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ORIGINAL PAPER

Increased winter precipitation benefits the native plant pathogen *Ustilago bullata* that infects an invasive grass

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Abstract *Ustilago bullata* is a fungal pathogen that infects grasses in western North America. It infects the grass *Bromus tectorum*, sometimes at epidemic levels, and has been considered as a biocontrol agent in regions where *B. tectorum* is invasive. During a study of the effects of variation in precipitation on *B. tectorum* demography in Colorado, USA, we observed infection by *U. bullata* and recorded data on variation in infection rates among treatments receiving different amounts of winter precipitation. Over 3 years, increased winter precipitation was correlated with a higher prevalence of infection by *U. bullata*. In one of those years (2012), infection was associated with a 21 % decrease in *B. tectorum* seed yield in plots that received supplemental winter precipitation. While *B. tectorum* may exhibit higher rates of growth and/or reproduction if winter precipitation increases, results of our pathogen surveys suggest that associated population increases could be moderated by increased rates of fungal infection. Our observations suggest that although invasive species may benefit from climate change, some pathogens may also benefit, and decrease success of invasive plant populations in the future. These results highlight the importance of both direct and interactive effects of climate change on success of invasive species.

Keywords *Bromus tectorum* · Cheatgrass · Climate change · Invasive species · Precipitation change

Introduction

Global climate change will affect the abundance and success of plant species (Dukes and Mooney 1999; Thuiller et al. 2007; Hellmann et al. 2008) and plant pathogens (Coakley et al. 1999; Pautasso et al. 2012; Chakraborty 2013). Further, changing climatic conditions may alter the frequency and intensity of biotic interactions between plants and pathogens (Garrett et al. 2006; Tylianakis et al. 2008). Infection by pathogens can have strong effects on plant growth (Van der Putten et al. 1993) and climate induced changes in the interactions between plants and pathogens can greatly affect plant success (Van der Putten and Peters 1997; Pautasso et al. 2012). While the effects of climate change on invasive plant species have been extensively considered (e.g. Hellmann et al. 2008; Dukes et al. 2011), relatively few studies have examined how invasive plants may interact with pathogen pressure in a changing climate (Tylianakis et al. 2008; Seastedt 2014). Increasing temperature and precipitation associated with climate change may

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benefit invasive plants more than native ones, at least in portions of North American rangelands (Zelikova et al. 2013; Concilio et al., in press). However, the overall effects of global climate change on invasive plant populations could be strongly influenced by changing dynamics of plant/pathogen interactions.

Most research on plant pathogens and climate change concerns how success of crop pathogens will be influenced by changing climate (Coakley et al. 1999; Chakraborty et al. 2000). Another interesting, and less well-studied, impact of global change may be changes in success of pathogens on invasive species. Success of invasive plant species in new environments is often attributed to enemy release, or an escape from predators and pathogens in their home range (Klironomos 2002; Mitchell and Power 2003; Reinhart et al. 2003; Callaway et al. 2004). However, novel enemies in the new ranges can impact invasive plant abundance (Mack 1996; Parker and Gilbert 2004; Mitchell et al. 2006; Callaway et al. 2013). Changing climatic conditions have the potential to alter the abundance of both invasive plant species and novel enemies in the future.

Here, we report observational data on plant/pathogen interactions collected during a study examining the effects of increased precipitation on populations of an invasive plant. We designed a precipitation manipulation experiment to simulate changes in precipitation caused by climate change. We hypothesized that increased winter precipitation would benefit the invasive winter-annual *Bromus tectorum* (cheatgrass). After one year of manipulations, we observed the native fungal pathogen, *Ustilago bullata,* infecting seed heads of *B. tectorum* in our study plots. We decided to record presence and abundance of *U. bullata* to examine how simulated precipitation change would influence infection by the pathogen on an invasive grass.

