

Climate influences the demography of three dominant sagebrush steppe plants

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Abstract. Climate change could alter the population growth of dominant species, leading to profound effects on community structure and ecosystem dynamics. Understanding the links between historical variation in climate and population vital rates (survival, growth, recruitment) is one way to predict the impact of future climate change. Using a unique, long-term data set from eastern Idaho, USA, we parameterized integral projection models (IPMs) for *Pseudoroegneria spicata*, *Hesperostipa comata*, and *Artemisia tripartita* to identify the demographic rates and climate variables most important for population growth. We described survival, growth, and recruitment as a function of genet size using mixed-effect regression models that incorporated climate variables. Elasticities for the survival + growth portion of the kernel were larger than the recruitment portion for all three species, with survival + growth accounting for 87–95% of the total elasticity. The genet sizes with the highest elasticity values in each species were very close to the genet size threshold where survival approached 100%. We found strong effects of climate on the population growth rate of two of our three species. In *H. comata*, a 1% decrease in previous year's precipitation would lead to a 0.6% decrease in population growth. In *A. tripartita*, a 1% increase in summer temperature would result in a 1.3% increase in population growth. In both *H. comata* and *A. tripartita*, climate influenced population growth by affecting genet growth more than survival or recruitment. Late-winter snow was the most important climate variable for *P. spicata*, but its effect on population growth was smaller than the climate effects we found in *H. comata* or *A. tripartita*. For all three species, demographic responses lagged climate by at least one year. Our analysis indicates that understanding climate effects on genet growth may be crucial for anticipating future changes in the structure and function of sagebrush steppe vegetation.

Key words: *Artemisia tripartita*; climate change; demography; *Hesperostipa comata*; integral projection models; population dynamics; *Pseudoroegneria spicata*; sagebrush steppe; U.S. Sheep Experiment Station, Idaho, USA.

INTRODUCTION

Forecasting the ecological effects of climate change on plant species is an urgent challenge for ecosystem conservation and management. Impacts of climate change on plant species include altered flowering phenologies (Miller-Rushing et al. 2008), shifts in geographic ranges (Colwell et al. 2008), rapid evolution (Franks and Weis 2008), and demographic effects such as increased mortality (van Mantgem and Stephenson 2007) and altered seed size and quality (Hovenden et al. 2008). Altered population growth of dominants could have profound effects on community structure and ecosystem function.

Population models can be powerful tools for predicting species response to climate change (Pacala and Hurtt

1993, Coulson et al. 2001, Mysterud et al. 2001, Botkin et al. 2007, Adler and HilleRisLambers 2008, Forcada et al. 2008). Understanding how populations have responded to historical climatic variation should aid in predicting population responses to future climate change. The first step is to identify the demographic rates (e.g., survival, growth, or recruitment) with the greatest impact on population dynamics. For long-lived, dominant species, climate effects on survival and growth will likely have a larger impact on population dynamics than recruitment (Franco and Silvertown 2004). The second step is to quantify the influence of climate variables on critical demographic rates. The resulting models could be used to project population growth under a variety of climate scenarios (e.g., Adler and HilleRisLambers 2008).

A long-term data set collected from a sagebrush steppe plant community in the early 20th century offers a unique opportunity to examine the link between climate and demography for several plant species. Range ecologists at the U.S. Sheep Experiment Station

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(USSES) in Idaho, USA, annually mapped the size and location of all plants in 1-m² permanent plots from the 1920s to the 1950s. Using digitized versions of these maps, we can track the fates of individual plants and parameterize population models. Historical climate records from the same location allow us to examine the relationship between climate variables and recruitment, growth, survival, and overall population growth. Because the maps include size (cover) measurements, the data are an ideal application of integral projection models (IPMs) in which growth, survival, and fecundity are continuous functions of individual size (Easterling et al. 2000, Ellner and Rees 2006, 2007).

Global circulation models (Christensen et al. 2007) predict substantial temperature increases at the USSES which could alter plant populations through effects on physiology and soil moisture, a key limiting resource at this semiarid site. Historical climate data do not show significant increases in mean annual temperature at the USSES, but, on average, winter temperatures have increased significantly over the last century (Appendix A). While model predictions for precipitation are uncertain, two historical trends in precipitation are potentially important for plant populations. First, annual precipitation has increased (Appendix A), which could offset decreases in soil moisture caused by future warming. Second, annual snowfall has decreased (Appendix A), indicating that more winter precipitation is falling as rain. Historically, snow comprised 80% of December–March precipitation. A shift from a snow- to rain-dominated winter precipitation regime would alter the timing of soil moisture pulses, potentially hurting species dependent on snowmelt, and increase frost damage (e.g., Inouye 2000).

We used stochastic IPMs to model the population dynamics of two of the most abundant forage grasses in the community, *Pseudoroegneria spicata* (bluebunch wheatgrass) and *Hesperostipa comata* (needle-and-thread grass), as well as the dominant shrub, *Artemisia tripartita* (three-tipped sagebrush). For each species, we parameterize vital rate functions that include climate as predictors of demographic rates. We then use elasticity analysis to determine both the key vital rates (survival, growth, recruitment) and the effects of climate on population growth for these three dominant species.

METHODS

Site and data set descriptions

The USSES is 9.6 km north of Dubois, Idaho, USA (44.2° N, 112.1° W). During the years of this study (1926–1956), annual precipitation averaged 270 ± 64 mm. Average temperatures during the study period were –8°C (January) and 21°C (July). The vegetation is dominated by the drought-tolerant native shrub, *A. tripartita*, which flowers in late summer, and the native, C₃, caespitose perennial bunchgrasses *P. spicata* and *H. comata*, which flower May–June, with seed dispersal mainly in July–August.

In 1923, researchers established four permanent 1-m² quadrats at the USSES. By the early 1930s, 22 quadrats had been added for a total of 26 permanent quadrats. Eighteen quadrats were distributed among four ungrazed exclosures, and eight were distributed in two paddocks grazed at medium intensity spring through fall. All quadrats were located on similar topography and soils. Distances between quadrats within each group (paddock or exclosure) are in the tens and hundreds of meters, while distances between groups are roughly 1–3 km. Using a pantograph (Hill 1920), researchers mapped the basal cover of grasses and the canopy cover of shrubs within each quadrat (see Plate 1). For this study, we used demographic data from 19 year-to-year mapped transitions between 1931 and 1952. Cover of *H. comata* and *A. tripartita* increased over the study period, while cover of *P. spicata* showed a slight decline (Appendix B).

