Cheatgrass is favored by warming but not CO_2 enrichment in a semi-arid grassland

DANA M. BLUMENTHAL[1], JULIE A. KRAY[1], WILLIAM ORTMANS[2], LEWIS H. ZISKA[3] and ELISE PENDALL[4,5]

[1]Rangeland Resources Research Unit, USDA Agricultural Research Service, Fort Collins, CO, USA, [2]Biodiversity and Landscape Unit, Gembloux Agro-Bio Tech, University of Liege, Gembloux, Belgium, [3]Crop Systems and Global Change Laboratory, USDA Agricultural Research Service, Beltsville, MD, USA, [4]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, Australia, [5]Department of Botany & Program in Ecology, University of Wyoming, Laramie, WY, USA

Abstract

Elevated CO_2 and warming may alter terrestrial ecosystems by promoting invasive plants with strong community and ecosystem impacts. Invasive plant responses to elevated CO_2 and warming are difficult to predict, however, because of the many mechanisms involved, including modification of phenology, physiology, and cycling of nitrogen and water. Understanding the relative and interactive importance of these processes requires multifactor experiments under realistic field conditions. Here, we test how free-air CO_2 enrichment (to 600 ppmv) and infrared warming (+1.5 °C day/3 °C night) influence a functionally and phenologically distinct invasive plant in semi-arid mixed-grass prairie. *Bromus tectorum* (cheatgrass), a fast-growing Eurasian winter annual grass, increases fire frequency and reduces biological diversity across millions of hectares in western North America. Across 2 years, we found that warming more than tripled *B. tectorum* biomass and seed production, due to a combination of increased recruitment and increased growth. These results were observed with and without competition from native species, under wet and dry conditions (corresponding with tenfold differences in *B. tectorum* biomass), and despite the fact that warming reduced soil water. In contrast, elevated CO_2 had little effect on *B. tectorum* invasion or soil water, while reducing soil and plant nitrogen (N). We conclude that (1) warming may expand *B. tectorum's* phenological niche, allowing it to more successfully colonize the extensive, invasion-resistant northern mixed-grass prairie, and (2) in ecosystems where elevated CO_2 decreases N availability, CO_2 may have limited effects on *B. tectorum* and other nitrophilic invasive species.

Keywords: climate change, global warming, Great Plains grasslands, growing season length, nitrogen limitation, plant invasion, plant phenology, rangeland ecosystems

Introduction

Increasing atmospheric carbon dioxide and consequent changes in climate are expected to alter the species composition and distribution of plant communities, and therefore a wide range of ecosystem functions (Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Williams *et al.*, 2007; Suding *et al.*, 2008). One type of community change that may be especially problematic is the potential for increasing plant invasion (Dukes & Mooney, 1999; Thuiller *et al.*, 2007; Walther *et al.*, 2009; Bradley *et al.*, 2010). To date, however, invasive plant responses to the most pervasive global changes, elevated atmospheric CO_2 and warming, have been inconsistent and remain poorly understood (Sorte *et al.*, 2013).

Mechanistic understanding of invasive plant responses to CO_2 and temperature is impeded by the fact that these changes influence plants both directly, by altering physiological rates and growing season length, and indirectly, by altering water and N cycling (Williams *et al.*, 2007; Morgan *et al.*, 2011; Wolkovich & Cleland, 2011). Strong CO_2 responses of some invasive species have been attributed to their ability to increase photosynthesis, water use, growth rates, resource use efficiency, and rooting depth as carbon becomes less limiting (Ziska, 2003; Nagel *et al.*, 2004; Dukes *et al.*, 2011; Blumenthal *et al.*, 2013). Warming may promote invasion by increasing survival, accelerating growth, and opening phenological niches not occupied by native species, or may inhibit invasion by decreasing water availability and recruitment (Williams *et al.*, 2007; Walther *et al.*, 2009; Sandel & Dangremond, 2012; Wolkovich *et al.*, 2013; Zelikova *et al.*, 2013). The few studies to test for CO_2 by warming interactions have also had inconsistent results, with warming

Correspondence: Dana M. Blumenthal, Rangeland Resources Research Unit, USDA-ARS, 1701 Center Ave. Fort Collins, CO 80526, USA, tel. 970-492-7122, fax 970-492-7160, e-mail: dana.blumenthal@ars.usda.gov

counteracting CO_2-induced increases in invasion in some cases (Williams et al., 2007; Dukes et al., 2011; Blumenthal et al., 2013).

CO_2 and warming effects on plants are also context dependent, as the importance of their direct and indirect effects varies with the strength of C, N, and water limitation (Shaver et al., 2000; Morgan et al., 2004; Norby & Luo, 2004; Nowak et al., 2004; Reich et al., 2006). In particular, decreases in competition due to land use and disturbance may increase resource availability, allowing invasive species to respond more strongly to other global changes (Eskelinen & Harrison, 2014). The opposite may also be true, however, as observed for Centaurea solstitialis, which benefitted more from elevated CO_2 under competitive conditions than when grown in monoculture (Dukes et al., 2011). The context dependence of CO_2 and warming effects underscores the need for both multifactor field experiments with realistic levels of water and nutrient limitation, and experimental manipulation of disturbance and competition (Norby & Luo, 2004; Kroel-Dulay et al., 2015).

Synergy between global change and invasive species may be particularly harmful if the invasive species have strong community and ecosystem impacts. Bromus tectorum L. (cheatgrass), a winter annual grass native to Europe, southwestern Asia, and northern Africa, can decrease fire return times from centuries to decades or less in its invaded range, with subsequent declines in native species diversity, forage production, and carbon storage (Mack, 1981; Melgoza et al., 1990; Whisenant, 1990; D'Antonio & Vitousek, 1992; Rice, 2005; Bradley et al., 2006; Balch et al., 2013). It has now invaded tens of millions of hectares in western North America (DiTomaso, 2000; Rice, 2005; Bradley & Mustard, 2006). Economic costs of controlling fires associated with B. tectorum have been estimated at $20 million annually (Knapp, 1996).

As global change proceeds, B. tectorum is predicted to become more invasive in cooler, high-elevation, and high-latitude areas, and in areas where water availability increases in the winter or decreases in the summer (Bradley, 2009; Mealor et al., 2012; Concilio et al., 2013; Prevey & Seastedt, 2014; Bradley et al., 2015; West et al., 2015). Furthermore, warming may directly increase fire frequency and lengthen fire seasons (Westerling et al., 2006; Littell et al., 2009), strengthening positive feedbacks between B. tectorum invasion and wildfires (D'Antonio, 2000; Abatzoglou & Kolden, 2011; Bradley et al., 2015). Field experiments in the Intermountain Region of the United States, where B. tectorum is most problematic, have shown that warming can promote B. tectorum invasion in wet years, particularly at cooler high-elevation sites (Zelikova et al., 2013; Compagnoni

& Adler, 2014a,b). It is not clear whether these climatic changes will also allow B. tectorum to expand its invasive range to the north and east, particularly in the extensive grasslands of the western Great Plains (Bradley, 2009).

Also missing from predictions of future B. tectorum invasion is an understanding of how it will respond to elevated CO_2. In controlled environment comparisons, B. tectorum photosynthesis, growth, seed production, and flammability all increased with increasing CO_2 (Smith et al., 1987; Ziska et al., 2005). Elevated CO_2 also increased seed production and seed banks of a closely related species, Bromus rubens, during a wet El Niño year in the Nevada Desert free-air CO_2 enrichment experiment (Smith et al., 2000, 2014). These studies raise the prospect that elevated CO_2 may intensify effects of warming on B. tectorum. However, no studies have yet evaluated effects of elevated CO_2 on B. tectorum in the field, under competitive conditions with limited resource availability, or in combination with warming. Each of these factors can regulate CO_2 responses, and each represents a substantial gap in our ability to predict B. tectorum responses to global change (Poorter & Navas, 2003; Luo et al., 2004; Dukes et al., 2011; Morgan et al., 2011; Dieleman et al., 2012; Bradley et al., 2015).

Here, we describe the results of a 2-year study of warming, elevated CO_2, and competition on B. tectorum invasion of northern mixed-grass prairie. This plant community represents the largest remaining intact grassland (36 700 000 ha) in North America (Samson et al., 2004). While B. tectorum is sufficiently abundant within some parts of the northern mixed-grass prairie to warrant management, it remains much less abundant than it is in the Intermountain Region (Haferkamp et al., 2001; Ogle & Reiners, 2002; Ogle et al., 2003; Bradley & Mustard, 2006). Resistance to B. tectorum invasion may stem from summer-dominated precipitation regimes, relatively cool winters, and/or dominant grass species that tolerate domestic grazing (Mack & Thompson, 1982; Milchunas et al., 1988; Knapp, 1996; Bradley, 2009). If B. tectorum becomes more invasive in the future, it would have significant consequences for both livestock production and biological diversity (Haferkamp et al., 2001; Knick et al., 2003; Rice, 2005).