Ustilago bullata is native to North America, and it infects several cool-season grass species, including the invasive *B. tectorum* (Stewart and Hull 1949; Mack and Pyke 1984; Gossen and Turnbull 1995). Spores of *U. bullata* germinate and develop into sporidia in soil, and fuse to create hyphae that infect grasses during the seedling stage. The pathogen grows systemically inside the host until flowering, when it entirely co-opts seed production of the plant, causing it to produce spores of the fungus instead of viable seeds. These spores then disperse to the soil to repeat the cycle (Alexopoulos et al. 1996; Meyer et al. 2008). Introduced species, such as *B. tectorum*, did not evolve with, and may have less resistance to, native pathogens such as *U. bullata*, and thus may be more easily infected than native species (Mack 1996; Parker and Gilbert 2004; Verhoeven et al. 2009; Callaway et al. 2013). In the past, there have been instances where this pathogen has reached epidemic proportions, wiping out entire populations of *B. tectorum* (Stewart and Hull 1949; Klemmedson and Smith 1964; Mack and Pyke 1984). Because of this, and because it is native to North America, *U. bullata* has been suggested as a potential biocontrol mechanism for *B. tectorum* (Meyer et al. 2001, 2008). Observing how changing precipitation patterns affect *U. bullata* will inform considerations for use of this pathogen as a possible biocontrol in the future.

Pathogens that complete part of their life cycle in soil, such as *U. bullata*, may be particularly affected by changes in precipitation and soil moisture availability. Plant microbial pathogens, especially fungal pathogens, often benefit from increased soil moisture (Schafer and Kotanen 2003; Wagner and Mitschunas 2008). Studies show that adequate soil moisture influences the abundance of *U. bullata* (Mack and Pyke 1984; Meyer et al. 2008), so future changes in precipitation and soil moisture availability should impact success of the pathogen.

For 3 years, we recorded observations of the fungal pathogen in different precipitation treatments to address two questions: How does seasonality and amount of precipitation affect the abundance of *B. tectorum* infected by *U. bullata*? Does presence of the pathogen significantly reduce seed yield of the invasive grass *B. tectorum* in precipitation manipulation treatments?

Methods

Observations of infection by the fungal pathogen were made in a precipitation manipulation experiment at a site associated with a semi-arid grassland ecosystem near Boulder, Colorado, USA (40° 07′N, 105° 18′W). The site has an elevation of 1798 m, a mean annual precipitation of 475 mm, and a mean annual temperature of 10.5 °C (WRCC 2014). The site has a continental climate, with most precipitation falling as rain in spring and early summer, and c.a. 26 % of precipitation falling as snow over the winter (WRCC 2014). A precipitation manipulation experiment was established in 2010 with five precipitation manipulations: control, winter-wet, winter-wet/summer-dry, winter-wet/summer-wet, and winter-dry/summer-wet. The winter and summer-dry treatments were accomplished using rain-out shelters that block 50 % of incoming precipitation, and the winter and summer wet-treatments were accomplished with water additions from a local water source designed to increase precipitation 50 % above ambient. There were ten replicates of each treatment. All plots of the experiment were located within 1 ha of each other, on the same slope and with similar soils. More information on the experimental design of the precipitation manipulations can be found in Prevéy and Seastedt (2014).

We measured prevalence of *U. bullata* in plots of all treatments in June 2011–2013, after all *B. tectorum* in plots had senesced. Infected plants produce black teliospores of *U. bullata* instead of seeds, and these remain on the plant after senescence. We visually inspected each plot for presence of the pathogen on seed heads of *B. tectorum*. In addition, we harvested six *B. tectorum* individuals per plot in June of 2011 and 2012 and eight individuals per plot in June of 2013 to quantify seed yield and infection status. Plants were collected at 0.25 m intervals along a transect running through the middle of each plot. We dried and weighed harvested plants, and then counted the number of seeds produced per individual and recorded the presence of infection by *U. bullata*.

In June 2012 and 2013 we also measured the proportion of *B. tectorum* infected with *U. bullata* within 0.1 m^2 subplots in each treatment. Subplots were created in November 2011 to monitor demographic responses of *B. tectorum* to precipitation manipulations (Prevéy 2014). On November 15, 2011, 0.1 m^2 subplots were disturbed to remove surface vegetation. Fifty *B. tectorum* seeds were sown in each subplot. On June 20, 2012, after all *B. tectorum* in subplots had senesced; we harvested aboveground biomass in subplots. Harvested *B. tectorum* were visually inspected for infection by *U. bullata*. On October 18, 2012, we planted another 50 seeds in each subplot, and on June 26, 2013, all *B. tectorum* was harvested from subplots and *U. bullata* infection was recorded.