Extracting demographic data from mapped quadrats

We classified genets in the mapped quadrats based on their spatial locations (Lauenroth and Adler 2008). A genet in year $t + 1$ that overlaps in area with a conspecific genet present in year t inherits the identity of the established genet. A genet in year $t + 1$ that is >5 cm from any conspecific genet present in year t is classified as a recruit. We included plants present in the first year by visually comparing the first and second year's maps from each quadrat and assigning each polygon or cluster of polygons a unique genet number. A group of polygons that comprise a genet (i.e., have the same genet number) may fragment and/or coalesce over the study period. The caespitose growth form of our study grasses gave us confidence in these subjective decisions.

Stochastic integral projection model

The integral projection model describes how a continuously size-structured population changes through discrete time (Easterling et al. 2000). The population is represented by a probability density function, $n(x, t)$, which can be considered the proportion of individuals of size x at time t . The stochastic integral projection model for the proportion of individuals of size y at time $t + 1$ is given by

$$n(y, t + 1) = \int_{\Omega} [p(y, x, \theta_t) + f(y, x, \theta_t)]n(x, t) dx + \int_{\Omega} k(y, x, \theta_t)n(x, t) dx \quad (1)$$

where the kernel, $k(y, x, \theta_t)$, describes all possible transitions from size x to size y , including recruitment, and the vital rates are a function of genet size (x) and vector of time-varying climate variables (θ_t). The integral is evaluated over all possible sizes, Ω , set to the interval $(0.9 \times \min[\text{observation}], 1.1 \times \max[\text{observation}])$.

The kernel contains two vital rate functions, a survival–growth function, $p(y, x, \boldsymbol{\theta}_t)$, and a fecundity function, $f(y, x, \boldsymbol{\theta}_t)$. The survival–growth function is

$$p(y, x, \boldsymbol{\theta}_t) = s(x, \boldsymbol{\theta}_t)g(y, x, \boldsymbol{\theta}_t) \quad (2)$$

where $s(x, \boldsymbol{\theta}_t)$ and $g(y, x, \boldsymbol{\theta}_t)$ specify the size- and climate-dependent probabilities of survival and growth, respectively. The fecundity function is

$$f(y, x, \boldsymbol{\theta}_t) = [\mu_f(\boldsymbol{\theta}_t) \times x]f_a(y, x) \quad (3)$$

where $\mu_f(\boldsymbol{\theta}_t)$ is the mean number of recruits produced per square centimeter of genet as a function of climate, $\boldsymbol{\theta}_t$, x is the size of the genet, and $f_a(y, x)$ is a probability distribution of recruits of size y , for genets of size x .

Statistical modeling of vital rate functions

We modeled survival and growth as functions of genet size and used random year effects and fixed effects of climate to incorporate temporal variability.

Survival probability was modeled as a logistic regression:

$$\begin{aligned} \logit[s(x, \boldsymbol{\theta}_t)] = & \beta_{0,t} + \beta_{s,t}x + \beta_Q + \beta_{c,1}\theta_{1,t} \\ & + \cdots + \beta_{c,i}\theta_{i,t} + \varepsilon_t \end{aligned} \quad (4)$$

where x is the log of genet basal area (for the grasses) or canopy area (for the shrub), $\beta_{0,t}$ is a random-year intercept parameter, β_Q is a random effect of quadrat group location, Q , $\beta_{s,t}$ a random-year slope parameter for size, $\boldsymbol{\theta}_t$ is a vector of climate variables for i number of variables, $\beta_{c,i}$ is a fixed slope parameter for the i th effect of climate, and ε_t is the error term.

Mean growth in genet basal (or canopy) area from one year to the next can be described as a linear function:

$$\mu_g(x, \boldsymbol{\theta}_t) = \beta_{0,t} + \beta_{s,t}x + \beta_Q + \beta_{c,1}\theta_{1,t} + \cdots + \beta_{c,i}\theta_{i,t} + \varepsilon_{x,t} \quad (5)$$

where $\mu_g(x, \boldsymbol{\theta}_t)$ is predicted genet size at time $t + 1$, and $\beta_{0,t}$, β_Q , $\beta_{s,t}$, $\beta_{c,i}$ and $\boldsymbol{\theta}_t$ are as described in the previous paragraph. The error term, $\varepsilon_{x,t}$, is a standard normal deviate with a mean of 0 and a variance of $\sigma_{x,t}^2$. The variance term, which describes how variable growth is for each size of genet, was also dependent on size. We modeled the variance $\sigma_{x,t}^2$ as

$$\sigma_{x,t}^2 = a \exp[c \times \mu_g(x, \boldsymbol{\theta}_t)] \quad (6)$$

where $\mu_g(x, \boldsymbol{\theta}_t)$ is the log of genet basal (or canopy) area predicted from Eq. 5, and a and c are constants. We parameterized the growth function using the normal probability density function:

$$g(x, y, \boldsymbol{\theta}_t) = \frac{1}{\sqrt{2\pi\sigma_{x,t}^2}} \exp\left(-\frac{[y - \mu_g(x, \boldsymbol{\theta}_t)]^2}{2\sigma_{x,t}^2}\right) \quad (7)$$

with $\mu_g(x, \boldsymbol{\theta}_t)$ given by Eq. 5 and $\sigma_{x,t}^2$ given by Eq. 6.