Our objectives were (1) to learn how elevated CO_2 and warming influence B. tectorum recruitment, growth, and seed production under realistic conditions in the field, and (2) to determine whether effects of elevated CO_2 and warming are regulated by the intensity of competition, water availability, and/or N availability. To answer these questions, we seeded B. tectorum into subplots within the Prairie Heating and CO_2 Enrichment (PHACE) study (Morgan et al., 2011),

varied the intensity of competition by removing resident plants, and measured soil resource availability together with phenological, physiological, growth, and reproductive responses of *B. tectorum*. We predicted that elevated CO$_2$ would promote *B. tectorum* invasion by increasing photosynthesis or water use efficiency, and that warming would have no net effect on *B. tectorum*, due to opposing effects of reduced temperature limitation and increased water limitation. We also predicted that reduced competition would increase the availability of below-ground resources and allow *B. tectorum* to respond more positively to global change treatments.

Materials and methods

Study site

The PHACE experiment was located at the High Plains Grassland Research Station, near Cheyenne, WY, USA (latitude 41°11′N, longitude 104°54′W, elevation 1930 m). This site falls at the southern edge of the northern mixed-grass prairie. The climate is semi-arid, with a mean annual temperature of 7.6 °C and mean annual precipitation of 385 mm, approximately 60% of which falls during the growing season (late March through September) (Carrillo *et al*., 2012). Plant production is frequently water limited (Derner & Hart, 2007), and when water is present, belowground nutrients, particularly N, can be limiting (Blumenthal, 2009; Dijkstra *et al*., 2010). The site is dominated by perennial graminoids, including both cool season species, principally *Pascopyrum smithii* (Rydb.) A. Love, *Hesperostipa comata* Trin and Rupr., and *Carex eleocharis* L. Bailey, and warm season species, principally *Bouteloua gracilis* (H.B.K) Lag. It also includes a diverse array of forbs and subshrubs, and one native winter annual grass, *Vulpia octoflora* (Walter) Rydb. *Bromus tectorum* is widely distributed at the High Plains Grassland Research Station and is abundant in some areas, but was not present within study plots prior to this experiment.

Experimental design

We imposed five replications of each of four treatments: (1) control; (2) free-air CO$_2$ enrichment (FACE) to 600 ppmv; (3) infrared warming to increase canopy temperature by 1.5 °C during the day and 3 °C at night; and (4) CO$_2$ enrichment plus warming. Achieved treatment levels were 600.5 ppmv CO$_2$ ±50.4 (SD, measured at 1-min intervals), and +1.6 ± 0.3 °C (SD, measured at 1-h intervals) during the day and + 3.0 ± 0.3 °C at night (see Morgan *et al*., 2011 and LeCain *et al*., 2015 for additional system performance details). The CO$_2$ and temperature levels were chosen to match projections for the late 21st century in this region, which call for atmospheric CO$_2$ concentration to rise to 500–800 ppm and mean annual temperature to increase 2.5–4 °C, under low and high emissions scenarios, respectively (Kunkel *et al*., 2013; Shafer *et al*., 2014).

Warming and CO$_2$ enrichment treatments were applied to 7 m^2 rings starting in 2006 and 2007, respectively. Untreated rings were outfitted with mock heaters and CO$_2$ enrichment tubing to control for potential infrastructure effects. To ensure that treatment effects on soil water were not diluted by water movement between plots and surrounding prairie, rings were isolated belowground by installing a 60 cm deep plastic barrier. Throughout the construction and operation of the experiment, work was conducted from raised platforms to minimize disturbance to vegetation and soil within the rings. To account for within-site variation in belowground properties, we randomized rings within two soil-type blocks: Ascalon Variant Loam (fine-loamy, mixed-mesic) and Altvan Loam (fine-loamy over sandy, mixed-mesic).

The warming treatment was imposed year-round, and often accelerated snowmelt during winter periods with measurable snow accumulation (D. Blumenthal, personal observation). Enrichment of CO$_2$ was limited to daylight hours during periods warm enough for plant growth. To ensure that the CO$_2$ treatment was applied even during cooler portions of the *B. tectorum* growing season, we enriched CO$_2$ throughout each full 24-h period when the daily temperature maximum reached 7 °C or above. We then calculated the proportion of growing degree days between *B. tectorum* germination and maturation for which CO$_2$ enrichment was applied. Conservatively assuming that *B. tectorum* growth occurs down to but not below 3 °C (Young, 2000), CO$_2$ was enriched during 100% (ambient temperature plots) and 98% (warmed plots) of growing degree days in 2012, and 97% and 95%, respectively, of growing degree days in 2013.

We seeded *B. tectorum* into a single 0.7 × 0.5 m plot within each ring in two consecutive years. One year prior to seeding, in August 2010, we removed competitors from a 0.5 × 0.3 m strip in the center of each plot with glyphosate, while protecting surrounding vegetation with vertical barriers. Thus, each plot contained two 0.5 × 0.2 m strips of undisturbed native vegetation (the 'high-competition' treatment) bordering a single strip with little vegetation (the 'low-competition' treatment) (Figure S1). The low-competition treatment did not represent the complete absence of competition because it may have contained roots from plants in adjacent undisturbed strips, soil resources could move among strips, and native species were allowed to recolonize the disturbed strips (little aboveground recolonization occurred, but belowground recolonization may have been greater). For each of two *B. tectorum* growing seasons (Year 1: 2011–2012; Year 2: 2012–2013), we collected *B. tectorum* seed locally in June and seeded it by hand in August across the 0.7 × 0.5 m plot at a rate of 22 g m^{-2}, approximately 8000 seeds m^{-2}, within the range of reported seed production values for *B. tectorum* (Humphrey & Schupp, 2001; Hempy-Mayer & Pyke, 2008; Mazzola *et al*., 2011).

Measurements

At 3-week intervals during the period of active growth (October–November, and March–June), we counted all *B. tectorum* individuals and measured the height of 10 randomly selected individuals within each competition treatment of each plot.

Average plant height was closely correlated with average per-plant biomass at maturity ($R^2 = 0.70$ in Year 1 and 0.75 in Year 2).

We harvested individual *B. tectorum* plants when they contained mature seed, but had not yet begun to drop seed. Because plants matured at different times under different treatments, we harvested from all plots weekly for 6 weeks each year, at each date removing only mature plants by clipping at ground level. Mature plants were identified as those for which >50% of florets were purple and contained hardened seeds. All harvested plants were stored in paper bags and oven-dried for 72 h at 60 °C. Total aboveground plant biomass was determined for each subplot in each year. We then separated seed biomass (spikelets, including seeds, palea, lemma, and awns) from stems and leaves. Seed biomass including associated reproductive structures was closely correlated with biomass of seeds alone ($R^2 = 0.99$), determined by weighing seeds from a random 0.2 g subsample of spikelets (or all spikelets if seed biomass was <0.2 g). We harvested native species at the end of the study in Year 2, but not in Year 1, to avoid reducing competition in high-competition subplots. Native species biomass was measured across competition treatments because very low recolonization of low-competition subplots combined with their proximity to high-competition treatments precluded accurate measurement of recolonization.

We calculated *B. tectorum* N concentration and carbon isotope discrimination ($\Delta^{13}C$) as indicators of N limitation and water use efficiency integrated over the growing season. The $\Delta^{13}C$ value is a function of both the supply of CO_2 to the leaf—regulated by the external CO_2 concentration and leaf stomatal conductance (g_s)—and the photosynthetic demand for CO_2 (Ainsworth & Long, 2005; Cernusak *et al.*, 2013). Smaller $\Delta^{13}C$ values (lower discrimination against ^{13}C) result from lower leaf-internal CO_2 concentrations, which may be due to reduced stomatal conductance and/or increased photosynthetic carboxylation capacity (V_{cmax}). Thus, smaller $\Delta^{13}C$ values often indicate higher water use efficiency. Larger $\Delta^{13}C$ values (greater discrimination against ^{13}C) indicate higher leaf-internal CO_2 concentrations, suggesting either higher stomatal conductance or lower carboxylation capacity (which can, in turn, result from nutrient limitation of photosynthesis).

All *B. tectorum* stem and leaf tissue were combined across harvest dates for each subplot, finely ground, and analyzed for N and $\delta^{13}C$ on an elemental analyzer connected to a mass spectrometer (20-20 Stable Isotope Analyzer; Europa Scientific, Cheshire, UK). We calculated $\Delta^{13}C$ using equation 1 below, where $\delta^{13}C_{atm}$ and $\delta^{13}C_{plant}$ are the measured $^{13}C/^{12}C$ ratios of atmosphere and plant tissue, respectively. Annual atmospheric CO_2 concentrations measured at PHACE were averaged to determine $\delta^{13}C_{atm}$ isotope ratios as -9.19 ± 0.1 in ambient plots and -19.43 ± 0.09 in elevated CO_2 plots.

$$\Delta^{13}C = (\delta^{13}C_{atm} - \delta^{13}C_{plant})/(1 + \delta^{13}C_{plant}) \qquad (1)$$

We measured leaf xylem pressure potential (Ψ) as a relative index of leaf-level water stress. *Bromus tectorum* mid-day leaf xylem pressure potential was measured on 24 May and 4 June in Year 2, using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, USA). On each date, we sampled leaves from three plants of similar size and appearance from each ring; measurements could only be conducted on larger plants and were therefore limited to the low-competition treatment. Leaves were sampled during cloudless 45-min periods between 1200 and 1400 h.

