Oecologia (2010) 164:821–832
DOI 10.1007/s00442-010-1749-3

GLOBAL CHANGE ECOLOGY - ORIGINAL PAPER

Effects of climate and snow depth on *Bromus tectorum* population dynamics at high elevation

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Received: 22 January 2010 / Accepted: 30 July 2010 / Published online: 26 August 2010

Abstract Invasive plants are thought to be especially capable of range shifts or expansion in response to climate change due to high dispersal and colonization abilities. Although highly invasive throughout the Intermountain West, the presence and impact of the grass *Bromus tectorum* has been limited at higher elevations in the eastern Sierra Nevada, potentially due to extreme wintertime conditions. However, climate models project an upward elevational shift of climate regimes in the Sierra Nevada that could favor *B. tectorum* expansion. This research specifically examined the effects of experimental snow depth manipulations and interannual climate variability over 5 years on *B. tectorum* populations at high elevation (2,175 m). Experimentally-increased snow depth had an effect on phenology and biomass, but no effect on individual fecundity. Instead an experimentally-increased snowpack inhibited population growth in 1 year by reducing seedling emergence and early survival. A similar negative effect of increased snow was observed 2 years later. However, a strong negative effect on *B. tectorum* was also associated with a naturally low-snow winter, when seedling emergence was reduced by 86%. Across 5 years, winters with greater snow cover and a slower accumulation of degree-days coincided with higher *B. tectorum* seedling density and population growth. Thus, we observed negative effects associated with both experimentally-increased and naturally-decreased snowpacks. It is likely that the effect of snow at high elevation is nonlinear and differs from lower elevations where wintertime germination can be favorable. Additionally, we observed a doubling of population size in 1 year, which is alarming at this elevation.

Keywords Climate change · Invasive · Sierra Nevada · Periodic matrix model · Snow fence

Introduction

Anthropogenic climate change is anticipated to affect the margins of species and population ranges, and there is extensive evidence that indicates this is already occurring (Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006). Range expansions and contractions may be particularly pronounced along elevational gradients where local climates change rapidly across small spatial scales. Wintertime conditions and snowpack dynamics at higher elevations can substantially affect organisms, and changes in these climatic factors may favor some species and hinder others (Billings and Bliss 1959; Dunne et al. 2003; Klanderud and Birks 2003; Pauli et al. 2007). In particular, the ability of terrestrial plants to respond to climate change may be highly variable among species due to large variation in life histories and dispersal abilities (Walther 2004).

Invasive plant species may be especially capable of rapid range shifts or expansion in the face of climate change because of generally high dispersal abilities and a proven ability to thrive in new habitats (Dukes and Mooney

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Communicated by Jon Keeley.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-010-1749-3) contains supplementary material, which is available to authorized users.

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1999; Walther 2000; Walther et al. 2002). The rate of anthropogenic climate change is expected to be far greater than previous natural climatic changes, and dispersal ability will be crucial for plants to follow suitable climates (Simberloff 2000). Many invasive plants also exhibit short juvenile periods with high fecundity, and may be able to respond rapidly to climate change at the population level (Dukes and Mooney 1999; Simberloff 2000; Theoharides and Dukes 2007). It is therefore important to understand how climatic variables affect invasive plant populations at the edge of their elevational distribution.

The invasive annual grass *Bromus tectorum* L. (Poaceae; 'cheatgrass', 'downy brome') has profoundly altered ecosystems and fire regimes across the Great Basin Desert and Intermountain West (Billings 1990; D'Antonio and Vitousek 1992; Knapp 1996). It is estimated that areas invaded by *B. tectorum* are up to 500 times more likely to burn than native communities (BLM 2000). At higher elevations in the western Great Basin and eastern Sierra Nevada, the impact has been limited. However, the potential for plant invasions at high elevation has recently attracted attention (Pauchard et al. 2009) and *B. tectorum* populations are common along the base of the eastern Sierra Nevada escarpment (personal observation). Previous research has demonstrated that cold temperatures and winter snowfall can negatively impact *B. tectorum* survival, growth, and fecundity (Mack and Pyke 1983; Pierson and Mack 1990a; Chambers et al. 2007), which may help explain its limited presence in the eastern Sierra Nevada. While there remains uncertainty, several future climate scenarios for eastern California predict an upward elevational shift of climate regimes (Hayhoe et al. 2004; Leung et al. 2004; Snyder and Sloan 2005; Cayan et al. 2008). Under these scenarios, a release from climatic constraints could facilitate the invasion of *B. tectorum* into higher elevations in the Sierra Nevada.

Compared to research in alpine/subalpine and arctic/subarctic systems, there has been relatively little work that examines the effect of wintertime snowpack on winter annuals, such as *B. tectorum*, at high elevation. Winter snowpack can exert both positive and negative influences on plant populations and communities depending on snow depth, melt timing, and snowpack duration (Billings and Bliss 1959; Bell and Bliss 1979; Jackson and Bliss 1984; Smith et al. 1995; Walker et al. 1995; Inouye et al. 2002). For *B. tectorum*, the timing of germination and environmental influences on germination can be variable (Mack and Pyke 1983, 1984; Beckstead et al. 1996; Meyer et al. 1997), and may further complicate the effects of snowpack dynamics.

The underlying question addressed by this study is whether winter snowpack limits the expansion of *B. tectorum* into high-elevation habitats. Specifically, we tested the hypotheses that (1) an experimentally-increased snowpack would negatively affect *B. tectorum* demographic rates and population growth, and (2) that winters with naturally deep and long-lasting snowpacks would have similar negative effects on demographic rates and population growth, in contrast to patterns following more mild winters. Our approach utilized experimental snowpack manipulations to isolate effects associated with winter conditions, and used this information to better understand the population-level response to natural climate variability among years. We conducted our research on a *B. tectorum* population at 2,175 m in elevation, typical of those established along the base of the eastern Sierra Nevada. We chose to primarily investigate demographic responses because of the specific relevance to the potential expansion and persistence of invasive species near the range margin.