In contrast to survival and growth, which we modeled at the individual level, we modeled recruitment at the quadrat level because we could not determine which recruits were produced by which potential parent genets. Recruitment refers to new genets only; clonal expansion of the grasses is modeled in the growth function. We assumed that the number of individuals, y , recruiting at time $t + 1$ in quadrat q follows a negative binomial distribution (the observations appeared overdispersed relative to a Poisson model):

$$y_{q,t+1} \sim \text{NegBin}(\lambda_{q,t+1}, \phi) \quad (8)$$

where λ is the mean intensity and ϕ is the size parameter. In turn, λ depends on the composition of the quadrat in the previous year:

$$\lambda_{q,t+1} = C'_{q,t} e^{(\beta_{0,t} + \beta_Q + \beta_{c,1}\theta_{1,t} + \cdots + \beta_{c,i}\theta_{i,t})}. \quad (9)$$

$C'_{q,t}$ is the “effective cover” (in 100 cm²) of the focal species in quadrat q at time t , and $\beta_{0,t}$, β_Q , $\beta_{s,t}$, $\beta_{c,i}$, and $\boldsymbol{\theta}_t$ are as described after Eq. 4. The value of the exponent term gives $\mu_f(\boldsymbol{\theta}_t)$ of Eq. 3. By estimating each species’ effective cover in a quadrat, we recognized that plants outside the mapped quadrat may contribute recruits to the focal quadrat, and vice versa. We estimated effective cover as a mixture of the observed cover, C , in the focal quadrat, q , and the mean cover across the group, Q , in which the quadrat was located:

$$C'_{q,t} = pC_{q,t} + (1 - p)\bar{C}_{Q,t} \quad (10)$$

where p is the mixing fraction between 0 and 1. Our model assumes that recruitment increases linearly with genet area and that the size distribution of recruits is not influenced by maternal genet area (Weiner et al. 1997).

We combined the vital rate functions to create the kernel (Eq. 1) and projected the model using a “kernel selection” approach. We parameterized a kernel for each of the 19 years in our study and then projected the population forward in time from an arbitrary initial stage distribution. At each time step we randomly selected a kernel representing one of the 19 observed years along with the observed climate variables from the same year. By using the observed climate data for each year, rather than simulating it from observed distributions, we automatically incorporated covariance among climate variables. Our simulations assume that kernels and climate variables at time $t + 1$ are independent of time t , consistent with the absence of autocorrelation in the climate record. We evaluated the IPM at each time step using the midpoint rule approximation and matrix multiplication, using a range of mesh sizes to ensure accuracy of our estimates of population dynamics (Ellner and Rees 2006).

Incorporating climate in vital rate functions

The full list of climate predictors we examined included annual precipitation (a July–June water year), previous year’s annual precipitation, seasonal precipita-

tion, monthly precipitation, annual snowfall, seasonal snowfall, monthly snowfall, average yearly temperature, average seasonal temperature, and average monthly temperature. We found that February plus March snowfall was a superior predictor to February or March snowfall alone, so we also included February plus March snowfall in our analyses. All climate variables were measured at the USSSES, except for February and March snowfall in 1951, which was measured at a station in nearby Dubois, Idaho. The correlation between the long-term snow records at the two stations was high ($\rho = 0.89$).

Our first step in selecting climate variables to include in the vital rate functions was to create a short list of the potentially important climate variables for each vital rate within each species. We began by parameterizing the vital rate functions using only random effects of year. Next, we examined the correlations between the random year effects and the full list of climate variables. Any climate variable that was correlated with a vital rate parameter with $P < 0.1$ was included on the short list of climate variables. In addition, we added the temperature or precipitation variable measured at the same time as short-listed variables, even if the correlation did not meet our P value threshold.

After building the short list of climate variables, we conducted model selection for the survival and growth functions in a fixed-effects framework. We fit a series of candidate models that incorporated fixed quadrat group effects and all combinations of the short-listed climate variables as main effects for each vital rate. We did not include explanatory variables that were highly correlated within the same model; for example, winter precipitation and February plus March snow were not included in the same model because they were highly correlated. We considered interactions only between temperature and precipitation variables from the same time period (i.e., spring precipitation \times spring temperature). We used Bayes Information Criterion (BIC) to compare our candidate models (Schwarz 1978). Finally, we refit the model with the smallest BIC value as a mixed effects model with year and quadrat group as random effects and the selected climate variables as fixed effects. We used `lm` and `glm` functions for the fixed-effects models, `lmer` and `glmer` functions for the mixed models, and `nls` for the variance of the growth function in R 2.7 (R Development Core Team 2007). We calculated a measure of the proportional reduction in deviance when climate parameters were included in the model as

$$D = 1 - \left(\frac{\text{dev}_1}{\text{dev}_2} \right) \quad (11)$$

where dev_1 is the deviance of the fixed-effects model that included genet area, group parameters, and climate parameters and dev_2 is the deviance of the fixed-effects model that included only genet area and group parameters (Zheng 2000). Thus, D is a measure of the

amount of deviance explained by the climate parameters.

We fit the parameters of the recruitment model using a hierarchical Bayesian approach implemented in WinBUGS 1.4 (Lunn et al. 2000). We used diffuse priors (relative to the posterior), ran the Markov Chain Monte Carlo simulation for 10 000 iterations after a 10 000 iteration burn in period, and checked for convergence of two parameter chains using Brooks and Gelman's (1998) potential scale reduction factor (all values of \hat{r} were < 1.1). We fit a final, mixed-effects model for each species that included all the climate variables that were significantly correlated with the random year effects on recruitment. We did not conduct additional model selection because of the complexities of model selection when using a hierarchical Bayesian approach and because the initial models included only one or two climate variables for each species.

Elasticity analysis of vital rate functions and climate parameters

We calculated the stochastic population growth rate, λ_s , as

$$\lambda_s = \exp\left(\frac{1}{T} \sum_{t=0}^{T-1} r_t\right) \quad (12)$$

where

$$r_t = \log\left(\frac{\|n_{t+1}\|_1}{\|n_t\|_1}\right) \quad (13)$$

and $T = 50\,000$. Elasticities measure the effect of proportional changes in the kernel on λ_s (Easterling et al. 2000, Ellner and Rees 2006). We calculated the stochastic elasticity to survival + growth and recruitment separately following the methods of Rees and Ellner (2009). We calculated the elasticity of climate variables by perturbing the mean of one climate variable and calculating the proportional change in λ_s (e.g., see Koons et al. 2007). For example, to perturb winter precipitation, we added 0.1% of the mean winter precipitation to the winter precipitation observed in each year. This altered the mean of the parameter, but not the variance (Tuljapurkar et al. 2003).

RESULTS

Statistical models for survival

For all species, survival increased with genet size. Survival of genets $> 7\text{ cm}^2$ approached 100% for both grass species (Appendix C). Shrubs $> 20\text{ cm}^2$ had high survival ($> 80\%$), with survival approaching 100% beyond 400 cm^2 (Appendix C).

