Can life-history traits predict the response of forb populations to changes in climate variability?

Harmony J. Dalgleish*, David N. Koons and Peter B. Adler

Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main Hill, Logan, UT 84322, USA

Summary

1. Climate change will cause changes in average temperature and precipitation as well as increased fluctuations around the mean, yet few studies have considered the impacts of altered climate variability on plant populations. We tested whether life-history traits (expected life span, generation time and seed size) can predict plant responses to increased environmental variability across similar plant species sharing the same habitat.

2. We combined long-term demographic data on 10 prairie forb species with stochastic demography techniques to estimate the effects of potential changes in matrix element means and variances on the long-term stochastic population growth rate.

3. For all 10 species, recruitment had higher contribution and elasticity values than survival, meaning that climate change is more likely to influence population growth through effects on recruitment than on survival for these relatively short-lived forbs. Species with longer generation times had lower elasticities to increases in matrix element variability.

4. *Synthesis.* Our analysis of a unique, long-term data set suggests that longer-lived plant species will be less vulnerable to the effects of future increases in climate variability. While this relationship was previously reported for diverse taxa from many locations, our results show that it also applies within a guild of short-lived species from a single community. The generality of the pattern demonstrates the potential for using life-history traits to make predictions about which species may be the most vulnerable to climate change.

Key-words: climate change, elasticity, life history, matrix models, mixed-grass prairie, short-lived perennial, stochastic demography

Introduction

Anthropogenic climate change will cause changes in average temperature and precipitation as well as increased fluctuations around the mean (Salinger 2005; IPCC 2007). Much ecological research has focused on how species might respond to changes in mean climate variables (e.g. Parmesan & Yohe 2003; Pounds *et al.* 2006), but few studies have considered the impacts of altered climate variability (Knapp & Smith 2001; Knapp *et al.* 2002; Adler *et al.* 2006). At a demographic level, increased climate variability may increase the variability of survival and recruitment (i.e. vital rates) for many species (Boyce, Haridas & Lee 2006). Both theoretical and empirical studies indicate that increased variability of vital rates decreases population growth rate (Lewontin & Cohen 1969; but see Doak *et al.* 2005; Drake 2005), implying that increased climate variability could have important consequences for population persis-

tence, species coexistence and conservation (Morris *et al.* 2006).

Life-history theory may help predict which species will be most vulnerable to increased climate variability. For example, longer life span, longer generation times and polycarpy are favoured in variable environments (Schaffer 1974). Seed traits such as large seed size (Rees 1994) or low germination fraction (Venable 2007) may also be favourable in variable environments. Comparative analyses across plant species can test which life-history traits indicate sensitivity to increased climate variability.

Stochastic demographers have recently derived new elasticities that are ideal for testing the relationship between life-history traits and the potential effects of changes in vital rate or matrix element variability (Tuljapurkar, Horvitz & Pascarella 2003; Haridas & Tuljapurkar 2005). These elasticities measure the proportional change in the long-term stochastic population growth rate, λ_s, which results from a proportional change in either the mean ($E^{S\mu}$) or the variance ($E^{S\sigma}$) of a given vital rate

*Correspondence author. E-mail: h.dalgleish@usu.edu

or matrix element. Because traditional elasticities (E^s) perturb both the mean and the variance simultaneously [while keeping the coefficient of variation (CV) of the vital rates constant], computing both the $E^{s\mu}$ and $E^{s\sigma}$ allows one to separate the effects on λ_s of perturbing the mean from the effects of perturbing the variability.

Despite a recognized need to compare the impact of environmental variability on population dynamics across species (Boyce, Haridas & Lee 2006), only a few recent studies exist (Forcada, Trathan & Murphy 2008; Morris *et al.* 2008). Morris *et al.* (2008) analysed multi-year demographic data for 36 animal and plant species from around the globe and found that short-lived species were more sensitive to increased vital rate variability than long-lived species. If this same pattern applies to co-occurring plant species, then it may be possible to use life-history theory to predict the effect of climate change on community structure.