Soil water content and N availability were measured in low-competition subplots only, due to space and resource constraints. Although we were not able to measure soil water and N within high-competition subplots seeded with *B. tectorum*, measurements in other similarly undisturbed subplots within the same rings provide a picture of belowground resource availability in the absence of *B. tectorum* (Dijkstra *et al.*, 2010; Carrillo *et al.*, 2012). To measure soil N availability, we buried Plant Root Simulator (PRS) resin probes (Western Ag Innovations, Saskatoon, Canada) from March to June in Year 1 and April to June in Year 2, in the low-competition subplots only. Probes were cleaned with deionized water, extracted with 0.5 N HCl solution, and analyzed colorimetrically for NH_4^+ and NO_3^- by Western Ag Innovations on a flow injection analyzer (Seal Analytical, Mequon, WI, USA). We measured volumetric soil water content (VWC) from 0 to 15 cm depth continuously with Decagon 10 HS probes and recorded hourly average values on Em50 data loggers (Decagon Devices, Pullman, WA, USA). Probes were installed perpendicular to the ground surface, at a central location within the low-competition subplots. We used factory calibrations based on the Topp equation, which are expected to measure VWC within ±3% in mineral soils.

Statistical analysis

Analyses were conducted using mixed models in JMP (version 11, Cary, NC, USA) and, for *B. tectorum* numbers only, generalized linear models in SAS (version 9.2, Cary, NC, USA). Response variables measured in both competition treatments (*B. tectorum* biomass, seed biomass, plant N content, and $\Delta^{13}C$) were analyzed with split-plot repeated measures mixed models that included CO_2, warming, competition, year and associated interactions as fixed effects and block, replication*CO_2*warming and replication*CO_2*warming*competition as random effects, to account for correlation between subplots within a plot, and between years within a subplot. *Bromus tectorum* height and numbers, which were measured multiple times per year, were analyzed with the same model structure but with day of year in place of year. Separate models were run for each year. For *B. tectorum* numbers, a Poisson distribution was used with a log link function. As competition rarely interacted with main treatment effects, most response variables were averaged across competition levels for presentation and follow-up analyses to examine significant CO_2 by warming and climate treatment by time interactions. Separate data for each competition treatment are presented in the supplementary materials. Note that in Year 1, *B. tectorum* was absent from two high-competition subplots, leading to more limited statistical power.

Response variables measured across subplots (native species biomass, harvest date) or in low-competition subplots only (soil water content and resin-available N) were analyzed with repeated measures models including CO_2, warming, year and associated interactions as fixed effects, and block and replication*CO_2*warming as random effects, to account for correlation between years within a plot. Prior to analysis, hourly soil water content records for each plot were averaged seasonally to represent the autumn and spring portions of *B. tectorum's* growing season, omitting winter records when soils were frozen and probes did not reliably record water content. Soil water content records from the following dates were averaged for each season: October 1–November 6 in 2011 (Year 1 autumn), March 15–June 15 in 2012 (Year 1 spring), October 1–November 9 in 2012 (Year 2 autumn), and March 28–June 15 in 2013 (Year 2 spring). Data were log, square-root or fifth-root (for biomass and seed biomass) transformed when necessary to meet assumptions of normality and heteroscedasticity. Significant interactions were investigated further using post hoc mixed models; Bonferroni-adjusted alpha values were used to evaluate significance.

Results

Strong interannual variation in weather led to interactions between year and treatments in all analyses; thus, we present all results by year. Average maximum, mean, and minimum temperatures during the *B. tectorum* September–June growing season were 14.0 °C, 5.8 °C, and −0.7 °C, respectively, in Year 1 (2011–2012), and 12.3 °C, 4.5 °C, and −1.7 °C in Year 2 (2012–2013), close to the long-term averages of 11.8 °C, 5.1 °C, and −1.6 °C (Western Regional Climate Center, station 481675). September–June precipitation was 177 mm in Year 1, and 194 mm in Year 2, lower than the long-term average for the same time period: 291 mm. Spring precipitation (March–May), however, was unusually low in Year 1 (17 mm) but not Year 2 (112 mm), which likely caused the tenfold difference in *B. tectorum* biomass between years (Fig. 1; Table 1).

Warming increased *B. tectorum* biomass approximately fourfold and seed production more than threefold, while elevated CO_2 had little effect (Fig. 1; Table 1). Despite large differences in total biomass, warming effects were consistent across years. *B. tectorum* biomass production in warmed plots exceeded that of nonwarmed plots even though plants matured 3.5 days earlier with warming in both years ($F_{1,16} = 46.60$, $P < 0.0001$). Reducing competition increased both plant and seed mass more than eightfold, but competition did not interact with either warming or elevated CO_2. Despite a marginally significant CO_2*competition interaction for biomass, CO_2 effects were not significant in either competition treatment.
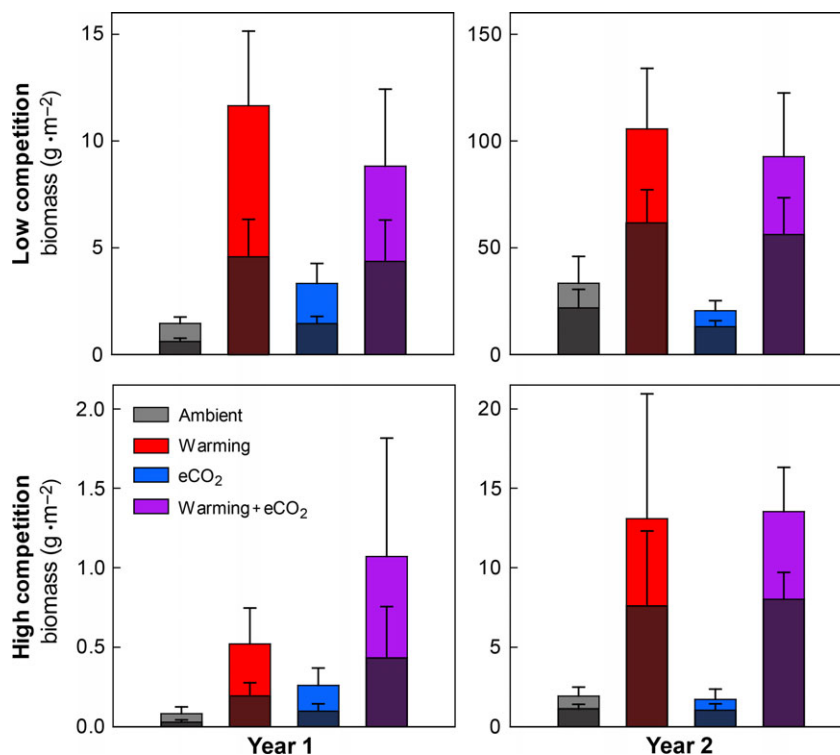

Fig. 1 Cumulative effects of elevated CO_2 (eCO_2) and warming on *Bromus tectorum* aboveground biomass (solid bars) and seed mass (shaded bars). Note the tenfold scale differences across both competition level and year. See Table 1 for statistical results. Error bars are ± 1 SE.

Table 1 Model results for *Bromus tectorum* and soil N responses measured at yearly time steps

Variable	Biomass (g m^{-2})		Seed mass (g m^{-2})		Leaf Δ^{13}C		Soil N (μg cm^{-2})		Plant N (%)	
	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P
CO$_2$	$0.13_{1,15}$	0.7245	$0.27_{1,15}$	0.6129	$3.16_{1,63}$	0.0803	**$6.56_{1,32}$**	**0.0154**	**$56.4_{1,63}$**	**<.0001**
Warming	**$20.7_{1,15}$**	**0.0004**	**$15.4_{1,15}$**	**0.0014**	$0.45_{1,63}$	0.5060	$0.21_{1,32}$	0.6480	$0.42_{1,63}$	0.5170
CO$_2$*Warming	$0.32_{1,15}$	0.5819	$0.07_{1,15}$	0.7919	$1.19_{1,63}$	0.2785	$0.21_{1,32}$	0.6521	$3.37_{1,63}$	0.0710
Competition	**$262_{1,16}$**	**<.0001**	**$264_{1,16}$**	**<.0001**	$0.83_{1,63}$	0.3646			**$17.1_{1,63}$**	**0.0001**
CO$_2$*Competition	$4.13_{1,16}$	0.0592	$3.43_{1,16}$	0.0825	$0.15_{1,63}$	0.7038			$1.63_{1,63}$	0.2068
Warming*Competition	$0.28_{1,16}$	0.6066	$0.22_{1,16}$	0.6425	$0.06_{1,63}$	0.8023			$0.51_{1,63}$	0.4783
CO$_2$*Warming*Competition	$0.55_{1,16}$	0.4709	$0.49_{1,33}$	0.4930	$0.17_{1,63}$	0.6849			$0.08_{1,63}$	0.7815
Year	**$176_{1,33}$**	**<.0001**	**$238_{1,33}$**	**<.0001**	**$6.62_{1,63}$**	**0.0125**	**$77.1_{1,32}$**	**<.0001**	**$59.7_{1,63}$**	**<.0001**
Year*CO$_2$	$1.51_{1,33}$	0.2273	$1.99_{1,33}$	0.1669	$3.41_{1,63}$	0.0697	**$4.27_{1,32}$**	**0.0469**	$1.11_{1,63}$	0.2958
Year*Warming	$3.62_{1,33}$	0.0660	**$5.28_{1,33}$**	**0.0280**	$1.65_{1,63}$	0.2043	$0.14_{1,32}$	0.7144	$1.03_{1,63}$	0.3150
Year*CO$_2$*Warming	$3.50_{1,33}$	0.0701	$2.39_{1,33}$	0.1319	**$5.16_{1,63}$**	**0.0265**	$0.02_{1,32}$	0.8919	$0.50_{1,63}$	0.4829
Year*Competition	$2.85_{1,33}$	0.1006	**$4.40_{1,33}$**	**0.0437**	$0.01_{1,63}$	0.9226			**$10.7_{1,63}$**	**0.0017**
Year*CO$_2$*Competition	$0.00_{1,33}$	0.9575	$0.02_{1,33}$	0.8788	$0.21_{1,63}$	0.6506			$0.05_{1,63}$	0.8281
Year*Warming*Competition	$0.00_{1,33}$	0.9832	$0.04_{1,33}$	0.8490	$0.21_{1,63}$	0.6499			$0.07_{1,63}$	0.7938

Bold text indicates significant effects ($P < 0.05$).