For all three species, lagged effects of climate seemed to have the greatest effect on survival. For the bunchgrasses, climate in the winter previous to the initial genet measurement influenced survival. For example, for survival of a genet from June 1931 to June

TABLE 1. Functions and mean parameter values for the survival and mean growth functions of three dominant sagebrush steppe species at the U.S. Sheep Experiment Station, eastern Idaho, USA.

Species and vital rate	Candidate climate variables	Final model	Mean (variance) parameter estimates	D
<i>Pseudoroegneria spicata</i>				
Survival ($n = 6913$)	winter ppt (1), mean winter temp (1), Feb + Mar snow (1), Feb + Mar temp (1), Feb + Mar ppt (1)	$\text{logit}[s(x, \theta_{T_{\text{win}1,t}}, \theta_{\text{snow}_{\text{FM}1,t}})]$ $= \beta_{T_{\text{win}1}} \theta_{T_{\text{win}1,t}} + \beta_{\text{snow}_{\text{FM}1}} \theta_{\text{snow}_{\text{FM}1,t}}$ $+ \beta_{T_{\text{win}1} \times \text{snow}_{\text{FM}1}} \theta_{T_{\text{win}1,t}} \theta_{\text{snow}_{\text{FM}1,t}}$ $+ \varepsilon_t$	$\beta_{0,t} = 1.18$ (0.43), $\beta_{s,t} = 1.79$ (0.13), $\beta_{\text{snow}_{\text{FM}1}} = 0.01$ (0.02), $\beta_{T_{\text{win}1}} = 0.22$ (0.07), $\beta_{T_{\text{win}1} \times \text{snow}_{\text{FM}1}} = -0.005$ (0.003)	0.11
Growth ($n = 4500$)	summer ppt (2), fall ppt (2), mean fall temp (2), mean summer temp (2)	$\mu_g(x, \theta_{T_{\text{fall}2,t}}, \theta_{\text{ppt}_{\text{sum}2,t}})$ $= \beta_{T_{\text{fall}2}} \theta_{T_{\text{fall}2,t}} + \beta_{\text{ppt}_{\text{sum}2}} \theta_{\text{ppt}_{\text{sum}2,t}}$ $+ \varepsilon_{x,t}$	$\beta_{0,t} = 0.30$ (0.13), $\beta_{s,t} = 0.89$ (0.02), $\beta_{T_{\text{fall}2}} = -0.10$ (0.04), $\beta_{\text{ppt}_{\text{sum}2}} = -0.001$ (0.001)	0.04
<i>Hesperostipa comata</i>				
Survival ($n = 3706$)	winter ppt (1), mean winter temp (1), Feb + Mar snow (1), Feb + Mar temp (1), Feb + Mar ppt (1)	$\text{logit}[s(x, \theta_{T_{\text{win}1,t}}, \theta_{\text{snow}_{\text{FM}1,t}})]$ $= \beta_{T_{\text{win}1}} \theta_{T_{\text{win}1,t}} + \beta_{\text{snow}_{\text{FM}1}} \theta_{\text{snow}_{\text{FM}1,t}}$ $+ \beta_{T_{\text{win}1} \times \text{snow}_{\text{FM}1}} \theta_{T_{\text{win}1,t}} \theta_{\text{snow}_{\text{FM}1,t}}$ $+ \varepsilon_t$	$\beta_{0,t} = 1.64$ (0.33), $\beta_{s,t} = 1.52$ (0.12), $\beta_{\text{snow}_{\text{FM}1}} = 0.02$ (0.009), $\beta_{T_{\text{win}1}} = 0.24$ (0.05), $\beta_{T_{\text{win}1} \times \text{snow}_{\text{FM}1}} = -0.003$ (0.001)	0.07
Growth ($n = 2552$)	summer ppt (2), spring ppt (1 and 2), mean summer temp (2), mean spring temp (1 and 2), previous year's ppt (-1)	$\mu_g(x, \theta_{\text{ppt}_{-1,t}}, \theta_{T_{\text{spr}2,t}}, \theta_{\text{ppt}_{\text{spr}2,t}})$ $= \beta_{\text{ppt}_{-1}} \theta_{\text{ppt}_{-1,t}} + \beta_{T_{\text{spr}2}} \theta_{T_{\text{spr}2,t}}$ $+ \beta_{\text{ppt}_{\text{spr}2}} \theta_{\text{ppt}_{\text{spr}2,t}}$ $+ \beta_{T_{\text{spr}2} \times \text{ppt}_{\text{spr}2}} \theta_{T_{\text{spr}2,t}} \theta_{\text{ppt}_{\text{spr}2,t}} + \varepsilon_{x,t}$	$\beta_{0,t} = 5.78$ (3.03), $\beta_{s,t} = 0.87$ (0.03), $\beta_{\text{ppt}_{-1}} = 0.004$ (0.0008), $\beta_{T_{\text{spr}2}} = -0.58$ (0.29), $\beta_{\text{ppt}_{\text{spr}2}} = -0.07$ (0.04), $\beta_{T_{\text{spr}2} \times \text{ppt}_{\text{spr}2}} = 0.006$ (0.003)	0.10
<i>Artemisia tripartita</i>				
Survival ($n = 1732$)	previous year's ppt (-1)	$\text{logit}[s(x, \theta_{\text{ppt}_{-1,t}})]$ $= \beta_{\text{ppt}_{-1}} \theta_{\text{ppt}_{-1,t}}$ $+ \beta_{\text{ppt}_{-1} \times x} \theta_{\text{ppt}_{-1,t}} x + \varepsilon_t$	$\beta_{0,t} = -1.97$ (1.04), $\beta_{s,t} = 1.77$ (0.29), $\beta_{\text{ppt}_{-1}} = 0.005$ (0.004), $\beta_{\text{ppt}_{-1} \times x} = -0.004$ (0.001)	0.05
Growth ($n = 1024$)	summer ppt (1), winter ppt (2), mean summer temp (1), mean winter temp (2)	$\mu_g(x, \theta_{\text{ppt}_{\text{win}2,t}}, \theta_{T_{\text{sum}1,t}}, \theta_{\text{ppt}_{\text{sum}1,t}})$ $= \beta_{\text{ppt}_{\text{win}2}} \theta_{\text{ppt}_{\text{win}2,t}} + \beta_{T_{\text{sum}1}} \theta_{T_{\text{sum}1,t}}$ $+ \beta_{\text{ppt}_{\text{sum}1}} \theta_{\text{ppt}_{\text{sum}1,t}}$ $+ \beta_{T_{\text{sum}1} \times \text{ppt}_{\text{sum}1}} \theta_{T_{\text{sum}1,t}} \theta_{\text{ppt}_{\text{sum}1,t}}$ $+ \varepsilon_{x,t}$	$\beta_{0,t} = -10.91$ (2.68), $\beta_{s,t} = 0.87$ (0.06), $\beta_{\text{ppt}_{\text{win}2}} = 0.008$ (0.002), $\beta_{T_{\text{sum}1}} = 0.59$ (0.14), $\beta_{\text{ppt}_{\text{sum}1}} = 0.10$ (0.03), $\beta_{T_{\text{sum}1} \times \text{ppt}_{\text{sum}1}} = -0.006$ (0.001)	0.08