Materials and methods

Study system

Research was conducted in a Great Basin Desert shrubland ecosystem adjacent to the Valentine Eastern Sierra University of California Natural Reserve (VESR) near Mammoth Lakes, CA (37°36′51″N, 118°49′47″W, 2,175 m elevation). Annual precipitation at the site is roughly 325 mm year^{-1}, and occurs mostly as snow during the winter. Surface soils at this site (0–100 cm deep) are composed of sandy loam and gravelly sandy loam, are slightly acidic ($pH = 6.0$), and are underlain by glacial alluvium deposits. The site is dominated by the native shrubs *Artemisia tridentata* Nutt. (Asteraceae; 'big sagebrush') and *Purshia tridentata* (Pursh) DC (Rosaceae; 'antelope bitterbrush'). Other, less common, shrubs include *Chrysothamnus nauseosus* and *Prunus andersonii*. Native perennial bunchgrasses are scattered and include *Achnatherum hymenoides*, *Elymus elymoides*, and *Hesperostipa comata*. Other herbaceous species include *Gayophytum diffusum*, *Phacelia bicolor*, *Viola purpurea*, and *Eriastrum sparsiflorum*. The site has been annually grazed for 1 month during the summer for at least 50 years (Dan Dawson, personal communication) with an average density of less than 0.25 calf/cow pairs ha^{-1}. During the period of this study, grazing occurred after *B. tectorum* senescence.

Experimental design

In October 2005, we constructed four experimental snow fences with the goal of manipulating snow depth in experimental plots (Online Resource 1). Each fence measured 30 m in length and 1.8 m in height and consisted of 16 vertical t-posts sunk 0.6 m into the ground. Plastic mesh fencing (50% porosity) was secured along the fence, leaving a 50-cm gap at the bottom (essential for proper snow fence functionality; Tabler 1991, 1994). This design allowed for the removal of the plastic fencing after each winter (April–October) to avoid the unwanted effects of shading and wind disruption during the growing season, although effects on wintertime wind scouring during snow-free periods remained possible. All fences were oriented perpendicular to the prevailing winter wind (240°) and remained in effect throughout the study.

Snow fences create zones of increased snow accumulation immediately downwind of the fence followed by an area of reduced snow accumulation farther downwind. Plots were established in the spring of 2005 at three snow fence sites prior to the snow manipulations to provide baseline information. Plots at the fourth snow fence were established in the spring of 2006 after the first snow manipulation winter. For each fence, plots were established downwind in association with areas of increased (2 m from each fence) and decreased (15 m from each fence) snow accumulation. Control plots were established both upwind (15 m from each fence) and farther downwind (40 m from each fence) where snow depth is unaffected by the fence. Two sets of control plots were deemed necessary as it is not possible to randomize the spatial order of snow manipulation plots. Within each snow depth treatment zone, we established sampling plots in association with three microhabitats: under adult *A. tridentata* canopies, under adult *P. tridentata* canopies, and in intershrub spaces. This is necessary to fully capture landscape-level population dynamics as microhabitat can significantly affect *B. tectorum* demography at this site (Griffith 2010). Plots varied in size in order to capture a sufficient number of *B. tectorum* individuals ($\geq$24) while remaining within each microhabitat (mean shrub microhabitat plot area = 480 cm^2, mean intershrub plot area = 896 cm^2).

Whereas our goal was to incorporate both increased and decreased snow accumulation treatments, the size of the snow fences was apparently not large enough to produce a significant reduction in snow accumulation (increased snow accumulation remained a robust treatment—see "Results"). In general, areas of snow reduction downwind of snow fences are much more spread out compared to the narrow and focused snow accumulation zone. Thus, we have excluded the reduced snow accumulation treatment from this study as there was not a robust treatment application nor can it be considered a true control. Also, there were never any significant effects on *B. tectorum* detected in these plots. The final experimental design presented in the paper thus includes four snow fences, each with zones designated as 'upwind control', 'downwind control', and '+snow', and three subplots (one in each microhabitat) within each snow manipulation zone.

Snow depth and climatic variables

Snow depth and cover were examined in three ways. First, snow depth in the experimental plots was manually measured monthly during winter, except for winters when there was no persistent snowpack. Second, daily modeled ambient snow depth and cover data were obtained from the National Operational Hydrologic Remote Sensing Center's (NOHRSC) KMMH station, which is less than 1 km from our research site. These values of snow depth are generated from an energy-and-mass-balance, multi-layer snow model. Third, the percentage of days with snow cover for each winter was estimated from NOHRSC satellite observations. This was deemed necessary as the modeled snowpack data from 2008/2009 was in contrast to the observation of no persistent snowpack during that winter (this may be a result of difficulties in modeling the snowpack for a site near the elevational snow line). We estimated the percentage of snow cover days as a range, such that the low end includes days with satellite estimates of 60–100% snow cover. The high end is less conservative and includes days with 20–100% snow cover.

We calculated total precipitation during the winter (defined as December 1–April 14) and the growing season (defined as April 15–June 30) from a permanent weather station at VESR. Accumulated degree-days were calculated between September 1 and April 14 using hourly air temperature and modeled snowpack data, such that degree-days accumulated only when air temperature was above zero and when the modeled snow depth was less than 1 cm. We also calculated potential evapotranspiration (PET) during the growing season based on daily minimum and maximum temperature, relative humidity, solar radiation (0.285–50 μm), and average wind speed using the Penman–Monteith method (Allen et al. 1998).

Demographic sampling

In this paper, we present two complementary and overlapping demographic datasets that examine the response of a naturally-occurring, high-elevation *B. tectorum* population to both experimental snow depth manipulations and to natural climatic variability. First, we used a 2-year detailed demographic dataset based on the complete life cycles of over 1,600 individual plants. These data were used to build matrix population models to better understand how the response of individuals translates into the response of the population. Second, we continued to monitor *B. tectorum* seedling density every April in these plots for 5 years (2005–2009) to provide a more long-term perspective on the population-level response to snow manipulations and natural climatic variation.

The fates of 1,603 *B. tectorum* individuals were monitored in demographic plots during the 2005 and 2006 growing seasons. Sampling was conducted twice in 2005 (28 April–May 1 and June 9–11), and three times in 2006 (April 25–27, May 12–14, and June 5–7). After measuring the density of *B. tectorum* in each plot in April, up to 24 individual plants were marked with uniquely identifiable toothpicks. These plants were measured for survivorship, number of leaves, length of the longest leaf, maximum culm height, and number of spikelets (in 2006, spikelets were not fully developed during the June sampling period, and we returned on June 26 to record the final spikelet counts). We also measured gravimetric soil moisture content at 15 cm depth adjacent to each plot during each sampling period.