Plant and seed mass were 10 and 14.5 times greater, respectively, in the wetter year compared with the drier year. A warming*year interaction for seed mass (investigated for this and subsequent interactions using post hoc mixed models by year, treatment, or date within year), indicated a stronger warming effect in Year 2 ($F_{1,16} = 18.77$, $P = 0.0005$) than Year 1 ($F_{1,16} = 5.71$, $P = 0.03$).

In contrast to the response of *B. tectorum*, there was no significant change in native species biomass with warming (86.5 g m^{-2} under ambient temperature vs. 81.7 g m^{-2} under warming; $F_{1,15} = 0.15$; $P = 0.7$) or elevated CO$_2$ (78.5 g m^{-2} with ambient CO$_2$ vs. 89.7 g m^{-2} with elevated CO$_2$; $F_{1,15} = 0.81$; $P = 0.4$). As a result, warming doubled the proportion of total plot biomass contributed by *B. tectorum* (52% vs. 24%, $F_{1,16} = 11.26$, $P < 0.004$, measured in Year 2 only), while elevated CO$_2$ had no significant effect.

Increases in plant number and size both contributed to the success of *B. tectorum* with warming (Fig. 2; Table 2; Figs S2 and S3). *Bromus tectorum* plants germinated in October of each year, following autumn precipitation pulses >10 mm (seedlings first observed on October 20, 2011 and October 1, 2012). By late November in both years, there were significantly more plants in warmed than ambient temperature plots ($P < 0.0004$ on both dates). Warming*date interactions indicated that the strong positive effect of warming on plant number persisted from late November to mid-April in Year 1 ($P < 0.0002$ on all dates), at which point it diminished and became nonsignificant, and persisted throughout the spring in Year 2 ($P < 0.0009$ on all

dates). A significant CO$_2$*warming interaction in Year 2 indicated that CO$_2$ also increased *B. tectorum* numbers, but only in combination with warming ($F_{1,9} = 7.75$, $P = 0.02$).

Warming increased average per-plant height in both years, and warming*date interactions indicated that the height increase was significant between March 15 and May 15 in Year 1 ($P < 0.002$ on all dates) and on all dates except October 9 and November 19 in Year 2 ($P < 0.009$ on all other dates). Although we also observed a significant CO$_2$*date interaction in Year 1, the effect of CO$_2$ was not significant on any individual date.

Warming increased leaf-level water stress in *B. tectorum*, as indicated by lower leaf xylem pressure potentials (Fig. 3; Table 2). Leaf xylem pressure potential was 0.27 and 0.55 MPa more negative with warming in May and June of Year 2, respectively (May 2013, $F_{1,15} = 9.13$, $P = 0.009$; June 2013, $F_{1,15} = 7.0$, $P = 0.02$). A trend toward lower leaf water stress under elevated CO$_2$ was not significant. Neither warming nor CO$_2$ influenced leaf Δ^{13}C in Year 1, whereas elevated CO$_2$ led to more leaf-level discrimination against ^{13}C in Year 2 (CO$_2$ effect: $F_{1,16} = 6.56$, $P = 0.02$; Fig. 4; Table 1; Fig. S4). Larger Δ^{13}C values (greater discrimination against ^{13}C) result from an increase in the leaf-internal CO$_2$ concentration, suggesting either an increase in leaf stomatal conductance (g_s) or a reduction in carboxylation capacity (V_{cmax}).

Warming reduced average soil volumetric water content in the rooting zone of *B. tectorum* (Fig. 2; Table 2). Warming*date interactions in each year indicated sig-
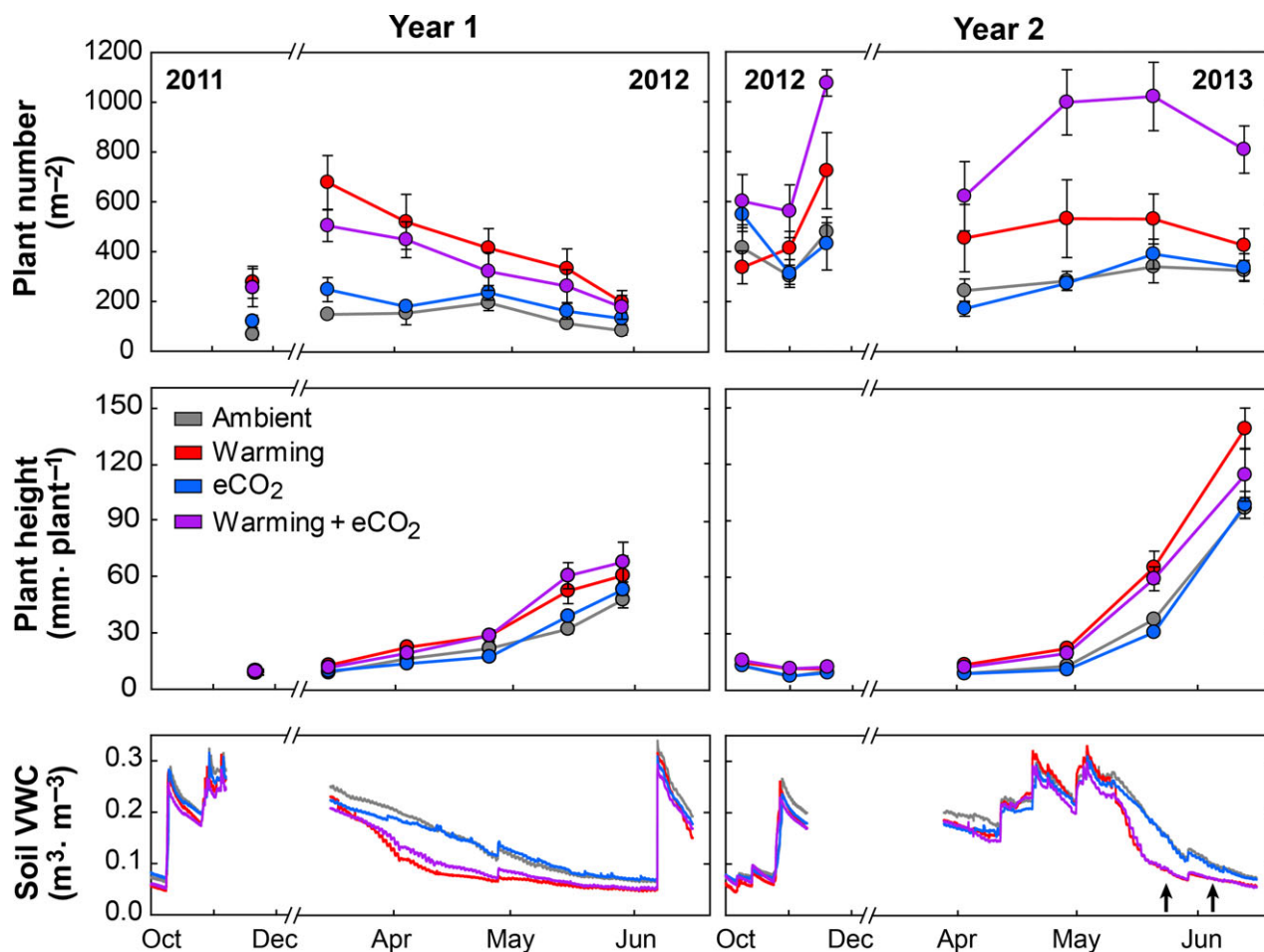
Fig. 2 Effects of elevated CO$_2$ (eCO$_2$) and warming on plant number and per-plant height of *Bromus tectorum* (averaged across competition treatments), and average soil volumetric water content (VWC) from 0 to 15 cm depth (measured in low-competition subplots). Arrows indicate dates of leaf xylem pressure potential measurements in Year 2. See Table 1 for statistical results, and Figures S2 and S3 for plant number and height results within each competition treatment. Error bars are ± 1 SE.

nificantly lower soil water content with warming in spring (Year 1, $F_{1,16} = 24.31$, $P = 0.0002$; Year 2, $F_{1,15} = 5.91$, $P = 0.03$), but not autumn. Warming reduced average spring soil water content by 26% in Year 1, and 18% in Year 2. Elevated CO$_2$ had no detectable effect on soil water content in either season of either year.