A long-term data set collected in mixed-grass prairie near Hays, KS (USA), in the early 20th century offers an unparalleled opportunity to explore interactions between life history and the demographic effects of temporal variability on many co-occurring plant species. The data set contains information on the key demographic rates of survival and recruitment and is long enough (*c.* 30 years) to estimate historical variation in those rates. In addition, the data set encompasses a large-enough number of species to permit synthesis based upon plant life-history traits.

Using stochastic demography techniques, we conducted a comparative analysis of 10 prairie forbs to address two questions. Our first question concerns the basic demography of these ten species: Is survival or recruitment most influential for population growth? We hypothesized that the relative importance of survival and recruitment to population growth should be related to life history: species with shorter generation times and life span should be more sensitive to changes in recruitment than to changes in survival (Heppell, Caswell & Crowder 2000; Sæther & Bakke 2000; Oli & Dobson 2003; Franco & Silvertown 2004; Gaillard *et al.* 2005; Garcia, Pico & Ehrlen 2008). Second, how do life-history traits influence the response of populations to increased variability in survival and recruit-

ment that will likely be caused by increases in climate variability? We hypothesized that species with longer generation times, longer life span and larger seed size will be less elastic to changes in variability.

Materials and methods

STUDY SITE AND DATA SET DESCRIPTION

The study site is located two miles west of Hays, Kansas, USA (38.8° N, 99.3° W), in native southern mixed-grass prairie. During 1938–1972 (the years of data collection for this study), annual precipitation ranged from a low of 267 mm in 1957 to a high of 1101 mm in 1951, with a mean of 590 mm and a standard deviation of 143 mm. Almost 80% of the yearly precipitation falls between April and September. Mean annual temperature is 12 °C.

In the early 1930s, researchers from Fort Hays State University established over 50 permanent 1-m^2 quadrats at the site. Every summer until 1972, with few exceptions, they used pantographs (Hill 1920) to map the basal cover of all plants in each of the quadrats (Albertson & Tomanek 1965). Most quadrats were located inside livestock exclosures, although 15 did receive light to moderate spring and summer grazing. The original maps have been digitized and the data and metadata are available in tabular or spatial formats along with monthly precipitation and temperature data (Adler, Tyburczy & Lauenroth 2007). In this study, we analysed the population dynamics of 10 forb species (Table 1). Although perennial forbs constitute a small proportion of biomass in the grass-dominated communities at Hays, they represent much of the species diversity (Adler 2004).

MODEL STRUCTURE AND PARAMETER ESTIMATION

We built a stage-classified, birth-pulse model that projects the population from 1 year to the next by

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t,$$

where $\mathbf{n}$ is a vector of abundance in each age class and $\mathbf{A}$ is a projection matrix with an annual time step. The population model contains two age classes: one for plants that are 1 year old and another for plants that are 2 years old or older. We approximated the life cycle with a matrix model:

$$\mathbf{A} = \begin{bmatrix} f & f \\ s_1 & s_2 \end{bmatrix},$$

Table 1. The 10 study species are all coexisting perennial forbs native to mixed grass prairie. Sample size is the number of stems occurring in the data set. Expected life span measures the expected life span past 1 year of age (from Lauenroth & Adler 2008). We calculated generation time from the deterministic models as μ_1, the average age of the parents of the offspring produced by a cohort over its lifetime (Caswell 2001:129)