Individual aboveground biomass was estimated by measuring (as above) and then harvesting 147 additional *B. tectorum* individuals from areas nearby demographic plots to avoid disturbance within the plots. Samples were weighed after drying for 96 h at 60°C, and the data were used to estimate the biomass of individual plants in the field using allometric relationships ($r^2 = 0.87$; Griffith 2010). Aboveground relative growth rates (RGR, mg mg^{-1} day^{-1}) between sampling periods were calculated as, RGR = $(\ln \text{Biomass}_2 - \ln \text{Biomass}_1)/(t_2 - t_1)$ (Hunt 1978).

To estimate seed production from non-destructive spikelet counts, we harvested a total of 118 plants adjacent to the experimental plots and counted the number of fertile florets per spikelet. An average value of 1.78 seeds per spikelet was assumed for all individuals as there were no significant differences among snow depth treatments ($F_{3,114} = 2.08$, $P = 0.107$). The rate of seedling emergence was calculated as the density of established seedlings in April divided by the estimated seed output density from the previous year.

Statistical analysis and demographic modeling

To examine univariate differences among snow depth treatments within a year, we used a split-plot analysis of variance (ANOVA) that included the following factors: snow fence (random blocking effect, $n = 4$), snow depth treatment (fixed effect, $n = 3$), and microhabitat (fixed effect, $n = 3$). F ratios for both snow depth and microhabitat were calculated using their respective interactions with snow fence as the error term. We included the effect of microhabitat in the model to investigate possible interactions with snow depth, although the effect of microhabitat per se is not within the scope of this paper (see Griffith 2010). The snow depth by microhabitat interaction (using the 3-way interaction as the error term) was never significant for any response variable, and the effect of microhabitat was dropped from the model. The final statistical model therefore simplified to a block design, with snow fence as the block and snow depth treatment as the main factor (with each snow depth plot value an average of the three microhabitats within). We tested the hypothesis that increased snow depth would have a negative effect on *B. tectorum* demographic variables using a planned contrast of +snow plots against both sets of control plots. The F ratio of the entire model is not an appropriate test as we would not expect there to be any differences between the two sets of control plots. To satisfy the assumptions of ANOVA, values of biomass, spikelet number, and λ were log-transformed, and survivorship and establishment values were arcsin-square root transformed. Values of log-transformed variables presented in the paper have been subsequently back-transformed. All univariate analyses of the snow manipulations were performed using Systat (version 12, Systat Software, Point Richmond, CA, USA).

To examine differences in demographic variables due to natural variability between 2005/2006 and 2006/2007, we restricted our analyses to the snow depth control plots only (averaged across the three microhabitats). To statistically compare these 2 years, we used 2-sample, two-tailed randomization tests (Manly 1997; Caswell 2001) as no distributional assumptions are required. Changes in *B. tectorum* April seedling densities from 2005 to 2009 were calculated as April-to-April population growth rates (λ), where $\lambda = N_{t+1}/N_t$. Mean values of λ were calculated using log-transformed data.

We used periodic matrix models and life table response experiment (LTRE) analysis to estimate population growth (λ) and to examine how differences in demographic vital rates contributed to differences in λ. The population model is described in detail by Griffith (2010), with the exception here that seed germination and establishment rates are parameterized from natural seedling emergence data. We used the LTRE analysis to specifically examine λ differences among snow depth treatments (comparing +snow values to pooled values of control plots) and between years (using ambient snow depth plots only). All randomization tests and population modeling were conducted using Matlab (release 14, The Mathworks, Natick, MA, USA).

Results

Snow depth and soil moisture

During the first winter following the construction of the snow fences (2005/2006), average snow depth on +snow plots was consistently greater than on control plots (Fig. 1). The +snow snowpack remained substantial throughout the winter, whereas there was a measurable snowpack on control plots only on the January sampling date. The pattern was similar 2 years later in the 2007/2008 winter, with +snow plots having roughly twice the snow depth of control plots during periods of snow cover. During the 2006/2007 winter there was never a persistent snowpack in any plot due to low natural snowfall. Whereas sampled snow depth on control plots in the 2005/2006 and 2007/2008 winters was reasonably consistent with the NOHRSC modeled snowpack data (Fig. 1), on-site observations during the 2008/2009 winter were not consistent with the modeled snowpack in that virtually no persistent snowpack was observed in any plots that year.

Following the first winter of snow manipulations (the period in which we concurrently sampled detailed demographic parameters), soil moisture did not significantly vary among plots in April or June 2006 (Table 1). In May 2006, soil moisture on +snow and downwind control plots was significantly greater than on upwind control plots (Table 1).