Statistical analyses

We employed several analyses to examine how precipitation treatments affected abundance of *U. bullata*. First, we compared presence and absence of *U. bullata* in plots of each treatment in 2011–2013. Because the response variable was either presence or absence, we analyzed data with generalized linear models with binomial distributions. However, spatial heterogeneity in the presence of the pathogen in soil could result from factors other than precipitation treatment (Ettema and Wardle 2002), so only examining presence or absence data might not provide an accurate representation of the effects of precipitation timing and amount on pathogen prevalence. To evaluate the severity of infection in plots where we knew the pathogen was present, we performed correlation analyses that only included data from plots where we observed infection by the pathogen. We excluded plots in which infection was not observed and then calculated the average percent of *B. tectorum* infected with *U. bullata* among all plots in each precipitation treatment. To examine how winter precipitation might impact infection severity, we correlated the average percent of *B. tectorum* infected with *U. bullata* in each treatment in each year with the amount of winter precipitation received by that treatment in that year using linear models. We included percent cover of *B. tectorum* and average aboveground biomass of individual *B. tectorum* as covariates in initial correlation analyses. We performed correlation analyses for infection severity on transects in 2011–2013, and subplots in 2012–2013.

To determine if infection by *U. bullata* was negatively affecting the amount of seeds produced by *B. tectorum* at the field site, we examined the effects of pathogen infection on the average seed yield of *B. tectorum* in plots of each treatment in each year. We compared the average number of seeds per individual in each plot including *B. tectorum* with *U. bullata* infection (and thus no viable seeds), to the average number of seeds per individual excluding infected *B. tectorum,* to calculate the percent reduction in seed yield of *B. tectorum* per treatment, per year. All analyses were performed in the statistical program R (R Development Core Team 2012).

Results

Ambient winter precipitation varied over the 3 years of the study, with drier winters in 2010–2011 and 2012–2013, and a wetter than average winter in 2011–2012. Average winter temperatures were similar over the 3 years, although January 2012 was unseasonably warm (Fig. 1). There were no significant differences in presence of *U. bullata* between treatments in any year (all $p > 0.3$, Fig. 2). Overall, *U. bullata* was present in only 26 % of plots of all treatments in 2011, but was present in over 60 % of all plots in 2012 and 2013 ($p < 0.02$ for comparisons of presence in 2011 to 2012 or 2013, Fig. 2).

Neither percent cover nor aboveground biomass of *B. tectorum* explained significant variation in severity of infection with *U. bullata* ($p = 0.33$ and $p = 0.11$, respectively), so these variables were removed from final correlation analyses. Correlation coefficients for infection abundance in transects and subplots were similar (William's t test, $p = 0.41$), so we combined all measurements from transects and subplots for the correlation analysis. The percent of *B. tectorum* infected with *U. bullata* positively correlated with increasing winter precipitation in transects and subplots over the 3 years ($R^2 = 0.25$, $p = 0.01$, Fig. 3).

Across all plots in 2012 and 2013, infection with *U. bullata* was associated with a 3–4 % reduction in mean seed yield (Fig. 4). Among treatment/year combinations, the largest reduction (21 %, $p < 0.0001$) occurred

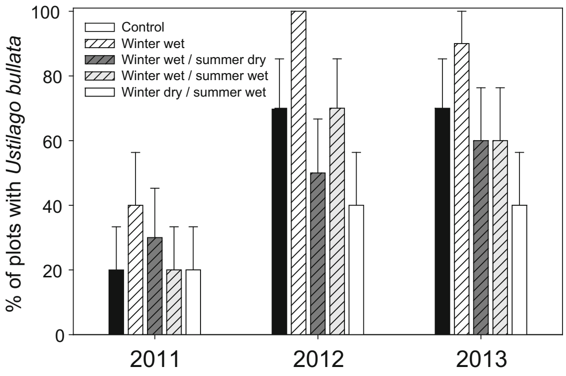

Fig. 2 Percent of plots in each precipitation treatment in which *U. bullata* was present in 2011–2013, +standard error