Notes: The final model for each vital rate included intercept, slope, and quadrat random effects ($\beta_{0,t} + \beta_{s,t}x + \beta_Q$) plus the fixed effects of climate variables (temp, temperature; ppt, precipitation). For simplicity, only the final climate variables are listed in the final model, though the mean parameter estimates and their variances (in parentheses) are given for all the parameters in the final model. Note that by construction, the mean quadrat random effect is 0 in all models. D is a measure of the proportional reduction in deviance when climate parameters were included in the fixed-effects model as compared to a model with only group and genet area effects (see *Methods* for more details). Subscript climate abbreviations are: T , mean temperature; ppt, precipitation; FM, February + March; sum, summer; spr, spring; and win, winter. Numbers following the candidate climate variables refer to the year in which they are measured relative to the vital rate. For example, for survival or growth measured from June 1931 to June 1932, (1) refers to measurement before June 1931, (2) refers to measurement after June 1931, and (-1) refers to measurement in 1930. For parameter estimates for all of the vital rate functions we used in the IPM (integral projection models) and goodness-of-fit measures; see Appendix D: Tables D1 and D2.

1932, higher snowfall and warmer temperatures in the winter of 1931 increased survival in both bunchgrasses (Table 1). For *A. tripartita*, previous year's precipitation influenced survival (Table 1). Analysis of deviance indicated that all models were a good fit for the data (Appendix D, Table 1). The proportional reduction in deviance when climate variables were added to the models ranged from 0.05 to 0.11 (Table 1).

Statistical models for growth

The average slope of the growth function was similar in all three species and was below 1, indicating that

retrogression (reversion to smaller size) was common as size increased (Table 1). The variance of growth decreased with size in all three species (Appendix D: Table D2).

In contrast to the lagged effects on survival, the majority of climate variables that emerged as potentially important for growth occurred between the two measurement points of each year-to-year transition (Table 1). While we identified several climate variables as potentially important for growth in all three species, the final models for each species were unique (Table 1). For *P. spicata*, a drier summer and cooler fall between