Species	Family	Sample size	Expected life span (years)	Average seed size ($\times 10^{-2}$ g)	Generation time (years)
Cirsium undulatum	*Asteraceae*	632	1.33	1.05	1.23
Echinacea angustifolia	*Asteraceae*	417	1.65	0.19	1.54
Hedyotis nigricans	*Rubiaceae*	731	1.45	0.01	1.18
Lesquerella ovalifolia	*Brassicaceae*	941	2.27	0.29	1.93
Paronychia jamesii	*Caryophyllaceae*	1064	1.33	0.06	1.35
Psoralea tenuiflora	*Fabaceae*	3487	1.20	2.26	1.15
Ratibida columnifera	*Asteraceae*	844	0.82	0.10	1.15
Solidago mollis	*Asteraceae*	2144	1.06	0.01	1.08
Sphaeralcea coccinea	*Malvaceae*	971	1.03	0.19	1.20
Thelesperma megapotamicum	*Asteraceae*	608	1.01	0.25	1.15

where f is the stage independent per capita recruitment rate (i.e. the number of newly established plants per plant), s_1 is the probability of surviving from age 1 to 2, and s_2 is the annual probability of survival for individuals aged 2 or older. This simple stage structure is supported by Lauenroth & Adler's (2008) survival analyses. Their study showed that 90–97% of all observed individuals of these species over the 30 years of data collection were < 3 years old. Furthermore, changes in survival rates past age 2 were small (Lauenroth & Adler 2008).

In contrast to the stage-specific survival information, we were not able to estimate stage-specific recruitment rates from the historical maps. Therefore, we used the same recruitment rate for each age class. To test whether our conclusions are robust to the assumption of stage-independent reproduction, we repeated the same analysis described below using an extreme stage structure in recruitment: only plants of age 2+ could reproduce. Although the assumption that plants of age 1 do not reproduce is clearly inaccurate (for all ten species, we observed recruitment in years where the entire reproducing population was in age 1), our results did not change with the added stage structure in recruitment. Therefore, our assumption of stage-independent recruitment is unlikely to alter our conclusions.

Annual matrix elements were estimated based upon pre-breeding census data taken from mapped quadrats. The maps record basal cover, meaning that the single-stemmed forb species used in this study are mapped as points. We used a computer program to identify survivors and recruits based on their spatial coordinates (Lauenroth & Adler 2008). The program uses two basic rules: First, a survivor is an individual < 5 cm from the location of a conspecific in the previous year. We chose 5 cm as the critical distance after considering both mapping error and the potential for vegetative growth (Fair, Lauenroth & Coffin 1999). If more than one individual was present in the neighbourhood in the previous year, the current year's plant inherits the identity of the closest 'parent', and only one individual inherits that identity. This last contingency means that the program tracks individual stems, not whole genets. Second, a new recruit is defined as an individual that appears in a location more than 5 cm away from any conspecific in the previous year.

Methods for statistical modelling of matrix elements using the information on the number of survivors and new recruits follow Adler & HilleRisLambers (2008) and are described in Appendix S1 in Supporting Information. Matrix element estimates do not incorporate density dependence and were made for individual stems, rather than genets. Although many prairie species can reproduce vegetatively, our focus was on year-to-year changes in ramet density. Therefore, we classified all new stems as recruits, regardless of the mode of reproduction.

Because we were unable to assign the recruits to a specific parent, we estimated the recruitment rate as the number of new recruits per number of parent plants at the quadrat level. Recruits, however, may come not only from the observed plants within the quadrat, but also from plants located outside the quadrat or from the seed bank. Therefore, we introduced a latent 'true parents' variable to represent the contribution from observed and unobserved sources (i.e. the seed bank) to the per capita recruitment rate (see Appendix S1 for details). Thus, our recruitment estimation implicitly allows for limited recruitment from a seed bank. Lack of detailed data on the seed bank for these ten species prevented us from including a specific seed stage within the model. However, preliminary data from a seed burial experiment at the site (H. J. Dalgleish, unpublished data) demonstrate that the seed bank may play a role in the life cycle for only three of the 10 species: *Cirsium undulatum*, *Psoralea tenuiflora* and *Thelesperma megapotamicum* all had seed survival rates of *c.* 5% after

1 year of burial. Four of the species in this study had no seeds surviving past 1 year (*Echinacea angustifolia*, *Hedyotis nigricans*, *Ratibida columnifera* and *Soldiago mollis*) and three species had seed survival rates of < 1% (*Lesquerella ovalifolia*, *Paronychia jamesii* and *Sphaeralcea coccinea*).