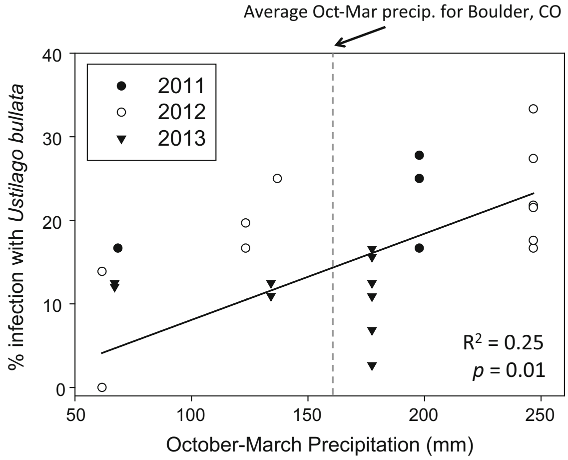

Fig. 3 Relationship between average percent of *B. tectorum* infected with *U. bullata* per treatment per year and cumulative precipitation received by that treatment from October to March. This analysis only includes plots where *U. bullata* was present

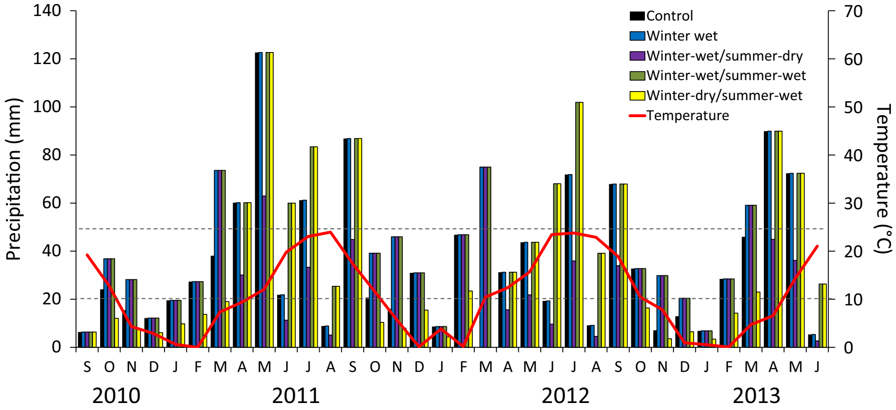

Fig. 1 Total precipitation received by each treatment in each month (*bars*) and average monthly temperature from September 2010 to June 2013 (*red line*). *Dotted lines* indicate the temperature range within which *U. bullata* is most successful at infecting seedlings (Boguena et al. 2007)

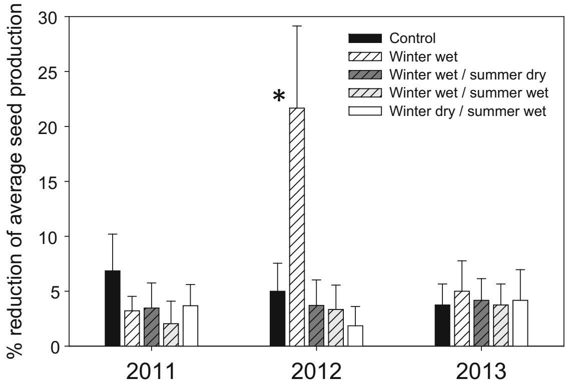

Fig. 4 Percent reduction in seed production resulting from *U. bullata* infection in precipitation treatments in 2011–2013, +standard error. Seed production was significantly reduced in winter wet treatments in 2012 compared to all other treatments ($p < 0.0001$)

in plots experiencing the winter-wet treatment in 2012. There was no difference across treatments in the effect of *U. bullata* on seed set of *B. tectorum*, with the exception of the winter-wet treatment in 2012.