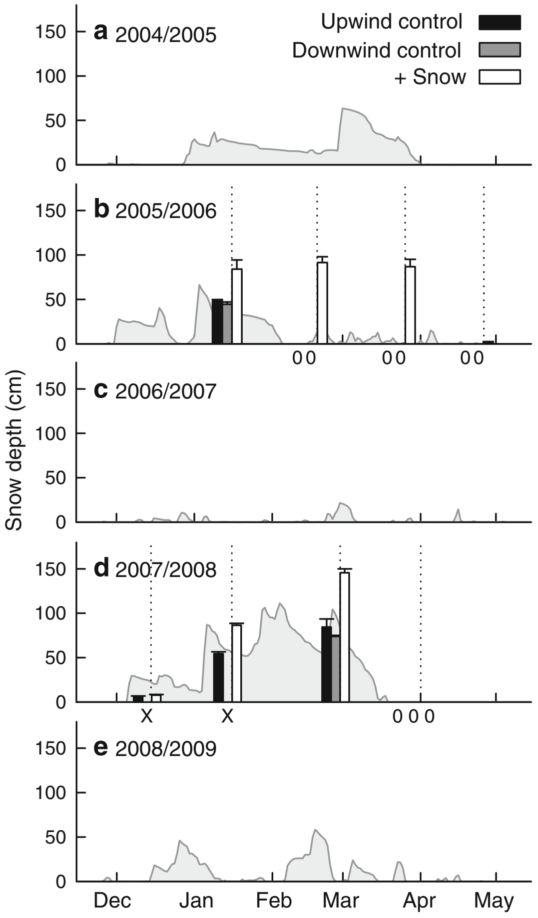

Fig. 1 Experimental snow depth and natural snowpack formation from 2004/2005 to 2008/2009. *Gray areas* depict NOHRSC modeled snow depth (see "Methods"). *Vertical bars* indicate the means + 1SE of manually-sampled snow depth in experimental plots during winters with a measureable snowpack (*dashed lines* sampling dates). *0* no snow cover, *X* missing data. Snow fences were not yet in effect during the 2004/2005 winter. NOHRSC modeled snow depth in 2008/2009 conflicts with on-site observations of no persistent snowpack (see "Results")

Table 1 Soil gravimetric percent water content (Θ) at 15 cm depth following the 2005/2006 snow depth treatments

Θ	Upwind control	Downwind control	+Snow
April	7.51 a	8.43 a	8.41 a
May	4.63 b	6.78 a	6.44 a
June	4.21 a	4.41 a	4.30 a

Values are means; letters indicate significant differences ($P < 0.05$) among snow depth treatment levels as revealed by Tukey's HSD test

Experimental snow depth manipulation: detailed demography

During the 2006 growing season, mean individual biomass on +snow plots was significantly and consistently lower than on control plots (Table 2). Most spikelets were visible during the June sampling period, but spikelet production had not finished. Between the early June sampling period and the final spikelet counts in late June, additional spikelet production was significantly greater on +snow plots. The final spikelet counts revealed no significant differences among snow depth treatments in terms of total individual spikelets (Table 2). Thus, it appears that the timing of spikelet production was affected by an increased snowpack, but final individual reproductive output was not. Survivorship between sampling periods varied significantly among snow depth treatments, although this is likely due to a combination of shifted phenologies and fixed sampling dates (e.g., early mortality was likely captured on +snow plots but not controls; see "Discussion").

Demographic rates from 2006 were incorporated into a periodic matrix population model in order to examine a

Table 2 *Bromus tectorum* biomass and spikelet production following the 2005/2006 snow depth treatment

Response variable	Upwind control	Downwind control		+Snow
April biomass	2.59	2.59	***	1.73
May biomass	4.13	4.43	**	3.27
June biomass	28.4	27.8	***	19.4
RGR (Apr–Jun)	0.058	0.058	NS	0.056
June spikelets	3.48	3.47	*	2.54
Late spikelet production	0.22	0.05	***	1.37
Final (July) spikelets	3.73	3.52	NS	4.03

Values are means; significant differences between +snow and control plots: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

NS indicates non-significance

Biomass in mg, RGR in mg mg^{-1} day^{-1}

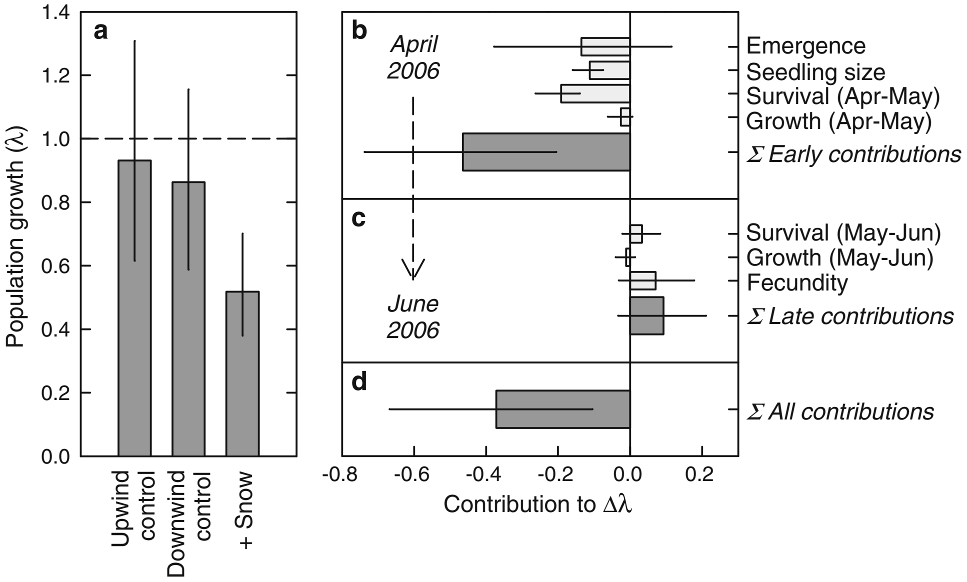

Fig. 2 Results from the periodic population model of *Bromus tectorum* comparing snow depth treatment effects in 2006 on **a** modeled population growth rates (means ± 95% CI). The life table response experiment (LTRE) analysis is separated into contributions from **b** demographic rates primarily influenced by the snowpack and immediate post snow melt environment, **c** those primarily influenced by growing season conditions, and **d** the total summed contributions of all effects (mean contributions ± 95% CI). More negative values indicate a greater contribution to the decrease in λ on +snow plots. Separate contributions from April–May survival and seedling emergence cannot be accurately interpreted due to shifted phenology on +snow plots, but their combined sum remains accurate (see "Discussion")

more synthetic response to the snow manipulation. Modeled population growth (λ) was significantly reduced on +snow plots ($P = 0.013$), with no overlap of the 95% confidence intervals and $\lambda = 1.0$ (Fig. 2a). The life table response experiment (LTRE) analysis revealed how differences in vital rates between +snow plots and control plots (pooled) contributed to the decrease in λ on +snow plots (Fig. 2b–d). The reduction of λ on +snow plots was primarily due to reduced demographic rates associated with initial seedling size, seedling emergence, and early survival, i.e. effects immediately following snowmelt. Demographic rates occurring later in the growing season (May–June survival, growth, and fecundity) were not different among snow depth treatments and thus did not contribute to the low λ on +snow plots.