DETERMINISTIC MODELS

We constructed a deterministic matrix model for each species using the mean values of each matrix element over the *c.* 30 years of annual estimates available from the Hays data set. We assumed density-independent matrix elements, a stable stage distribution and no (co)variation among the elements over time (i.e. constant environments). For each model, we calculated λ_1, the population's finite rate of growth in a constant environment, as the dominant eigenvalue of each matrix model.

We then conducted both prospective and retrospective analyses of vital-rate contribution to population growth for the 10 forb species. Retrospective analyses were used to examine the contribution of historical variation in matrix elements to observed changes in asymptotic population growth: λ_1 (Horvitz, Schemske & Caswell 1997). Prospective analyses were used to project the consequences of future change in the matrix elements on population growth.

Prospective analysis of deterministic models

To measure the effect of changes in each matrix element on λ_1, we calculated the sensitivity of λ_1 to unit changes in the matrix element means (Caswell 1978):

$$s_{ij} = \frac{\partial \lambda_1}{\partial a_{ij}},$$

where $a_{i,j}$ is the i, jth entry of **A**. Furthermore, we calculated 'elasticities' as the sensitivity of λ_1 to proportional changes in the matrix elements (de Kroon *et al.* 1986):

$$e_{ij} = \frac{a_{ij}}{\lambda_1} \frac{\partial \lambda_1}{\partial a_{ij}}.$$

Retrospective analysis of deterministic models

We evaluated inter-annual variation in survival and recruitment (s_1, s_2 and f) and their contribution to variance in asymptotic growth (λ_1) using a random-effects life table response experiment (LTRE, Caswell 2001). LTREs compare the observed difference in, or variance among, asymptotic population growth rates between two or more matrices and decompose this difference into contributions from individual matrix elements. Contribution values incorporate both the sensitivities of matrix elements and the observed changes in survival and recruitment estimates between matrices. Thus, variation in a matrix element in one matrix will have a larger contribution to variation in λ_1 when λ_1 is quite sensitive to that element, when the element changes a great deal between matrices, or when both are true.

Formally, the variance in λ_1 among matrices, $V(\lambda_1)$, can be calculated as:

$$V(\lambda_1) \approx \sum_{ij} \sum_{kl} C(ij, kl) s_{ij} s_{kl}$$

where $C(ij, kl)$ is the covariance of matrix elements a_{ij} and a_{kl}, and s_{ij} and s_{kl} are the vital rate sensitivities for these matrix elements evaluated at a reference matrix (Caswell 2001: 269). In our analysis, the random effect was year and the reference matrix was the matrix composed of mean vital-rate values across all

times. We used the 'covariance method' to calculate a single contribution value (χ_{ij}) for each matrix element (Horvitz, Schemske & Caswell 1997, p. 253):

$$\chi_{ij} = \sum_{kl} C(ij, kl) s_{ij} s_{kl}.$$

This sum incorporates the contribution of a_{ij} to $V(\lambda_1)$ and a portion of the contributions from the covariances of a_{ij} with all the other matrix elements, thus resulting in a single contribution value for each vital rate. While a random effects LTRE examines the influence of observed temporal variation in matrix elements, this type of analysis assumes a stable stage structure and asymptotic growth, λ_1, and is therefore a deterministic population analysis.

STOCHASTIC MODELS

Constant environments and age distributions are not likely to occur in nature (Fox & Gurevitch 2000). Rather, survival, recruitment and age distribution fluctuate over time as environmental conditions change. To examine the consequence of temporally fluctuating matrix elements and stage distribution on population dynamics, we developed a stochastic version of the model for each species:

$$\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t$$

where the elements of $\mathbf{A}_t$ vary over time. We generated probability distributions for each element according to the mean and standard deviation estimated from the data. Because s_1 and s_2 were probabilities bounded between 0 and 1, we assumed that they conform to a beta distribution. We assumed that recruitment followed a gamma distribution. To incorporate inter-annual covariation between the two elements, we created bivariate probability distributions, first estimating the correlation structure between two elements from the data and then using the correlation coefficients to link the univariate marginal distributions of relevant matrix elements (i.e. to link the beta distribution for survival to the gamma distribution for recruitment; Sklar 1959; see also Koons, Metcalf & Tuljapurkar 2008). A time sequence of 60 000 random values of correlated matrix elements was then generated from the bivariate distributions.

