have higher root growth and greater responsiveness to the large/infrequent precipitation regime (Old and Callihan, 1987); yet this species had least root growth and no responsiveness to precipitation. Clearly, our assumptions and hypotheses regarding 'newer' invaders need further empirical testing to understand the ecology of these invasives.

In general, all three species had similar responses to our soil and watering treatments, which rationalizes grouping them into a single functional group when making broad-scale assessments of invasive grasses within sagebrush-steppe ecosystems. Even so, medusahead had intrinsically more allocation of biomass to roots and greater root growth in response to our environmental manipulations compared to cheatgrass or ventenata. Resource-use efficiency is a key functional plant trait associated with successful invasion into native communities (Hart and Marshall, 2012). Greater root growth combined with high responsiveness to precipitation is an adaptive strategy for resource uptake in dry climates with variable precipitation. Consequently, medusahead may have a competitive advantage over other invasive grasses and thus spread

faster than others across the western USA in response to changing climate.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2014.01.010>.

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