Experimental snow depth manipulation: long-term density

Prior to the construction of the snow fences there was no difference in *B. tectorum* densities among plots (Fig. 3). After the snow fences were installed, mean seedling densities on +snow plots were generally lower than on control plots, but there was no difference in April 2009. Statistically, differences between +snow and control plots were marginally significant in June 2006 ($F_{1,6} = 3.773$, $P = 0.100$) and highly significant in April 2008 ($F_{1,6} = 40.60$, $P < 0.001$).

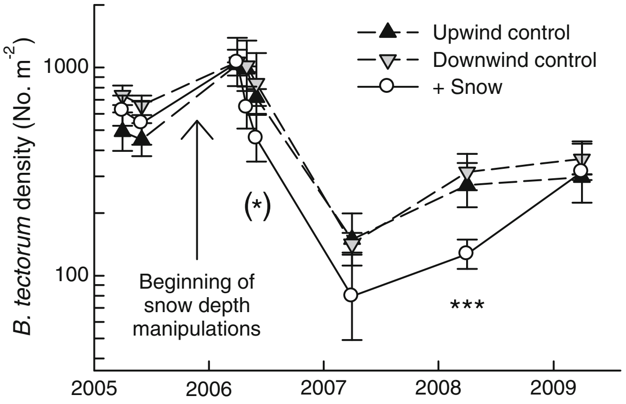

Fig. 3 Changes in *Bromus tectorum* densities in response to experimental snow depth treatments. Values are means ± 1SE (sample size varied depending on treatment and year—see text for details). Sampling occurred in late April of every year, June 2005, and May and June 2006. Significant differences between +snow and control plots: ***$P < 0.001$, (*)$0.05 < P < 0.10$

Natural interannual variability: detailed demography

The detailed demography dataset captured the natural variation of *B. tectorum* over two full years, from April 2005 to April 2007 (beginning and ending as seedlings).

Table 3 Values of response variables in 2005/2006 and 2006/2007 (snow depth control plots only)

Response variable	2005/2006		2006/2007
April soil Θ	7.40	NS	7.97
June soil Θ	3.58	NS	4.31
April biomass	3.28	**	2.59
June biomass	45.9	***	28.1
RGR (Apr–Jun)	0.063	(*)	0.058
Seedling emergence	0.19	***	0.04
Survivorship (Apr–Jun)	0.88	(*)	0.76
Spikelets	6.32	***	3.63

Values are means; significant differences: **$P < 0.01$, ***$P < 0.001$, (*)$0.05 < P < 0.10$

NS non-significance

Biomass in mg, RGR in mg mg^{-1} day^{-1}

Thus, each year included responses associated with different wintertime and growing-season conditions. Most demographic variables on unmanipulated, snow depth control plots were significantly different between years (Table 3). During the growing season, individual biomass (in April and June), and spikelet number were significantly greater in 2005 compared to 2006. A reduction in April-to-June RGR between 2005 and 2006 was marginally significant ($P = 0.060$). Similarly, decreased survivorship between 2005 and 2006 was marginally significant ($P = 0.068$). The mean emergence/establishment rate in 2005/2006 was 18.6% compared to 4.0% in 2006/2007. The timing of germination events and seedling establishment also apparently varied between years. In 2005 and 2006, there was no evidence of germination prior to April snowmelt. However, in April 2007, less than 2% of individuals were substantially larger than all previously measured seedlings, presenting two discrete seedling size class classes indicative of two cohorts that germinated at different times (data not shown).

Modeled λ was significantly greater ($P < 0.001$) in 2005/2006 ($\lambda = 1.85$) compared to 2006/2007 ($\lambda = 0.23$; Fig. 4a). LTRE analysis was used to examine differences in λ on control plots for these two annual periods (Fig. 4b). The decrease in seedling emergence rates between 2005/2006 and 2006/2007 accounted for 63% of the decrease in λ. Differences in fecundity, growth, and survival further accounted for 21, 8.9, and 6.8% of the decrease in λ, respectively. Thus, similar to the snow depth LTRE analysis, the greatest contribution to the decrease in λ was associated with effects on early life history stages compared to those later in the growing season.

Natural interannual variability: long-term density

From 2005 to 2009, *B. tectorum* density fluctuated greatly on control plots (Fig. 3). Positive population growth ($\lambda = N_{t+1}/N_t$) was observed during 2005/2006 ($\lambda = 1.67$), 2007/2008 ($\lambda = 2.03$), and 2008/2009 ($\lambda = 1.12$). These years contrasted with the precipitous population decline between 2006 and 2007 ($\lambda = 0.14$). Spanning the 5 years of sampling in April, *B. tectorum* seedling density on snow depth control plots was positively correlated with the antecedent winter's (December 1 to April 14) total precipitation ($r^2 = 0.85$, $P = 0.025$; Fig. 5a) and percentage of days with snow cover ($r^2 = 0.80$, $P = 0.040$; Fig. 5b). The relationship between seedling density and accumulated degree-days was marginally significant ($r^2 = 0.69$, $P = 0.082$; Fig. 5c). April seedling density did not correlate with potential evapotranspiration or total precipitation of the antecedent growing season.

Compared to density measurements, annual population growth of seedlings (April-to-April λ) did not significantly correlate with any climatic variables (Fig. 5f–j). However, as statistical power with only four data points is low, strong but nonsignificant relationships emerged between April-to-April λ and the percentage of days with snow cover

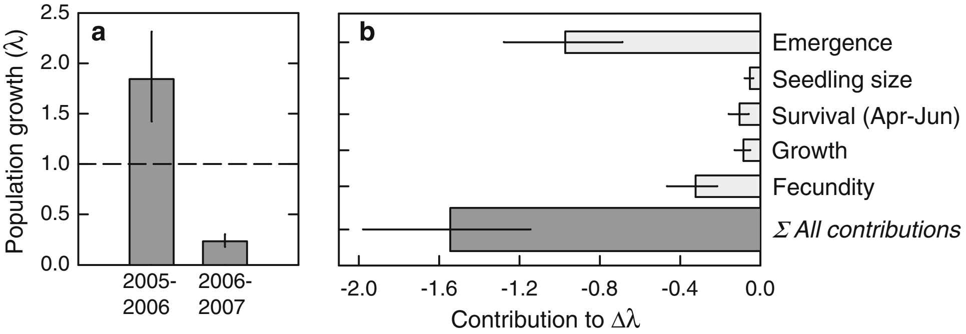

Fig. 4 Results from the periodic population model and LTRE analysis of *Bromus tectorum*, comparing natural variability between 2005/2006 and 2006/2007. **a** Modeled population growth rates (means ± 95% CI) among years, **b** contributions of changes in demographic rates to the decrease in λ between years (mean contributions ± 95% CI). More *negative values* indicate a greater contribution to the observed decrease in λ