In contrast to most other response variables, resin-available soil N and *B. tectorum* tissue N concentration were strongly influenced by elevated CO$_2$ (Fig. 5; Table 1). Tissue N concentration was lower in plants exposed to elevated CO$_2$ in both years. A year*CO$_2$ interaction indicated that elevated CO$_2$ reduced soil N, by 47%, only in the wetter year (Year 2; $F_{1,16} = 12.19$, $P = 0.003$). Warming did not influence soil N availability or plant N concentration in either year. Competition increased plant N concentration, but did not interact with elevated CO$_2$ or warming (Fig. S5).

Discussion

In contrast to our predictions, we found that experimental warming more than tripled *B. tectorum* biomass and seed production while elevated CO$_2$ had little effect. Warming effects were surprisingly consistent, occurring across CO$_2$ and competition treatments, and across years with very different precipitation patterns (Fig. 1). Furthermore, warming increased *B. tectorum* growth and reproduction despite the fact that it decreased water availability and increased leaf-level water stress during the late spring, when *B. tectorum* was growing most rapidly (Figs 2 and 3). These results suggest that the combination of global change and *B. tectorum* invasion will have profound impacts in some western North American ecosystems, and lower than expected impacts in others. In the relatively invasion-resistant northern mixed-grass prairie, which accounts

Table 2 Model results for *Bromus tectorum* and soil water responses measured at multiple time steps within years

Variable	Year 1 Plant number (m^{-2})		Year 2 Plant number (m^{-2})		Year 1 Plant height (mm)		Year 2 Plant height (mm)		Year 1 Soil water (m^3 m^{-3})		Year 2 Soil water (m^3 m^{-3})		Year 2 Leaf Ψ (MPa)	
	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P	F_{df}	P
CO_2	$0.38_{1,18}$	0.5465	$4.47_{1,18}$	**0.0488**	$0.13_{1,15}$	0.7186	$0.52_{1,15}$	0.4814	$0.14_{1,15}$	0.7114	$0.03_{1,15}$	0.8703	$3.40_{1,15}$	0.0840
Warming	$22.9_{1,18}$	**0.0002**	$27.1_{1,18}$	**<.0001**	$18.4_{1,15}$	**0.0007**	$35.2_{1,15}$	**<.0001**	$13.4_{1,15}$	**0.0023**	$3.82_{1,15}$	0.0696	$8.75_{1,15}$	**0.0093**
CO_2*Warm.	$3.53_{1,17}$	0.0773	$5.34_{1,18}$	**0.0332**	$0.00_{1,15}$	0.9454	$0.01_{1,15}$	0.9116	$0.10_{1,15}$	0.7537	$0.93_{1,15}$	0.3498	$1.54_{1,15}$	0.2324
Competition	$204_{1,181}$	**<.0001**	$99.6_{1,215}$	**<.0001**	$3.45_{1,16}$	0.0817	$83.1_{1,16}$	**<.0001**						
CO_2*Comp.	$0.03_{1,181}$	0.8551	$0.00_{1,215}$	0.9840	$0.37_{1,16}$	0.5502	$0.30_{1,16}$	0.5940						
Warm.*Comp.	$0.17_{1,181}$	0.6817	$2.88_{1,215}$	0.0909	$1.57_{1,16}$	0.2284	$0.44_{1,16}$	0.5155						
CO_2*Warm.*Comp.	$3.38_{1,181}$	0.0675	$2.19_{1,215}$	0.1408	$0.04_{1,16}$	0.8394	$0.04_{1,16}$	0.8447						
Date	$27.0_{5,181}$	**<.0001**	$20.0_{6,215}$	**<.0001**	$473_{5,165}$	**<.0001**	$856_{6,198}$	**<.0001**	$631_{1,16}$	**<.0001**	$95.8_{1,16}$	**<.0001**	$105_{1,15}$	**<.0001**
Date*CO_2	$0.71_{5,181}$	0.6170	$1.74_{6,215}$	0.1121	$4.00_{5,165}$	**0.0019**	$1.72_{6,198}$	0.1169	$1.47_{1,16}$	0.2436	$0.02_{1,16}$	0.8876	$0.22_{1,15}$	0.6486
Date*Warm.	$4.00_{5,181}$	**0.0018**	$9.19_{6,215}$	**<.0001**	$5.56_{5,165}$	**<.0001**	$6.24_{6,198}$	**<.0001**	$14.1_{1,16}$	**0.0017**	$7.66_{1,16}$	**0.0138**	$1.35_{1,15}$	0.2619
Date*CO_2*Warm.	$0.53_{5,181}$	0.7522	$0.44_{6,215}$	0.8524	$0.71_{5,165}$	0.6144	$1.83_{6,198}$	0.0953	$2.42_{1,16}$	0.1393	$0.67_{1,16}$	0.4257	$0.50_{1,15}$	0.4883
Date*Comp.	$4.93_{5,181}$	**0.0003**	$4.66_{6,215}$	**0.0002**	$11.2_{5,165}$	**<.0001**	$4.31_{6,198}$	**0.0004**						
Date*CO_2*Comp.	$0.42_{5,181}$	0.8320	$0.30_{6,215}$	0.9366	$0.19_{5,165}$	0.9646	$1.20_{6,198}$	0.3099						
Date*Warm.*Comp.	$1.07_{5,181}$	0.3775	$1.71_{6,215}$	0.1197	$1.14_{5,165}$	0.3401	$2.92_{6,198}$	**0.0095**						

Bold text indicates significant effects ($P < 0.05$).
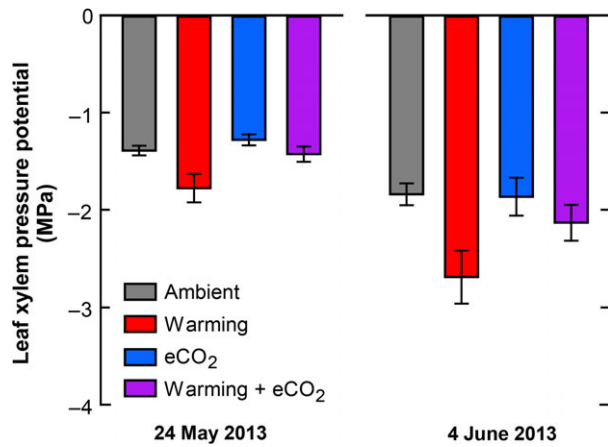Variable abbreviations are listed as follows: Warm. (Warming) and Comp. (Competition).

Fig. 3 Effects of elevated CO_2 (eCO_2) and warming on *Bromus tectorum* leaf xylem pressure potential, measured in May and June of 2013 (Year 2). More negative xylem pressure reflects greater relative water stress. Error bars are ± 1 SE. See Table 2 for statistical results.
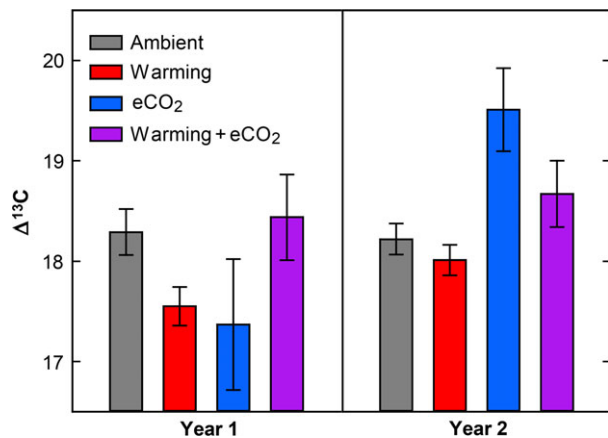

Fig. 4 Effects of elevated CO_2 (eCO_2) and warming on *Bromus tectorum* leaf $\Delta^{13}C$ in Year 1 and Year 2. Larger $\Delta^{13}C$ values indicate more discrimination against ^{13}C (reflecting an increase in the leaf-internal CO_2 concentration). Error bars are ± 1 SE. See Table 1 for statistical results and Figure S4 for $\Delta^{13}C$ results within each competition treatment.