Incorporating matrix element correlations between years into a population model has been shown to have an impact on the calculation of λ_s in some cases (Tuljapurkar, Horvitz & Pascarella 2003; Morris *et al.* 2006). However, we found no evidence for temporal autocorrelation in recruitment, the dominant driver of population dynamics in these 10 forb species. In addition, we found evidence for moderate temporal autocorrelation in survival for only three of the 10 species (correlation coefficients < 0.55). Based on weak evidence for between-year correlation, we did not include it in our analysis.

We used the sequence of matrix elements to construct time-specific matrices and projected the population forward in time from an arbitrary initial stage distribution for 60 000 time steps. The stochastic sequence of population dynamics was used to estimate the stochastic population growth rate (Heyde & Cohen 1985; Caswell 2001:396). We estimated the stochastic analogues of stable stage distribution ($\mathbf{u}_t$) and reproductive value ($\mathbf{v}_t$) using the procedure laid out in Caswell (2001:402–407; see also Tuljapurkar 1984, 1990).

Prospective analysis of stochastic models

We calculated three elasticities for the stochastic model as defined by Tuljapurkar, Horvitz & Pascarella (2003): the stochastic elasticity (*sensu* Caswell 2001), E^s; the elasticity to change in only the mean of a matrix element, $E^{s\mu}$; and the elasticity to change in only the variance of a matrix element, $E^{s\sigma}$. Examining the three different types of elasticity allowed us to compare the effects of different types of perturbation. The stochastic elasticity, E^s, perturbs both the mean and standard deviation by equal proportions and yields elasticity values that are non-negative, sum to 1 and are considered analogous to deterministic elasticities (Tuljapurkar, Horvitz & Pascarella 2003). The elasticity to the mean value of a matrix element, $E^{s\mu}$, measures the effect on population growth of a fixed proportionate perturbation to the mean while keeping the variance of the matrix element fixed. Such elasticities are ≥ 0, but do not sum to 1 as E^s does (Tuljapurkar, Horvitz & Pascarella 2003). The elasticity to the variance in matrix elements, $E^{s\sigma}$, measures the effect on population growth of a fixed proportionate perturbation to the variance of a matrix element while keeping the mean constant. This corresponds to perturbing matrix element i in year t by an amount that is proportional to the difference between its value in year t and its overall mean value (Morris *et al.* 2006). Such elasticities may be positive or negative and do not sum to 1 (Tuljapurkar, Horvitz & Pascarella 2003). All matrix calculations and analyses were conducted using MATLAB (The MathWorks, Inc. 2002, version 7.4.0).

LIFE-HISTORY TRAIT MEASURES

We measured three life-history traits for each species. Seed size was measured as the average dry weight of 300 seeds collected from the study site in 2007. We used estimates of expected life span (i.e. life expectancies) from Lauenroth & Adler (2008), who analysed life span using the mapped data. Because it is difficult to calculate and even to define a 'stochastic generation time', we calculated the generation time for each species from the deterministic model. Caswell (2001) lists three measures of generation time. We chose to calculate μ_1, which is defined as the average age of the parents of the offspring produced by a cohort over its lifetime (Caswell 2001:129).

STATISTICAL ANALYSIS

To test our prediction that elasticities should be related to life-history traits, we examined the relationship between each elasticity measure (Table 2) and expected life span and generation time using Spearman rank correlations in R (R Development Core Team. 2005).