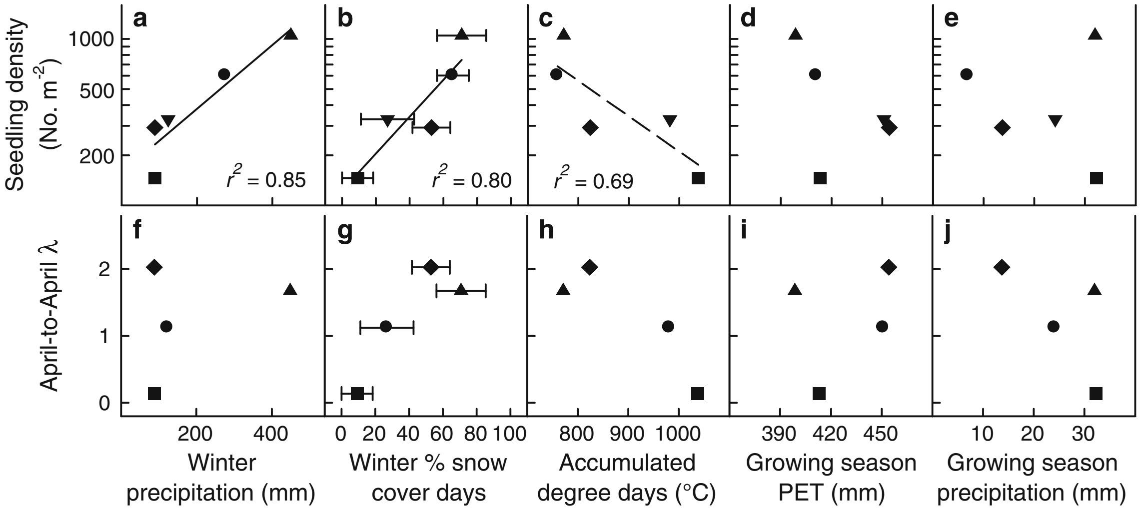

Fig. 5 Relationships between climatic variables and (**a**–**e**) mean *Bromus tectorum* April seedling density and (**f**–**j**) April-to-April λ from 2005 to 2009. For seedling density, all climatic variables are *antecedent*, e.g. the April seedling value for 2005 is related to the climatic conditions of the 2004/2005 winter and the 2004 growing season (**a**–**e***filled circle* 2005, *filled triangle* 2006, *filled square* 2007, *filled diamond* 2008, *inverted triangle* 2009). For λ, both winter and growing season climatic conditions fall *within* the April-to-April time span (**f**–**j***filled circle* 2005–2006, *filled triangle* 2006–2007, *filled square* 2007–2008, *filled diamond* 2008–2009). *Winter* spans December 1 to April 14 and *Growing season* April 15 to June 30. Accumulated degree-days were calculated between September 1 and April 14. Snow cover days are expressed as a range based on conservative and less conservative estimates of snow cover from satellite data (see "Methods"). Linear regressions are indicated as statistically significant (*solid linesP* < 0.05) and marginally significant (*dashed linesP* < 0.10)

($r^2 = 0.76$, $P = 0.125$; Fig. 5g) and accumulated degree-days ($r^2 = 0.79$, $P = 0.113$; Fig. 5h).

Discussion

Experimental snow depth manipulation

Consistent with our original hypothesis, we found a negative effect of experimentally-increased snow depth on *B. tectorum* population growth (λ), with λ on +snow plots reduced by nearly 50% of control plots. This period spanned the first winter of snow manipulations (2005/2006) when the snowpack on +snow plots was deeper and of longer duration than any natural snowpack in the study. The effects on individual plants were more nuanced. Smaller plants on +snow plots during the 2006 growing season is indicative of a phenological effect and corresponds with a delay in snow melt of 9 days compared to ambient snow depth plots. However, there was little lasting influence on growth over the next few months, consistent with no strong soil moisture differences among the plots, nor a difference in relative growth rates of individual plants.

Although individual biomass is a good predictor of fecundity for *B. tectorum* (Griffith 2010), the effect of increased snow on individual biomass was apparently not large enough to generate differences in fecundity by the end of the 2006 growing season (Table 2). This may be a result of continued growth and spikelet production on +snow plots after the early June sampling period via a phenological shift lasting through the end of the season. Many studies that have manipulated snow depth and duration report an influence on aspects of plant fecundity, such as flowering time and duration, flowering number, seed production, and/or seed weight (Bell and Bliss 1979; Galen and Stanton 1993; Dunne et al. 2003; Wipf et al. 2006; Lambrecht et al. 2007). However, these effects are often variable among species—both in sign and intensity—and demonstrate complicated trade-offs between insulation from harsh winter conditions and a longer growing season as a result of snowpack dynamics. These studies were conducted in alpine/subalpine and arctic/subarctic systems and focused primarily on perennial plant species. It may be difficult to compare the growing-season response of *B. tectorum* near its current upper elevational margin to plants with fundamentally different life histories that have evolved with deep winter snow cover.

In addition to effects on biomass, demographic data from 2006 showed an important negative effect of increased snow depth on early survivorship (Fig. 2b). This result is difficult to interpret as phenologies differed among snow depth treatments. Typical of many plants, *B. tectorum* at this site follows a type III survivorship curve, with the highest mortality associated with seedling establishment. It is possible that during the April sampling period in 2006, early mortality on +snow plots was ongoing (i.e. seedling establishment was not complete), whereas much of this mortality had already occurred on control plots due to shifted phenologies. We believe this is likely given that for 87% of individuals in +snow plots, only the coleoptile had emerged by the April sampling period. This is in contrast to the control plots where an average of 7% of individuals consisted only of the coleoptile. Therefore, we cannot meaningfully state that there was a true effect of snow depth on survivorship; rather this value is in part an artifact of shifted phenologies and fixed sampling times.