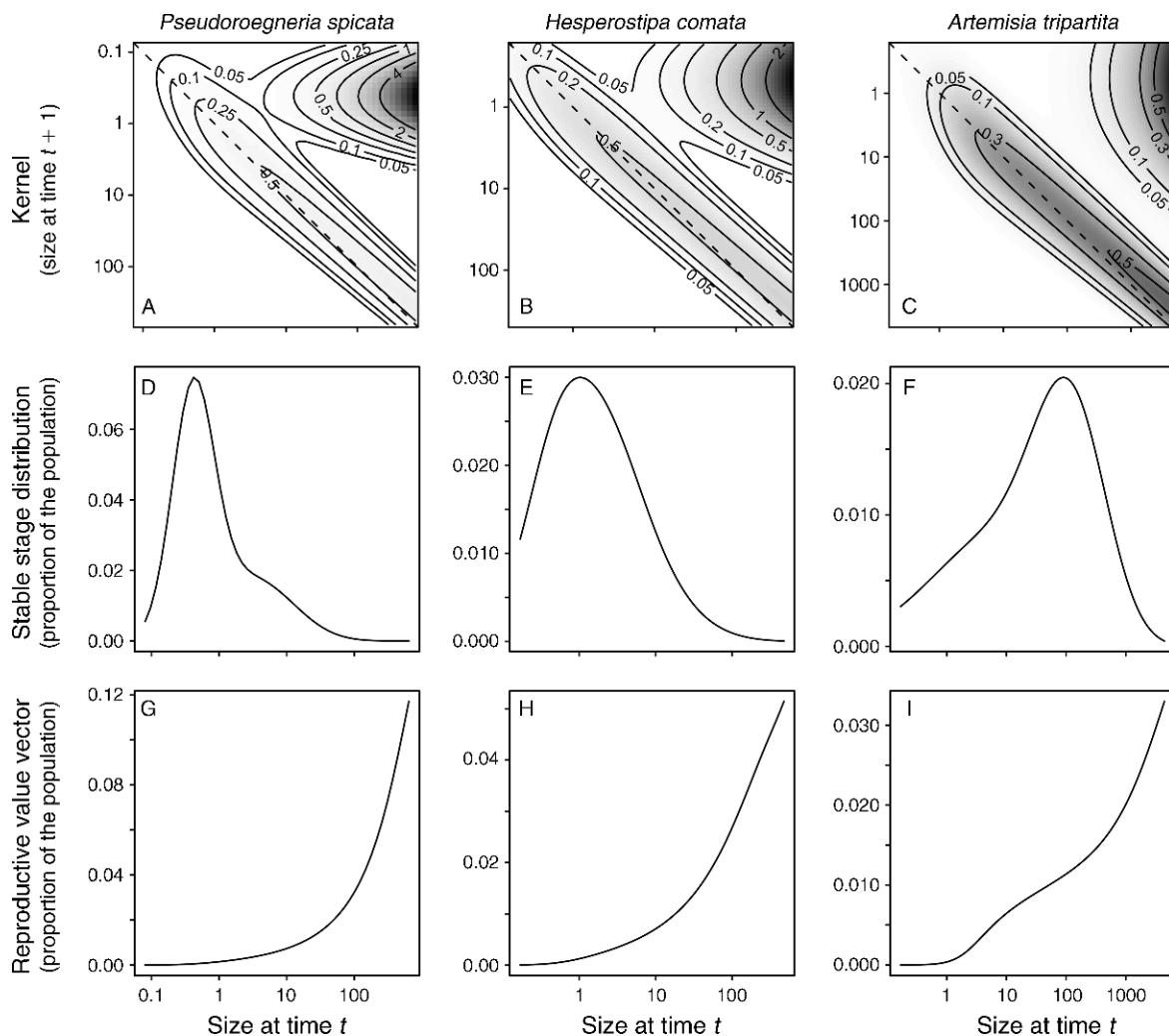


FIG. 1. Demographic measures for three dominant sagebrush steppe species at the U.S. Sheep Experiment Station, eastern Idaho, USA. (A–C) Kernels parameterized with mean parameter values for *Pseudoroegneria spicata* (bluebunch wheatgrass), *Hesperostipa comata* (needle-and-thread grass), and *Artemisia tripartita* (three-tipped sagebrush), respectively. (D–F) Stable stage distributions for the three species, respectively. (G–I) Reproductive value vectors for the three species, respectively. Size was measured as basal cover in cm² for the grasses (*P. spicata* and *H. comata*) and as canopy cover in cm² for the shrub (*A. tripartita*).

measurement points increased growth. In *H. comata*, previous year's precipitation positively affected growth, while spring precipitation and temperature between measurements negatively affected growth. The final shrub model included positive effects of summer climate prior to the first genet measurement and winter precipitation between measurements (Table 1). Values of R^2 for all fixed-effects growth regressions ranged from 0.75 to 0.83 (Appendix D: Table D1). The proportional reduction in deviance when climate variables were added to the models ranged from 0.04 to 0.10 (Table 1).

Statistical models for recruitment

Per capita recruitment was lowest in *A. tripartita* and highest in *H. comata* (Appendix D). Precipitation in April increased recruitment in all species, with higher

February + March snowfall increasing recruitment in *A. tripartita*.

Population structure and growth

All three species had similar shapes to their kernels with nonzero values along the diagonal and in the top right quadrant (Fig. 1A–C). The diagonal ridge of the kernel represents survival and stasis, the off-diagonal values represent survival plus growth (below) or retrogression (above), and the values at the top indicate recruitment.

The stable stage distributions for the grasses contained the largest proportion of the individuals as small genets, with medium-sized genets comprising the largest proportion in *A. tripartita* (Fig. 1D–F). The reproductive value vector for all three species was increasing (Fig.

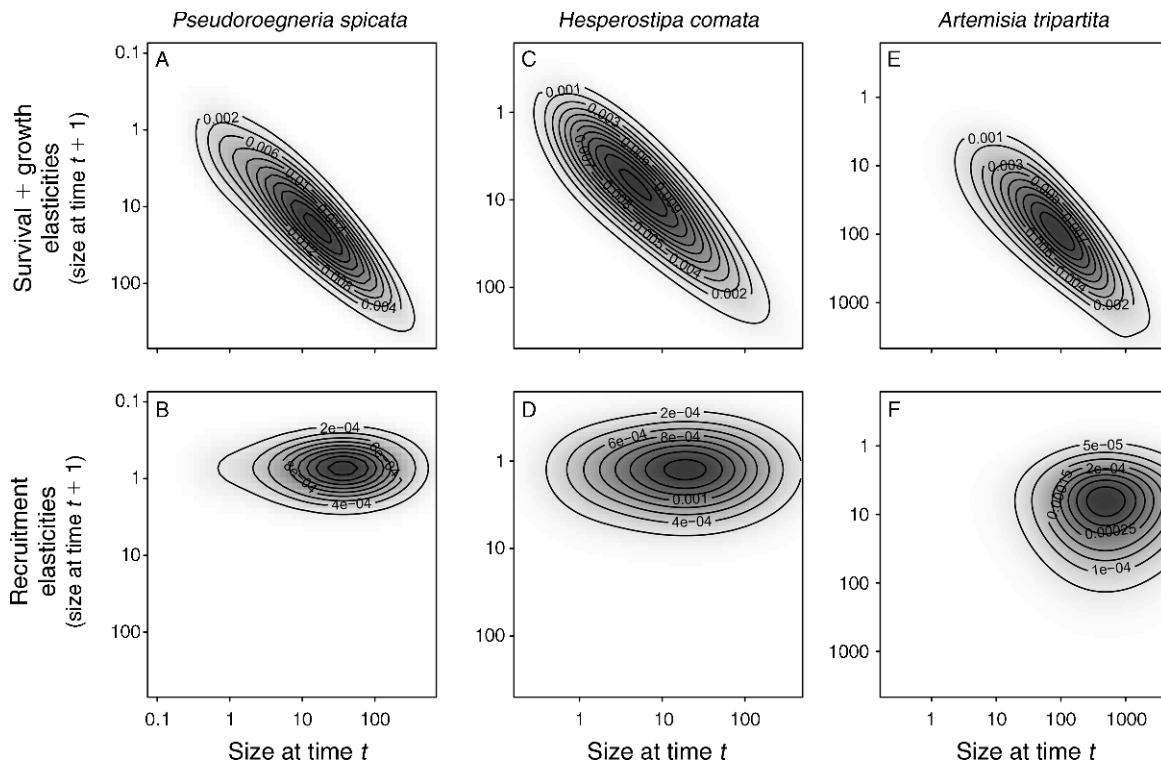


FIG. 2. Elasticity kernels for *P. spicata*, *H. comata*, and *A. tripartita*. (A, C, E) Survival + growth elasticities for the three species. (B, D, F) Recruitment elasticities for the three species. Size was measured as in Fig. 1.

1G–I). The λ_s for *P. spicata* was 1.03, for *H. comata* it was 1.20, and for *A. tripartita* it was 1.02.

Elasticity of vital rates

Perturbations of survival and growth have larger prospective effects on λ_s than perturbations of recruitment for all three species. For *P. spicata*, the survival + growth kernel accounted for 94% of the elasticity. In this species, elasticities were the highest for survival and growth of genets sized 20 cm² (Fig. 2). In *H. comata*, the survival + growth kernel accounted for 87% of the elasticity. Genets near 7 cm² had the highest elasticity values in *H. comata*. In *A. tripartita*, the survival + growth kernel accounted for 95% of the elasticity. Genets near size 150 cm² had the highest elasticities. The genet sizes with the highest elasticity values in each species were very close to the genet size threshold where survival approached 100%.