Results

HISTORICAL VARIATION IN SURVIVAL AND RECRUITMENT AND POPULATION GROWTH

Mean survival probabilities were similar for both age classes for six of the 10 species (Table 3, see Appendix S2). Four species, *E. angustifolia*, *L. ovalifolia*, *P. jamesii* and *S. coccinea*, had at least a 50% increase in survival from the first to the second age class (Table 3). Recruitment rates varied from a low of 0.67 ± 0.06 (mean $\pm$ 1 SE) for *E. angustifolia* to a high of 2.70 ± 1.10 for *R. columnifera* (Table 3). Variability in recruitment was approximately double that of variability in survival as measured by the CV for all species except for *S. coccinea*, which had CV values for survival and recruitment that were nearly identical (Table 3). Deterministic population growth

Table 2. Description of the different measures of population growth rate and elasticity used in the study

Term	Abbreviation	Definition
Deterministic growth rate	λ_1	Dominant eigenvalue of the mean matrix, matrix elements are constants
Long-term stochastic growth rate	λ_s	Long-run average of per time step growth in abundance on a log scale, matrix elements vary with year
Deterministic elasticity	E^d	Elasticity of λ_1 to change in the mean of a matrix element for a deterministic model
Stochastic elasticity	E^s	Elasticity of λ_s to change in a matrix element; the mean and variance are perturbed simultaneously with the CV remaining constant
Stochastic elasticity to the mean	$E^{s\mu}$	Elasticity of λ_s to change in the mean of a matrix element; the mean of the matrix element is perturbed, while keeping the variance constant
Stochastic elasticity to the variance	$E^{s\sigma}$	Elasticity of λ_s to change in the variance of a matrix element; the variance of the matrix element is perturbed, while keeping the mean constant

Table 3. Comparison of survival and recruitment for 10 forb species. Values are mean ± 1 standard error; CV, coefficient of variation; *f*, recruitment (which is the same for both age classes); s_1, survival for age class 1; s_2, survival for age class 2. See Appendix S2 for yearly values

| Species	s_1	s_2	f	s_1 CV	s_2 CV	f CV
Cirsium undulatum	0.18 ± 0.01	0.18 ± 0.01	1.03 ± 0.01	0.24	0.23	0.53
Echinacea angustifolia	0.25 ± 0.01	0.43 ± 0.02	0.67 ± 0.06	0.33	0.25	0.51
Hedyotis nigricans	0.10 ± 0.01	0.11 ± 0.02	1.46 ± 0.19	0.61	0.59	0.77
Lesquerella ovalifolia	0.32 ± 0.02	0.54 ± 0.02	0.79 ± 0.16	0.36	0.25	1.09
Paronychia jamesii	0.22 ± 0.02	0.31 ± 0.02	0.82 ± 0.11	0.50	0.43	0.8
Psoralea tenuiflora	0.11 ± 0.01	0.18 ± 0.01	1.29 ± 0.22	0.42	0.38	0.93
Ratibida columnifera	0.13 ± 0.02	0.13 ± 0.02	2.70 ± 1.10	1.06	1.05	2.56
Solidago mollis	0.06 ± 0.01	0.08 ± 0.01	1.67 ± 0.29	0.54	0.52	1.04
Sphaeralcea coccinea	0.15 ± 0.01	0.22 ± 0.02	0.86 ± 0.09	0.61	0.55	0.62
Thelesperma megapotamicum	0.12 ± 0.01	0.13 ± 0.01	0.92 ± 0.13	0.51	0.50	0.83

rates (λ_1) were near or above 1 for all species (see Appendix S2). Long-term stochastic population growth rates (λ_s) were lower than the deterministic population growth rates for each species (see Appendix S3). Species with the lowest variability in λ_s from year to year had the smallest differences between population growth rates, while species with the highest temporal variability in λ_s had the largest differences between population growth rates (see Appendix S3). There was neither a statistically significant relationship between λ_s and either of the life-history traits (generation time, expected life span, seed size), nor between λ_s and any of the elasticities we measured (data not shown).