Discussion

Ambient winter precipitation and precipitation manipulation treatments affected rates of *U. bullata* infection observed in our study, and these effects may have important implications for the utility of *U. bullata* as a biocontrol in future climate scenarios. Increased winter precipitation was correlated with an increase in the abundance of *U. bullata* in plots. Notably, treatments that received above average winter precipitation had the highest rates of infection, indicating that increases in future mean winter precipitation could benefit *U. bullata*, all else being equal.

Winter-wet treatments in 2012 had the highest infection abundance both in the percentage of plots with *U. bullata* present and in the percentage of plants infected, and also received the most winter precipitation of all treatments in all years. The fungal pathogen may need adequate soil moisture to survive in soil and infect emerging seedlings in late fall (Meyer et al. 2008), so treatments receiving additional winter precipitation have higher infection rates, whereas those receiving winter drought have lower rates. In addition to a wet winter, January 2012 was also warmer than other years (Fig. 1), and warm temperatures might also benefit *U. bullata*. *Ustilago bullata* at our field site may be able to infect more seedlings during mild temperatures in fall and winter than in cold temperatures. Boguena et al. (2007) found that *U. bullata* is most successful at infecting seedlings at temperatures ranging from 20 to 30 °C, and less successful in cold temperatures. Similar to our findings, Rua et al. (2014) observed that elevated temperature and precipitation led to increased infection of a non-native cool-season grass, *Schedonorus arundinaceus*, by viral pathogens in North America. In contrast, infection severity across treatments in 2013 was lower than the other years, even in treatments with supplemental winter precipitation. 2013 received the lowest winter precipitation of all years, and it is possible that experimental water additions did not alleviate dry periods between precipitation events in that year. Our results indicate that significantly higher than average winter precipitation may be needed to increase infection rates of *U. bullata*. Additionally, the high variability in presence and infection severity of *U. bullata* across treatments and years indicates that factors other than winter precipitation also influence abundance of this pathogen. Future experiments manipulating both temperature and the timing and quantity of precipitation will provide additional information on how climate influences success of *U. bullata*.

Overall, there were no differences across treatments in the effect of *U. bullata* on plot-level seed yield, and infection by *U. bullata* did not substantially lower average seed yield of *B. tectorum*. However, in 2012, seed set in winter-wet plots receiving greater than 250 mm of winter precipitation was reduced by over 20 %. Reducing seed yield by over 20 % could reduce propagule pressure and slow population growth of this invasive grass. Over the past 121 years, winter precipitation near the study area was greater than 200 mm in 20 % of the years, and greater than 250 in 8 % of the years (WRCC 2014). With an increasing probability of more winter precipitation along the Front Range of Colorado in the future (Knowles et al. 2006; Ray et al. 2008; IPCC 2013), *U. bullata* may become more abundant. *Bromus tectorum* does not form a long-lived seedbank (Smith et al. 2008), and pandemic levels of *U. bullata* can eliminate entire populations of *B. tectorum* from the landscape (Mack and Pyke 1984; Stewart and Hull 1949).

Additional research focusing on the mechanistic reasons for success of *U. bullata* in different precipitation scenarios is needed to understand how this pathogen will respond to climate change. Experiments testing the effects of different pathogen strains, winter temperatures, and plant resistance genotypes on success of infection will help inform the use of *U. bullata* as a biocontrol in the future. However, our results provide preliminary evidence that increased winter precipitation, and possibly warmer autumn temperatures, could benefit the pathogen *U. bullata*. Higher infection rates of *U. bullata* in the future may decrease abundance of the invasive grass *B. tectorum*. Most climate manipulation experiments focus on responses of individual species, or trophic levels, to climate manipulations, but interactions between trophic levels will influence responses of species to climate change as well (Tylianakis et al. 2008; Van der Putten et al. 2010). The observations of increased infection of *B. tectorum* by *U. bullata* in this climate manipulation experiment have important implications for interactions between invasive plant species and pathogens. Many invasive plants may become more successful as the climate changes; however, some pathogens may also benefit, and decrease success of invasive plants in the future.

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