To compare the elasticities associated with transitions to larger vs. smaller sizes and recruitment, we summed the elasticities to each of these components within a size (Fig. 3). The elasticities for transitions to larger sizes include the growth + survival elasticities while the elasticities for transitions to smaller sizes include the retrogression + survival elasticities. In *P. spicata*, transitions to larger sizes were more important than transitions to smaller sizes for small plants, while transitions to smaller size became more important in

genets greater than 100 cm² (Fig. 3A). The patterns for *H. comata* were similar to those for *P. spicata* with transitions to smaller size becoming more important near 90 cm² (Fig. 3B). However, recruitment became the most important vital rate in plants larger than 150 cm². In *A. tripartita*, transitions to smaller size became more important around 500 cm² (Fig. 3C).

Elasticity of climate variables

All of the climate variables with the largest elasticities operated on population dynamics through the survival or growth functions. For *P. spicata*, the climate variable with the largest elasticity was February + March snowfall, indicating that increases in snowfall would increase λ_s (Fig. 4A). In *H. comata*, previous year's precipitation had the largest elasticity, with increases in precipitation increasing λ_s (Fig. 4B). In *A. tripartita*, mean summer temperatures had the largest elasticity, with increases in summer temperatures increasing λ_s (Fig. 4C). Increases in five climate variables would decrease λ_s : winter and fall temperatures and summer precipitation in *P. spicata* and spring precipitation and temperature in *H. comata*.

DISCUSSION

Population structure

Our models showed that survival and growth are the important demographic transitions affecting population

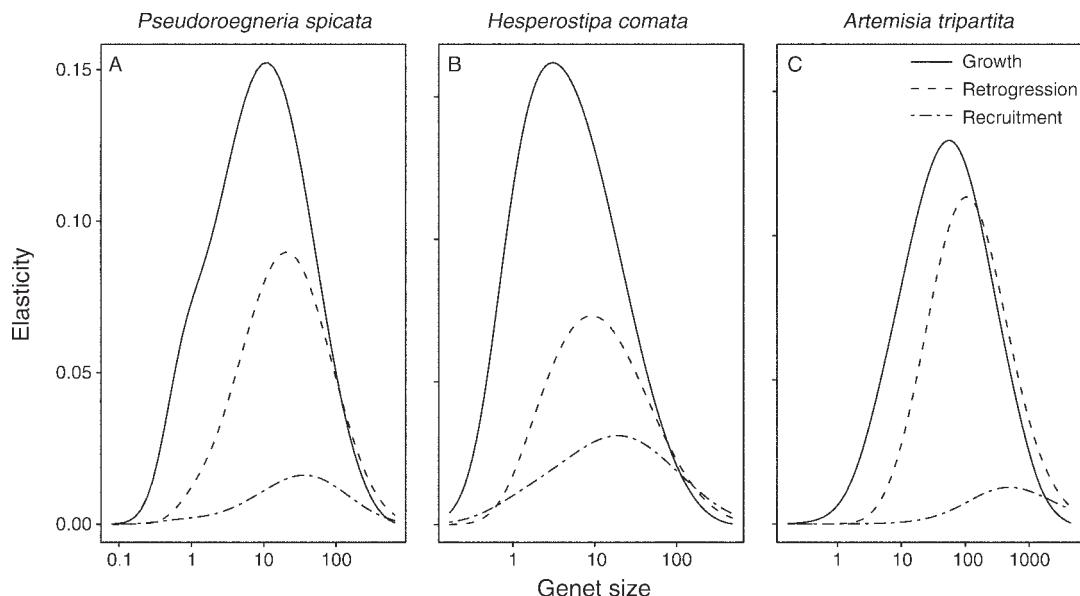


FIG. 3. Elasticities for the transitions to larger (growth) and smaller (retrogression) sizes and recruitment in relation to genet size. Genet size was measured as in Fig. 1.

growth for all three of our study species, which is consistent with other studies of long-lived plants (Silvertown et al. 1993, Franco and Silvertown 2004). The genet sizes with the highest elasticity values in each species were very close to the genet size threshold where survival approached 100%. For example, in *H. comata*, the highest elasticities occurred at the survival + growth transitions of genets ~ 7 cm², meaning that changes in the survival + growth of genets at this size would have a large impact on λ_s . Seven cm² is the size at which genet survival approaches 100%. We see the same pattern of elasticity peaking where survival reaches 100% in both *P. spicata* and *A. tripartita*.

Retrogression is an important demographic process in clonal plants, such as *P. spicata* and *H. comata* (Silvertown et al. 1993, Vega and Montana 2004). Vega and Montana (2004) showed that the importance of retrogression, stasis, and growth in a clonal perennial grass varies from year to year, with drier years having higher elasticities to retrogression. Though we were not able to completely separate the elasticities to growth, retrogression, and survival, our data show that once plants reached a size threshold, transitions to smaller size became the most important demographic process. The high survival probabilities for medium- and large-sized bunchgrass genets indicate that transitions to smaller size occur before mortality in many large individuals.

In semiarid systems, the cover of clonal forage grasses can be highly variable from year to year (Craddock and Forsling 1938, Lauenroth and Sala 1992, Oesterheld et al. 2001). Because the importance of growth, survival, and recruitment vary with genet size, the size distribution of the populations may help to inform management

strategies. For example, grazing can alter the size structure of bunchgrass populations (Pfeiffer and Hartnett 1995), potentially creating feedbacks between the size distribution of genets, the population growth rates, and the availability of forage. Understanding the interactions among grazing, size structure, and climate will be important for forecasting as well as managing for the effects of climate change.

Climate effects on demography and population growth

Though the proportional reductions in deviance were not large when climate variables were added to the vital rate models, the elasticity analysis revealed strong effects of climate on λ_s of two of our three species. For example, a 1% decrease in previous year's precipitation would result in a 0.6% decrease in λ_s of *H. comata*. A 1% increase in summer temperatures would result in a 1.3% increase in λ_s for *A. tripartita*. Despite being the most abundant grass species in the historical data set, the climate effects we found for *P. spicata* were among the smallest we measured. For example, a 1% increase in February plus March snowfall would result in only a 0.06% increase in λ_s .