QUESTION 1. INFLUENCE OF SURVIVAL AND RECRUITMENT ON POPULATION GROWTH RATES

Contribution values showed that recruitment accounted for more than 85% of the observed temporal variation in λ_1 for all 10 species (Table 4, see Appendix S4). Deterministic elasticities (E^d) followed a similar pattern and were much higher for recruitment than for survival in all species (Table 4). The stochastic elasticity values (E^s) for recruitment were larger than those for survival for all species except for *L. ovalifolia* (the longest-lived species) (Table 4). Stochastic elasticity to the mean ($E^{s\mu}$) was larger for recruitment in all species and

Table 4. Comparison of contribution values and elasticities for 10 forbs. *f* is recruitment summed over both age classes; *s* is survival summed over both age classes; *C* is the contribution to the observed variance in λ_1 over time; E^d is the deterministic elasticity; E^s is the stochastic elasticity; $E^{s\mu}$ is the stochastic elasticity to the mean; $E^{s\sigma}$ is the stochastic elasticity to the variance. See Appendix S4 for contribution, sensitivity and elasticity values for separate age classes

Species	Cf	Cs	$E^d f$	$E^d s$	$E^s f$	$E^s s$	$E^{s\mu} f$	$E^{s\mu} s$	$E^{s\sigma} f$	$E^{s\sigma} s$
Cirsium undulatum	1.00	0.00	0.84	0.16	0.81	0.19	1.04	0.18	−0.22	0.00
Echinacea angustifolia	0.85	0.15	0.64	0.36	0.60	0.40	0.72	0.43	−0.12	−0.03
Hedyotis nigricans	0.99	0.01	0.90	0.10	0.89	0.11	1.67	0.11	−0.78	−0.01
Lesquerella ovalifolia	0.91	0.09	0.61	0.39	0.45	0.55	0.86	0.63	−0.41	−0.08
Paronychia jamesii	0.96	0.04	0.76	0.24	0.67	0.33	1.08	0.37	−0.41	−0.04
Psoralea tenuiflora	0.98	0.02	0.91	0.09	0.82	0.18	2.00	0.21	−1.17	−0.04
Ratibida columnifera	1.00	0.00	0.95	0.05	0.53	0.47	2344.71	113.82	−2344.16	−113.37
Solidago mollis	1.00	0.00	0.96	0.04	0.90	0.10	3.54	0.13	−2.64	−0.03
Sphaeralcea coccinea	0.94	0.06	0.83	0.17	0.79	0.21	1.10	0.23	−0.31	−0.02
Thelesperma megapotamicum	0.98	0.02	0.87	0.13	0.81	0.19	1.59	0.22	−0.78	−0.03
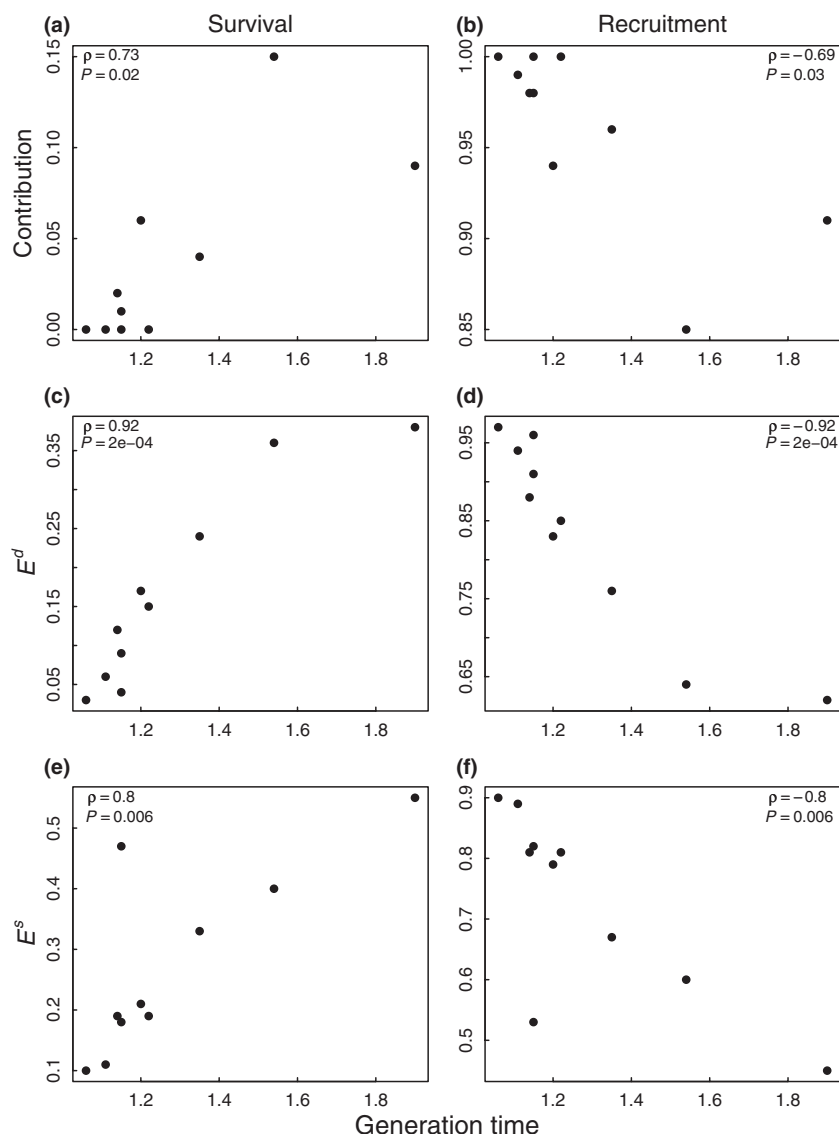
Fig. 1. Relationship between contribution values, deterministic elasticities (E^d) and stochastic elasticities (E^s) to survival (left) and recruitment (right) and generation time. Each point represents a different species. Note the difference in scale between the y-axes.