Fig. 5 Effects of elevated CO_2 (eCO_2) and warming on resin-available inorganic soil N (measured in low-competition subplots) and plant tissue N (averaged across competition treatments). Note that resin probe incubation period was longer in Year 1 than Year 2, to match a longer *Bromus tectorum* growing season (see Fig. 2), and caution should be used in comparing absolute values across years. Error bars are ± 1 SE. See Table 1 for statistical results and Figure S5 for plant N results within each competition treatment.

for more than one-third of remaining native grassland in the Great Plains (Samson *et al.*, 2004), increases in *B. tectorum* appear likely. Where its abundance increases, fire frequency may also increase, while biological diversity and forage production may decline (Haferkamp *et al.*, 2001; Rice, 2005; Abatzoglou & Kolden, 2011; Balch *et al.*, 2013). At the same time, the absence of a CO_2 effect in our study suggests that elevated CO_2 may not exacerbate *B. tectorum* invasion in all ecosystems. This finding contrasts with results from both controlled environment studies with *B. tectorum* (Smith *et al.*, 198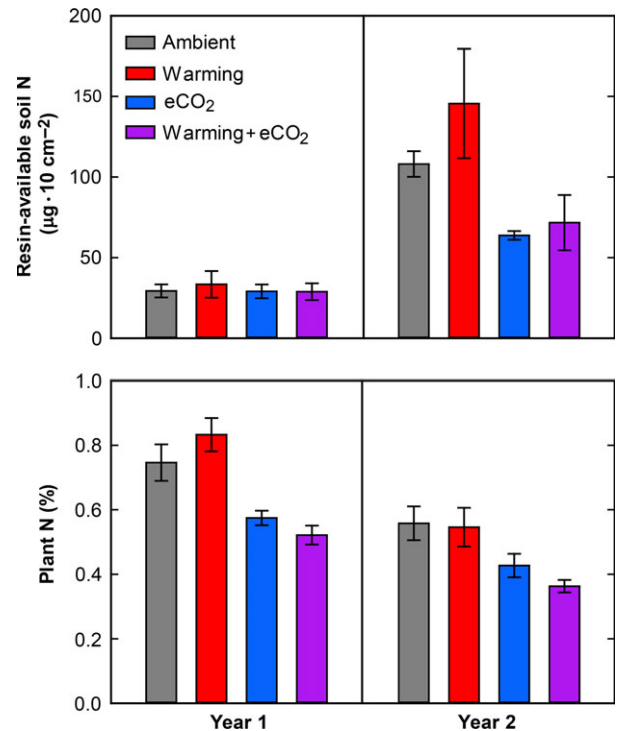7; Ziska *et al.*, 2005) and field studies with other invasive species at this site (Blumenthal *et al.*, 2013), demonstrating both the context and species dependence of invasive plant responses to elevated CO_2.

The most likely mechanism underlying *B. tectorum*'s warming response appears to be decreased temperature limitation of recruitment and growth. Because *B. tectorum* germinates in autumn or early spring (depending on autumn precipitation) and matures in late spring, low temperatures can limit its recruitment, survival, and growth (Mack & Pyke, 1983; Young, 2000; Bradford & Lauenroth, 2006; Chambers *et al.*, 2007; Bykova & Sage, 2012). Correspondingly, we found that warming increased *B. tectorum* numbers and growth during the cooler parts of its growing season (Fig. 2; Figs S2 and S3). Higher plant numbers, which reflect both germination and survival, were apparent soon after germination in the fall and were maintained through the course of each growing season. Larger plant size became apparent early in each spring and increased as growth continued, despite the fact that warming concurrently decreased soil water availability.

These patterns suggest that warming expanded the phenological niche occupied by *B. tectorum*, enhancing its ability to grow when native plants are inactive and competition for water and nutrients is least intense (Wolkovich & Cleland, 2014). Although warming of temperate grasslands has been predicted to open early-season phenological niches and lead to invasion by early-flowering species, previous work in the US Great Plains has not found this to be the case (Wolkovich *et al.*, 2013; Wolkovich & Cleland, 2014). Our results match both the predictions for temperate grasslands and the hypothesized mechanism: decreased temperature limitation at a time of limited competition (Wolkovich & Cleland, 2014).

Two studies conducted in the US Intermountain Region found warming to favor *B. tectorum* in wet years, but to have no effect or to inhibit *B. tectorum* in dry years (Zelikova *et al.*, 2013; Compagnoni & Adler, 2014b). Similarly, we found that warming increased seed production more in the wetter year, particularly in absolute terms, in accord with the idea that warming may have more positive effects on invasion when moisture is less limiting (Bradley *et al.*, 2010, 2015; Dukes *et al.*, 2011). Unlike in the Intermountain Region studies, however, warming strongly promoted *B. tectorum* in both wetter and drier years at our site. We speculate that increased recruitment and growth during the cool, wet part of the growing season outweighed effects of more limited water later in the season, or increased *B. tectorum's* root development and therefore access to water (Dukes *et al.*, 2011), leading to consistently positive warming effects. Together, experimental results to date support model predictions that *B. tectorum* could become more invasive at higher latitudes and elevations in response to projected temperature increases (Bradley, 2009; Bradley *et al.*, 2015; West *et al.*, 2015). Furthermore, stronger warming effects in wet years suggest that warming may interact with changes in precipitation to influence *B. tectorum*. In the northern mixed-grass prairie, predicted increases in winter and spring precipitation (Kunkel *et al.*, 2013; Shafer *et al.*, 2014) may not only promote *B. tectorum* invasion directly (Bradley, 2009; Prevey & Seastedt, 2014) but also strengthen warming effects on *B. tectorum*.

Surprisingly, elevated CO_2 had no net effect on *B. tectorum* growth or seed production. Previous field studies, including one within the PHACE experiment, have shown that elevated CO_2 often (but not always) promotes plant invasion (Hattenschwiler & Korner, 2003; Belote *et al.*, 2004; Williams *et al.*, 2007; Dukes *et al.*, 2011; Blumenthal *et al.*, 2013). *Bromus tectorum* responded strongly to elevated CO_2 in controlled environments with ample water and nutrients (Smith *et al.*,

1987; Ziska *et al.*, 2005). Furthermore, in the Mojave Desert, free-air CO_2 enrichment increased growth of *Bromus rubens*, a close relative of *B. tectorum*, in a wet year, leading to long-term increases in its seed bank (Smith *et al.*, 2000, 2014). These results have led to the expectation that elevated CO_2 will also favor *B. tectorum* in the field (Bradley *et al.*, 2015). In this study, however, elevated CO_2 did not increase either the biomass or seed production of *B. tectorum*. The only hints of a positive response to CO_2 were a nonsignificant trend toward a positive CO_2 effect on biomass in high-competition subplots in Year 1 (Fig. 1), and higher abundance with the combination of warming and elevated CO_2 in Year 2 (Fig. 2; Fig S2), which did not lead to greater biomass or seed mass.

The lack of a *B. tectorum* response to CO_2 may be due to indirect effects of CO_2 on N. Invasive plants, including *B. tectorum*, can be quite sensitive to N availability (Adair *et al.*, 2008; Perry *et al.*, 2010; James *et al.*, 2011; Concilio *et al.*, 2013; Chambers *et al.*, 2014; Seabloom *et al.*, 2015). For example, in the Mojave Desert, smaller CO_2 responses of *B. rubens* in open spaces between perennial plants were likely due to lower N availability in those microsites (Smith *et al.*, 2000, 2014). In a previous study at our site, reductions in N availability limited recruitment and growth of several introduced forbs (Blumenthal, 2009). While elevated CO_2 can often promote invasion, it also commonly reduces N availability (Luo *et al.*, 2004), which could indirectly limit CO_2 effects on invasion (Sorte *et al.*, 2013). Here, CO_2 reduced resin-available soil N by 47% in Year 2, and *B. tectorum* N concentration by 31% in Year 1 and 28% in Year 2 (Fig. 5), suggesting that CO_2 increased N limitation, as also observed in adjacent undisturbed subplots within PHACE (Dijkstra *et al.*, 2010). The decrease in *B. tectorum* N concentration was not due to dilution, as CO_2 did not increase *B. tectorum* biomass. Furthermore, given that elevated CO_2 did not influence soil water, the increase in ^{13}C discrimination in Year 2 most likely reflected increased N limitation of photosynthesis (Fig. 4) (Ainsworth & Long, 2005; Cernusak *et al.*, 2013). Thus, our study provides evidence, albeit circumstantial, that CO_2-induced reductions in N can limit CO_2 effects on invasion. To the degree that CO_2 effects on *B. tectorum* and other invasive species are constrained by N, this constraint could be intensified by progressive N limitation (Luo *et al.*; 2004), or alleviated by either N deposition (Kochy & Wilson, 2001; Fenn *et al.*, 2003), or positive feedbacks between invasion and N availability (Ehrenfeld, 2003; Stark & Norton, 2015).

We expected that elevated CO_2 might favor *B. tectorum* in part by improving plant water status (Ains-

worth & Long, 2005; Morgan *et al.*, 2011), as observed for the invasive forb *Linaria dalmatica* at this site (Blumenthal *et al.*, 2013). There was little evidence, however, that improved water relations influenced *B. tectorum* in this study. Although elevated CO_2 resulted in a marginally significant increase in *B. tectorum* leaf xylem pressure potential in May of Year 2, it also led to an increase in $\Delta^{13}C$, reflecting either *lower* water use efficiency or, more likely, downregulation of carboxylation capacity due to N limitation (Figs 4 and 5) (Ainsworth & Long, 2005; Cernusak *et al.*, 2013). Furthermore, elevated CO_2 did not increase soil water, as it has in other plots within the PHACE experiment (Morgan *et al.*, 2011). The absence of a CO_2 effect on soil water may be due to a paucity of active, transpiring native plants both during the *B. tectorum* growing season and in the low-competition subplots. These results suggest that species which complete their life cycle early, such as *B. tectorum*, may be less likely than other species to benefit from CO_2-induced increases in soil water.