We were able to partially resolve this issue by combining measures of early survivorship and seedling emergence through population modeling of the entire life cycle. For example, if early survivorship on +snow plots was artifactually reduced, then it is inherently compensated for by artifactually increased emergence, and it then only makes sense to examine the two together. The LTRE analysis demonstrated that the decrease in λ on +snow plots was due to the combined reduction in seedling emergence, size, and survivorship (Fig. 2b). We conclude that the negative effect of increased snowpack on λ resulted from factors operating during, or immediately following, snow cover and not during the bulk of the growing season.

The implications of confounded sampling dates and phenologies impose analytical challenges. In the context of anthropogenic climate change, it is important not only to document phenological shifts, but to understand how they affect populations and communities (Walther 2004; Cleland et al. 2007). However, demographic analyses for annual organisms, which are useful to this end, require repeated sampling periods. If the effect of interest is phenological, such analyses are difficult to conduct unless sampling is frequent and intervals are extremely short. Alternatively, one could attempt to stagger sampling dates across plots so that they are aligned with phenology. The drawback of this approach is that external effects (e.g., weather or disturbance events) may occur between sampling dates, again introducing artifacts and confounding results.

Across the 5 years of the study (Fig. 3), the only years with any decline in *B. tectorum* mean density on +snow plots were preceded by winters that produced large snowpacks on +snow plots (2005/2006 and 2007/2008). The snowpack on +snow plots in these years were apparently larger than any naturally occurring snowpacks during the study (Fig. 1) and suggest that only a very substantial snowpack exerts a negative effect on *B. tectorum* populations. In other years when there was no relative decline in *B. tectorum* density on +snow plots, there was only sporadic snow cover (even on +snow plots). These results highlight the complexity of population-level responses to climatic factors. In particular, populations can have a "memory" of antecedent climatic events such that the effect can be retained for several years, or effects may compound across years and amplify (Schwinning et al. 2004). Changes in the magnitude and duration of the snowpack are also likely to have important effects on soil nutrient dynamics due to altered rates of transformation and/or release (Groffman et al. 2001; Johnson et al. 2009). During the 2 years of detailed demography, we performed limited soil nutrient analyses (Griffith 2010). In April 2006, NO_3^- availability was slightly higher on +snow plots (0.89 vs 0.71 g m^{-2}; $P = 0.063$), but not for NH_4^+ or available P and K (nor were there any differences in June 2005). Thus, we have little evidence that snowpack-induced changes in nutrient availability were strongly driving our demographic results.

Natural interannual variability

The large population decline between 2005/2006 and 2006/2007 was primarily due to very low rates of seedling emergence/establishment in April 2007 (Fig. 4b). However, all other demographic variables also decreased between these periods with differences in survival, growth, and fecundity contributing to 37% of the decline in population growth. We will first discuss effects during the growing season ('post-establishment') followed by the major influence of seedling emergence/establishment ('pre-establishment'). We will then discuss the possible roles of climatic variables across the 5 years of *B. tectorum* density measurements.

Post-establishment effects

During the growing season, *B. tectorum* individuals are likely influenced by concurrent growing conditions and by both the timing of snow melt and its influence on soil moisture. A lack of soil moisture differences between 2005 and 2006 suggests that the differential response of *B. tectorum* was not driven by snowpack-derived soil moisture differences. Indeed, the period of snow depth influence on surface soil moisture may be quite short in this system. Seedling root systems of *B. tectorum* are not extensive or deep, and access to snowpack-derived soil moisture near the soil surface is likely to quickly diminish through rapid infiltration and evaporation (Loik et al. 2004; Loik 2007).

In contrast to a lack of soil moisture differences, an interannual phenological effect appears likely. April sampling in 2006 began only 3 calendar days later than in 2005, yet it was 27 days after final snow melt compared to 17 days in 2005. A phenological influence of snowpack on interannual biomass differences is consistent with the biomass differences among the experimental snow depth plots in 2006. Phenological effects induced by natural variation in snow melt timing have been shown to have significant effects on plant reproductive success (Walker et al. 1995; Inouye et al. 2002). From the data in this study, it is difficult to determine how much of the interannual fecundity difference is attributable to differences in phenology. However, results from the 2006 snow depth manipulations indicate that a slight phenological shift alone may not have a large impact on *B. tectorum* reproduction at this site. Instead slightly lower relative growth rates (RGR) in 2006 suggests that differences in growing-season environmental conditions may have contributed to differences in fecundity between years.

Increased potential evapotranspiration (PET) and reduced precipitation during the early growing season in 2006 could have limited periods of photosynthesis through stomatal closure (Noy-Meir 1973; Fischer and Turner 1978; Aphalo and Jarvis 1991; Tardieu and Simonneau 1998). For example, in the first 6 weeks following snow melt, cumulative PET was 161 mm in 2006 compared to 128 mm in 2005. Similarly precipitation during this period totaled 5.05 mm in 2006 compared to 16.4 mm in 2005. Thus, there was greater evaporative demand and less precipitation during the critical period of early seedling growth in 2006. Other factors that could have resulted in the reduced fecundity between 2005 and 2006 include herbivory and/or density-dependent processes, though there was little evidence for either of these. In general, instances of inferred herbivory were very low (less than 5% of individuals) and did not differ between years (data not shown). Whereas there was some indication of negative density dependence in 2006, the relationship was weak and cannot explain the fecundity differences between 2005 and 2006.