The climate variables with the largest elasticities (previous year's precipitation and summer temperature) affected λ_s by altering individual genet growth. Dahlgren and Ehrlen (2009) also found environmental effects on growth to have the largest influence on the demography of a perennial herb in a similar elasticity analysis of an IPM. However, the elasticities we report for climate effects are an order of magnitude larger than those reported for soil phosphorus by Dahlgren and Ehrlen (2009). Our elasticity analyses of the vital rates and the climate variables consistently illustrate that

understanding genet growth responses to climate will be crucial for anticipating the effect of climate change on sagebrush steppe plant populations.

While the elasticities for the climate variables influencing survival were lower than those influencing growth, we found that the same climate variables influenced survival in both *P. spicata* and *H. comata*: winter temperature and February plus March snow. Though snow is highly correlated to winter precipitation, survival models that included the amount of snow in February and March were superior to those that considered total winter precipitation or total winter snowfall. Warmer temperatures in the future will increase the importance of winter rain relative to snow (Knowles et al. 2006). Previous studies have shown that decreases in snowpack and duration can affect plants through two mechanisms (Bell and Bliss 1979, Dunne et al. 2003, Wahren et al. 2005, Wipf et al. 2006, Inouye 2008). First, the loss of insulating snowpack may lower soil temperatures, increasing the potential for plant damage and death due to frost (Inouye 2000, Bannister et al. 2005). Second, altered snowfall may change the timing of soil water availability, affecting plant growth and seedling establishment (Blumenthal et al. 2008). Our results emphasize that the timing and type of precipitation may impact the survival of these bunchgrasses.

Though the largest climate elasticities were different for each species (February + March snow in *P. spicata*, previous year's precipitation in *H. comata*, and summer temperatures in *A. tripartita*) the demographic response consistently lagged behind the observed climate variable. For example, snowfall in February and March of 1935 influenced survival in *P. spicata* from June 1935 through to June 1936, a one-year lag in snow effects on survival. We observed a similar lag in the effects of annual precipitation on growth for *H. comata* and summer temperatures on growth in *A. tripartita*. One potential explanation for the lagged response in survival may involve the bud bank (Dalglish and Hartnett 2006, Dalglish et al. 2008). Decreased snow cover may deplete the bud bank due to frost damage to the buds themselves, or because more buds are required to replace frost damaged tillers at the start of the season. Such losses of meristems may decrease the chance of genet survival into the next year. The lagged response we observed in survival and growth could also reflect resource availability: The lack of soil water though decreased snowmelt pulse, decreased annual precipitation, or increased summer temperatures could all reduce a plant's stored resources, and decrease its chance of survival or potential for growth. Distinguishing between these possible mechanisms will require experimental and physiological approaches.

Conclusions

Our work illustrates the potential importance of links between climate variability, the size structure of sage-

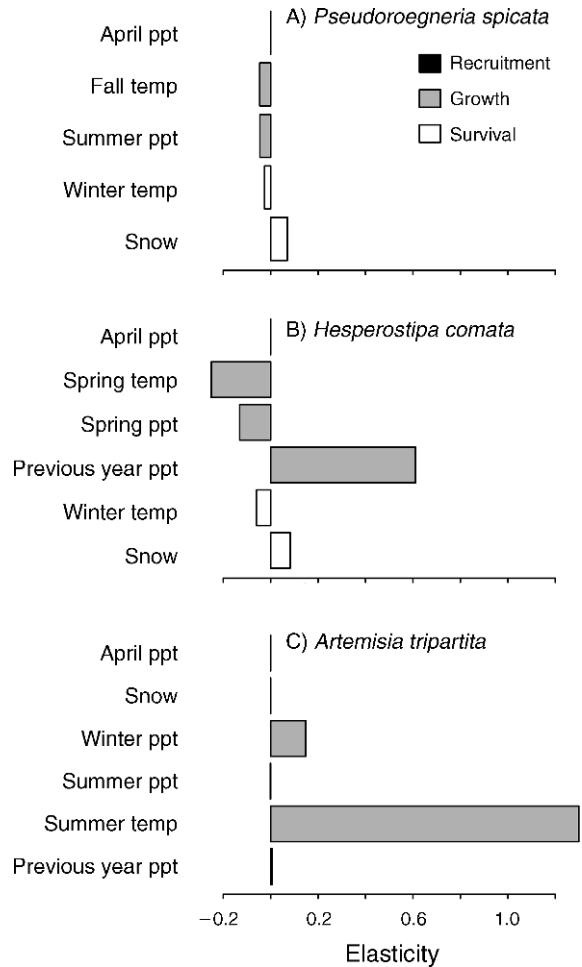


FIG. 4. Elasticities to climate variables within the vital rate functions for the three species. Abbreviations are: ppt, precipitation; temp, temperature. Small bars for April ppt in all three species and for snow in *A. tripartita* are elasticities of recruitment.

brush steppe plant populations, and their population dynamics. Future work should focus on understanding the interactions between grazing management (which can affect population size structure), and projected changes in climate variables, which may affect populations though changes in genet growth.

Our analysis emphasizes the potential impact of precipitation amount, timing and type, along with temperature, on plant demography. February and March snow, annual precipitation amount, and summer temperature emerged as important climate variables for sagebrush steppe dominants. Experimental manipulations will be needed to test our hypotheses about the importance of climate variables to demography. Fully evaluating the influence of climate variability on the population dynamics of these species will require several years of observations due to the lagged effects of climate on vital rates.



PLATE 1. Students mapping vegetation using a pantograph at the U.S. Sheep Experiment Station, Idaho, USA. Photo credit: P. B. Adler.

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APPENDIX A

Historical trends in winter temperature, annual precipitation, and annual snowfall at the USSSES (*Ecological Archives* E092-007-A1).

APPENDIX B

Abundance of *Pseudoroegneria spicata*, *Hesperostipa comata*, and *Artemisia tripartita* observed in the mapped quadrats over the study period (*Ecological Archives* E092-007-A2).

APPENDIX C

Graphs of mean vital rate functions for *Pseudoroegneria spicata*, *Hesperostipa comata*, and *Artemisia tripartita* (*Ecological Archives* E092-007-A3).

APPENDIX D

Statistical models describing the demography of *Pseudoroegneria spicata*, *Hesperostipa comata*, and *Artemisia tripartita* (*Ecological Archives* E092-007-A4).