To date, few experiments have tested how competition influences invasive species responses to elevated CO_2 or warming (Dukes *et al.*, 2011; Manea & Leishman, 2011; Compagnoni & Adler, 2014a). We predicted that reduced competition might, by increasing availability of limiting belowground resources (Carrillo *et al.*, 2012), strengthen *B. tectorum* responses to global change treatments. However, while competition strongly inhibited *B. tectorum*, it did not interact with either warming or elevated CO_2. Rather, effects of competition and global change treatments were additive. Reduced competition led to an eightfold increase in *B. tectorum* biomass, suggesting that resident mixed-grass prairie species provide strong biotic resistance against *B. tectorum* invasion. Warming increased *B. tectorum* biomass an additional fourfold. Similarly, competition rarely interacted with warming effects on *B. tectorum* in northern Utah (Compagnoni & Adler, 2014a). Notably, the fourfold effect of warming observed with both low and high competition in the present study led to a much greater absolute increase in seed production in low-competition plots (Fig. 1). Thus, while warming may have similar effects on *B. tectorum*'s ability to invade more and less competitive environments, its effects on seed production, and therefore, larger-scale population dynamics may be stronger in less competitive environments. The absence of a CO_2*competition interaction may be explained by reduced N availability and tissue N with elevated CO_2 even in low-competition subplots (Table 1; Fig. S5). While it remains difficult to predict how competition will interact with warming and elevated CO_2, the frequency with which it influences invasion suggests that competition needs to be taken into account when predicting future invasive species distributions and abundance (Ibanez *et al.*, 2009; Bradley *et al.*, 2010).

Adapting management to counteract effects of global change on *B. tectorum* will require monitoring changes in *B. tectorum* distribution, and management to increase ecosystem resistance to invasion and control *B. tectorum* populations in areas of expansion (Chambers *et al.*, 2014). Our results, combined with previous experiments (Concilio *et al.*, 2013; Compagnoni & Adler, 2014a; Prevey & Seastedt, 2014), suggest that climate envelope models are likely to be useful for guiding monitoring efforts. Not only are the warming and precipitation responses of *B. tectorum* in accord with predictions (Bradley, 2009; Bradley *et al.*, 2015; West *et al.*, 2015), but the lack of a CO_2 response suggests that the absence of CO_2 in such models may not be a concern for all ecosystems. Strategies for increasing ecosystem resistance in the face of warmer temperatures could include promoting native species with very early or late phenology. More broadly, the importance of competition across our global change treatments supports the idea that maintaining healthy stands of desired vegetation will continue to be essential for restricting cheatgrass invasion (Chambers *et al.*, 2007, 2014).

References

Abatzoglou JT, Kolden CA (2011) Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management*, **64**, 471–478.

Adair EC, Burke IC, Lauenroth WK (2008) Contrasting effects of resource availability and plant mortality on plant community invasion by *Bromus tectorum* L. *Plant and Soil*, **304**, 103–115.

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytologist*, **165**, 351–371.

Balch JK, Bradley BA, D'Antonio CM, Gomez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). *Global Change Biology*, **19**, 173–183.

Belote RT, Weltzin JF, Norby RJ (2004) Response of an understory plant community to elevated [CO₂] depends on differential responses of dominant invasive species and is mediated by soil water availability. *New Phytologist*, **161**, 827–835.

Blumenthal DM (2009) Carbon addition interacts with water availability to reduce invasive forb establishment in a semi-arid grassland. *Biological Invasions*, **11**, 1281–1290.

Blumenthal DM, Resco V, Morgan JA *et al.* (2013) Invasive forb benefits from water savings by native plants and carbon fertilization under elevated CO₂ and warming. *New Phytologist*, **200**, 1156–1165.

Bradford JB, Lauenroth WK (2006) Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance, and seed availability. *Journal of Vegetation Science*, **17**, 693–704.

Bradley BA (2009) Regional analysis of the impacts of climate change on cheatgrass invasion shows potential risk and opportunity. *Global Change Biology*, **15**, 196–208.

Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications*, **16**, 1132–1147.

Bradley BA, Houghton RA, Mustard JF, Hamburg SP (2006) Invasive grass reduces aboveground carbon stocks in shrublands of the western US. *Global Change Biology*, **12**, 1815–1822.

Bradley BA, Blumenthal DM, Wilcove DS, Ziska LH (2010) Predicting plant invasions in an era of global change. *Trends in Ecology & Evolution*, **25**, 310–318.

Bradley BA, Curtis CA, Chambers JC (2015) *Bromus* response to climate and projected changes with climate change. In: *Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US: Causes, Consequences, and Management Implications*. (eds Germino MJ, Chambers JC, Brown CS) pp. 257–274. Springer International Publishing, Cham.

Bykova O, Sage RF (2012) Winter cold tolerance and the geographic range separation of *Bromus tectorum* and *Bromus rubens*, two severe invasive species in North America. *Global Change Biology*, **12**, 3654–3663.

Carrillo Y, Dijkstra FA, Pendall E, Morgan JA, Blumenthal DM (2012) Controls over soil nitrogen pools in a semiarid grassland under elevated CO₂ and warming. *Ecosystems*, **15**, 761–774.

Cernusak LA, Ubierna N, Winter K, Holtum JAM, Marshall JD, Farquhar GD (2013) Environmental and physiological determinants of carbon isotope discrimination in terrestrial plants. *New Phytologist*, **200**, 950–965.

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A (2007) What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecological Monographs*, **77**, 117–145.

Chambers JC, Bradley BA, Brown CS *et al.* (2014) Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems*, **17**, 360–375.

Compagnoni A, Adler PB (2014a) Warming, competition, and *Bromus tectorum* population growth across an elevation gradient. *Ecosphere*, **5**, 1–18.

Compagnoni A, Adler PB (2014b) Warming, soil moisture, and loss of snow increase *Bromus tectorum*'s population growth rate. *Elementa*, **2**, 1–10.

Concilio AL, Loik ME, Belnap J (2013) Global change effects on *Bromus tectorum* L. (Poaceae) at its high-elevation range margin. *Global Change Biology*, **19**, 161–172.

D'Antonio CM (2000) Fire, plant invasions, and global changes. In: *Invasive Species in a Changing World* (eds Mooney HA, Hobbs RJ), pp. 65–93. Island Press, Washington, DC.

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.

Derner JD, Hart RH (2007) Grazing-induced modifications to peak standing crop in northern mixed-grass prairie. *Rangeland Ecology & Management*, **60**, 270–276.

Dieleman WIJ, Vicca S, Dijkstra FA *et al.* (2012) Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO₂ and temperature. *Global Change Biology*, **18**, 2681–2693.

Dijkstra FA, Blumenthal D, Morgan JA, Pendall E, Carrillo Y, Follett RF (2010) Contrasting effects of elevated CO₂ and warming on nitrogen cycling in a semiarid grassland. *New Phytologist*, **187**, 426–437.

DiTomaso JM (2000) Invasive weeds in rangelands: species, impacts, and management. *Weed Science*, **48**, 255–265.

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *Trends in Ecology & Evolution*, **14**, 135–139.

Dukes JS, Chiariello NR, Loarie SR, Field CB (2011) Strong response of an invasive plant species (*Centaurea solstitialis* L.) to global environmental changes. *Ecological Applications*, **21**, 1887–1894.

Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503–523.

Eskelinen A, Harrison S (2014) Exotic plant invasions under enhanced rainfall are constrained by soil nutrients and competition. *Ecology*, **95**, 682–692.

Fenn ME, Baron JS, Allen EB *et al.* (2003) Ecological effects of nitrogen deposition in the western United States. *BioScience*, **53**, 404–420.

Haferkamp MR, Grings EE, Heitschmidt RK, MacNeil MD, Karl MG (2001) Suppression of annual bromes impacts rangeland: animal responses. *Journal of Range Management*, **54**, 663–668.

Hattenschwiler S, Korner C (2003) Does elevated CO₂ facilitate naturalization of the non-indigenous *Prunus laurocerasus* in Swiss temperate forests? *Functional Ecology*, **17**, 778–785.

Hempy-Mayer K, Pyke DA (2008) Defoliation effects on *Bromus tectorum* seed production: implications for grazing. *Rangeland Ecology & Management*, **61**, 116–123.

Humphrey LD, Schupp EW (2001) Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist*, **61**, 85–92.

Ibanez I, Silander JA, Wilson AM, Lafleur N, Tanaka N, Tsuyama I (2009) Multivariate forecasts of potential distributions of invasive plant species. *Ecological Applications*, **19**, 359–375.

James JJ, Drenovsky RE, Monaco TA, Rinella MJ (2011) Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? *Ecological Applications*, **21**, 490–502.

Knapp PA (1996) Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert – history, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions*, **6**, 37–52.

Knick ST, Dobkin DS, Rotenberry JT, Schroeder MA, Vander Haegen WM, Van Riper C (2003) Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor*, **105**, 611–634.

Kochy M, Wilson SD (2001) Nitrogen deposition and forest expansion in the northern Great Plains. *Journal of Ecology*, **89**, 807–817.

Kroel-Dulay G, Ransijn J, Schmidt IK *et al.* (2015) Increased sensitivity to climate change in disturbed ecosystems. *Nature Communications*, **6**, 1–7.