Pre-establishment effects

Bromus tectorum population growth at this site is extremely sensitive to the rate of seedling establishment (Griffith 2010), and very low emergence/establishment (4%) in April 2007 primarily contributed to the decrease in population growth between years (Fig. 4b). This may have resulted from germination during a winter with very low snow cover that resulted in substantial early mortality. As a winter annual, *B. tectorum* seeds may germinate opportunistically between the autumn and spring given appropriate conditions (Young et al. 1969; Young and Evans 1975; Mack and Pyke 1983; Mack and Pyke 1984). The accumulated number of degree-days (above 0°C) has been shown to be an important predictor of *B. tectorum* germination (Roundy et al. 2007). Beginning in September, total snow-free degree-days was 771 by April 2006 compared to 1,037 by April 2007, while 771 degree-days had already been accumulated by early February 2007, suggesting that seeds may have been capable of germinating throughout the 2006/2007 winter when there was little snow cover. This indeed seems likely from the two clear seedling size classes seen in April 2007, when less than 2% of individuals were substantially larger than any seedlings previously encountered. From this observation, we infer that there were at least two seedling cohorts during the 2006/2007 winter, with the vast majority of surviving seedlings in the youngest cohort. Winter-time germination at this elevation may be detrimental and may reveal a positive influence of snow cover, by which it limits germination until conditions for survival are more favorable.

Long-term density

The 5-year *B. tectorum* density dataset suggests that winter-time climatic factors may be more important than growing season factors at this location (Fig. 5). Although 5 years of data (4 for values of λ) likely represents the minimum necessary to draw any conclusions from interannual climatic variability, the main results are consistent with those of the 2005–2007 detailed demography dataset discussed above: winters with greater snow cover and a slower accumulation of degree-days coincide with higher *B. tectorum* seedling density and population growth. This is in contrast to our original hypothesis, and indeed may be entirely opposite at lower elevations where winter-time germination may be favorable.

Of course, seedling density can never be predicted by climatic variables alone as prior seed production must be important. Although we do not have seed production data for all years, similar mean seed production in June 2005 and 2006 (6,465 vs 5,159 seeds m^{-2}, $P = 0.839$) was respectively followed by the highest (1,048 seedlings m^{-2}) and lowest (146 seedlings m^{-2}) April seedling densities in the study, indicating that climatic factors can likely overwhelm propagule supply.

Synthesis

Our original hypothesis of a negative effect of snowpack on *B. tectorum* populations was supported from an experimentally-increased snowpack in some years, yet relationships between natural variability in wintertime snow cover and *B. tectorum* populations were positive. These results are not necessarily in conflict with each other. Rather, they indicate that our original hypothesis was likely too simplistic and that the effects of the snowpack may be nonlinear at high elevation. Our hypothesis was largely based on previous *B. tectorum* demographic research (Mack and Pyke 1983, 1984; Pierson and Mack 1990a) that found high winter mortality in certain years. We hypothesized that winters at our high-elevation site adjacent to the Sierra Nevada would be much more severe (compared to the previous research below 1,000 m) and would represent a constraint on *B. tectorum* demography. However, a particular winter is only severe if seedlings have emerged to experience it. Similar to alpine and subalpine systems, *B. tectorum* populations may benefit from a continuous snowpack at higher elevation that serves as a barrier to germination when exposure to severe conditions is likely.

Modeled scenarios of anthropogenic climate change in eastern California project increased temperatures, rising snowlines, and reduced winter snowpack during this century (Hayhoe et al. 2004; Leung et al. 2004; Snyder and Sloan 2005; Cayan et al. 2008). With decreased snow cover, the direct consequences of climate change for *B. tectorum* at high elevation may depend on temperature and weather events during increasingly frequent snow-free periods. Whereas snow-free periods amid current climatic conditions may present challenges to *B. tectorum* establishment at high elevations, a future reduction in winter diel temperature range and higher daily minimum temperatures (Leung et al. 2004) could enhance establishment during these periods. Mack and Pyke (1983) observed that the fecundity of *B. tectorum* individuals that survived the winter was consistently and substantially greater than those that germinated in the spring. Thus, if a future climate increases survivorship of recruits during the winter period at high elevation, seed output could be multiplicatively increased, limiting the number of years in which $\lambda < 1$.

It is difficult to predict whether the invasion of *B. tectorum* will advance upwards into the Sierra Nevada under future climate change scenarios. At elevations not much above our study site, factors associated with the Sierran conifer forest will likely become important. Pierson and Mack (1990a) reported that *B. tectorum* seeds experimentally introduced into Washington and Idaho forests (<1,000 m) germinated in the autumn, suffered high wintertime mortality, and often failed to reproduce. They attributed this mainly to altered environmental conditions in the forest including shading, reduced temperatures, and greater snowpack. Our study has demonstrated that while population dynamics are variable, *B. tectorum* is capable of rapid population growth, with 3 years exhibiting annual seedling density increases of 12, 67, and 103%. However, as dispersal into Sierran forests is already likely, the general lack of *B. tectorum* there suggests that mechanisms associated with the forest (e.g., shading, litter, herbivory, soil quality) are currently restricting *B. tectorum* (Pierson and Mack 1990b).

Overall, the results of this study suggest that the response of *B. tectorum* to high elevation snowpack is likely nonlinear and differs from that at lower elevation. In particular, effects on seedling emergence and early survival can have a tremendous impact on population growth. Regardless, *B. tectorum* is capable of both rapid population growth and decline at high elevation. From a management standpoint, a doubling of population size in 1 year is alarming at this elevation. Although, we cannot yet state the frequency of 'boom' and 'bust' years, it is possible that several 'boom' years in a row could result in a rapid increase in *B. tectorum* biomass—and hence fuel load—along the eastern Sierra.

Acknowledgments We thank Holly Alpert, Amy Concilio, and Katie Griffith for fieldwork assistance, and Michael Kennedy, Isabel Schmidt, and Alexandre Sampaio for help with snow fence construction. Daniel Dawson and the entire staff of the U.C. Valentine Eastern Sierra Reserve provided invaluable support and assistance with lodging and logistics. Ingrid M. Parker, Daniel F. Doak, Julie Beckstead, Richard Lucas, Kristina Niovi Jones, and several anonymous reviewers provided helpful comments and suggestions that greatly improved this manuscript. Financial support for this study was provided by the STEPS Institute for Innovation in Environmental Research, the UCSC Environmental Studies Department, the Mildred E. Mathias Graduate Student Research Grant, the Valentine Eastern Sierra Reserve Graduate Student Research Grant, the David Gaines Memorial Award, and a California Native Plant Society (Bristlecone Chapter) Educational Grant. This research was conducted with permission of the United States Forest Service.

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