Kunkel KE, Stevens LE, Stevens SE *et al.* (2013) *Regional Climate Trends and Scenarios for the U.S. National Climate Assessment. Part 4. Climate of the U.S. Great Plains.* NOAA Technical Report NESDIS 142-4, Washington, DC.

LeCain D, Smith D, Morgan J, Kimball BA, Pendall E, Miglietta F (2015) Microclimatic performance of a free-air warming and CO₂ enrichment experiment in windy Wyoming, USA. *PLoS ONE*, **10**, 1–14.

Littell JS, McKenzie D, Peterson DL, Westerling AL (2009) Climate and wildfire area burned in western U.S. ecoprovinces, 1916-2003. *Ecological Applications*, **19**, 1003–1021.

Luo Y, Su B, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, **54**, 731–739.

Mack RN (1981) Invasion of *Bromus tectorum* L. into western North America – an ecological chronicle. *Agro-Ecosystems*, **7**, 145–165.

Mack RN, Pyke DA (1983) The demography of *Bromus tectorum* – variation in time and space. *Journal of Ecology*, **71**, 69–93.

Mack RN, Thompson JN (1982) Evolution in steppe with few large, hoofed mammals. *American Naturalist*, **119**, 757–773.

Manea A, Leishman MR (2011) Competitive interactions between native and invasive exotic plant species are altered under elevated carbon dioxide. *Oecologia*, **165**, 735–744.

Mazzola MB, Chambers JC, Blank RR *et al.* (2011) Effects of resource availability and propagule supply on native species recruitment in sagebrush ecosystems invaded by *Bromus tectorum*. *Biological Invasions*, **13**, 513–526.

Mealor BA, Cox S, Booth DT (2012) Postfire downy brome (*Bromus tectorum*) invasion at high elevations in Wyoming. *Invasive Plant Science and Management*, **5**, 427–435.

Melgoza G, Nowak RS, Tausch RJ (1990) Soil-water exploitation after fire – competition between *Bromus tectorum* (cheatgrass) and 2 native species. *Oecologia*, **83**, 7–13.

Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, **132**, 87–106.

Morgan JA, Pataki DE, Korner C *et al.* (2004) Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia*, **140**, 11–25.

Morgan JA, LeCain DR, Pendall E *et al.* (2011) C₄ grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature*, **476**, 202–206.

Nagel JM, Huxman TE, Griffin KL, Smith SD (2004) CO₂ enrichment reduces the energetic cost of biomass construction in an invasive desert grass. *Ecology*, **85**, 100–106.

Norby RJ, Luo YQ (2004) Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist*, **162**, 281–293.

Nowak RS, Ellsworth DS, Smith SD (2004) Functional responses of plants to elevated atmospheric CO$_2$ – do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist*, **162**, 253–280.

Ogle SM, Reiners WA (2002) A phytosociological study of exotic annual brome grasses in a mixed grass prairie/ponderosa pine forest ecotone. *American Midland Naturalist*, **147**, 25–31.

Ogle SM, Reiners WA, Gerow KG (2003) Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairies. *American Midland Naturalist*, **149**, 46–58.

Perry LG, Blumenthal DM, Monaco TA, Paschke MW, Redente EF (2010) Immobilizing nitrogen to control plant invasion. *Oecologia*, **163**, 13–24.

Poorter H, Navas M-L (2003) Plant growth and competition at elevated CO$_2$: on winners, losers and functional groups. *New Phytologist*, **157**, 175–198.

Prevey JS, Seastedt TR (2014) Seasonality of precipitation interacts with exotic species to alter composition and phenology of a semi-arid grassland. *Journal of Ecology*, **102**, 1549–1561.

Reich PB, Hungate BA, Luo YQ (2006) Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology Evolution and Systematics*, **37**, 611–636.

Rice PM (2005) Downy brome, *Bromus tectorum* L. In: *Invasive Plants of Range and Wildlands and Their Environmental, Economic, and Societal Impacts* (eds Duncan CA, Clark C), pp. 147–170. Weed Science Society of America, Lawrence, KS.

Samson FB, Knopf FL, Ostlie WR (2004) Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin*, **32**, 6–15.

Sandel B, Dangremond EM (2012) Climate change and the invasion of California by grasses. *Global Change Biology*, **18**, 277–289.

Seabloom EW, Borer ET, Buckley YM *et al.* (2015) Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nature Communications*, **6**, 1–8.

Shafer M, Ojima D, Antle JM *et al.* (2014) Chapter 19: Great plains. In: *Climate Change Impacts in the United States: The Third National Climate Assessment.* (eds Melillo JM, Richmond TC, Yohe GW), U.S. Global Change Research Program, Washington, DC, 441–461.

Shaver GR, Canadell J, Chapin FS *et al.* (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience*, **50**, 871–882.

Smith SD, Strain BR, Sharkey TD (1987) Effects of CO$_2$ enrichment on four Great Basin grasses. *Functional Ecology*, **1**, 139–143.

Smith SD, Huxman TE, Zitzer SF *et al.* (2000) Elevated CO$_2$ increases productivity and invasive species success in an arid ecosystem. *Nature*, **408**, 79–81.

Smith SD, Charlet TN, Zitzer SF, Abella SR, Vanier CH, Huxman TE (2014) Long-term response of a Mojave Desert winter annual plant community to a whole-ecosystem atmospheric CO$_2$ manipulation (FACE). *Global Change Biology*, **20**, 879–892.

Sorte CJB, Ibanez I, Blumenthal DM *et al.* (2013) Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecology Letters*, **16**, 261–270.

Stark JM, Norton JM (2015) The invasive annual cheatgrass increases nitrogen availability in 24-year-old replicated field plots. *Oecologia*, **177**, 799–809.

Suding KN, Lavorel S, Chapin FS *et al.* (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.

Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thuiller W, Lavorel S, Araujo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8245–8250.

Thuiller W, Richardson DM, Midgley G (2007) Will climate change promote alien plant invasions? In: *Biological Invasions, Ecological Studies* (ed Nentwig W), pp. 197–211. Springer-Verlag, Berlin.

Walther GR, Roques A, Hulme PE *et al.* (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution*, **24**, 686–693.

West AM, Kumar S, Wakie T, Brown CS, Stohlgren TJ, Laituri M, Bromberg J (2015) Using high-resolution future climate scenarios to forecast *Bromus tectorum* invasion in Rocky Mountain National Park. *PLoS ONE*, **10**, 1–15.

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increases western U.S. forest wildfire activity. *Science*, **313**, 940–943.

Whisenant S (1990) Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. In: *Proceedings of the Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management* (eds McArthur ED, Romney EM, Smith SD, Tueller PT), Forest Service General Technical Report INT-276, Intermountain Research Station, Las Vegas, NV, 4–10.

Williams AL, Wills KE, Janes JK, Schoor JKV, Newton PCD, Hovenden MJ (2007) Warming and free-air CO$_2$ enrichment alter demographics in four co-occurring grassland species. *New Phytologist*, **176**, 365–374.

Wolkovich EM, Cleland EE (2011) The phenology of plant invasions: a community ecology perspective. *Frontiers in Ecology and the Environment*, **9**, 287–294.

Wolkovich EM, Cleland EE (2014) Phenological niches and the future of invaded ecosystems with climate change. *AoB PLANTS*, **6**, 1–16.

Wolkovich EM, Davies TJ, Schaefer H *et al.* (2013) Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany*, **100**, 1407–1421.

Young JA (2000) *Bromus tectorum* L. In: *Invasive Plants of California's Wildlands* (eds Bossard C, Randall J, Hoshovsky M), pp. 76–80. University of California Press, Berkeley, CA.

Zelikova TJ, Hufbauer RA, Reed SC, Wertin T, Fettig C, Belnap J (2013) Eco-evolutionary responses of *Bromus tectorum* to climate change: implications for biological invasions. *Ecology and Evolution*, **3**, 1374–1387.

Ziska LH (2003) Evaluation of the growth response of six invasive species to past, present and future atmospheric carbon dioxide. *Journal of Experimental Botany*, **54**, 395–404.

Ziska LH, Reeves JB, Blank B (2005) The impact of recent increases in atmospheric CO$_2$ on biomass production and vegetative retention of cheatgrass (*Bromus tectorum*): implications for fire disturbance. *Global Change Biology*, **11**, 1325–1332.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. The Prairie Heating and CO$_2$ Enrichment (PHACE) study site, with simplified diagrams of the experimental rings and *Bromus tectorum* subplots.

Figure S2. Effects of elevated CO$_2$ (eCO$_2$) and warming on *Bromus tectorum* plant number by competition treatment and year. Error bars are $\pm$1 SE. See Table 2 for statistics.

Figure S3. Effects of elevated CO$_2$ (eCO$_2$) and warming on *Bromus tectorum* per-plant height by competition treatment and year. Error bars are $\pm$1 SE. See Table 2 for statistics.

Figure S4. Effects of elevated CO$_2$ (eCO$_2$) and warming on *Bromus tectorum* leaf Δ^{13}C by competition treatment and year. Error bars are $\pm$1 SE. See Table 1 for statistics.

Figure S5. Effects of elevated CO$_2$ (eCO$_2$) and warming on *Bromus tectorum* plant tissue N by competition treatment and year. Error bars are $\pm$1 SE. See Table 1 for statistics.