the difference between $E^{s\mu}$ values for recruitment and survival was the smallest in *L. ovalifolia* (the longest-lived species) (Table 4).

Both generation time and expected life span were significantly correlated with contribution values (C), deterministic elasticities (E^d) and stochastic elasticities (E^s) (Fig. 1 shows generation time results). Both C and E^d for survival increased with generation time (Fig. 1). A similar pattern was found for E^s as well, however, *R. columnifera* (the most variable species) was an outlier when stochasticity was added to the demographic model (Fig. 1). Generation time had a negative relationship with C, E^d and E^s for recruitment across species (Fig. 1). Although C, E^d and E^s values were larger for recruitment than survival across all 10 species, those species with long generation times had higher C, E^d and E^s to survival compared to species with short generation times. Seed size was not significantly related to either contribution values or elasticities.

QUESTION 2. LIFE-HISTORY TRAITS AND VARIABILITY IN SURVIVAL AND RECRUITMENT

Values of stochastic elasticity to the variance ($E^{s\sigma}$) were negative for all species, indicating that increased variability of survival and recruitment would result in a decrease of λ_s for all species (Table 4). Furthermore, $E^{s\sigma}$ was much larger for recruitment than for survival in all 10 species (Table 4). Among all the species, the relative effect of total variability in the life cycle on λ_s was higher in species with greater historical variability in recruitment (Fig. 2, $\rho = 0.78$, $P = 0.01$).

Generation time was significantly correlated with the elasticities to changes in the variance of matrix elements (Fig. 3). Species with shorter generation times showed a higher total elasticity to variance over all life stages ($\rho = -0.68$, $P = 0.03$, Fig. 3), a pattern entirely driven by the elasticity to variance in recruitment ($\rho = -0.70$, $P = 0.02$). A similar pattern was found between expected life span and total elasticity variance,
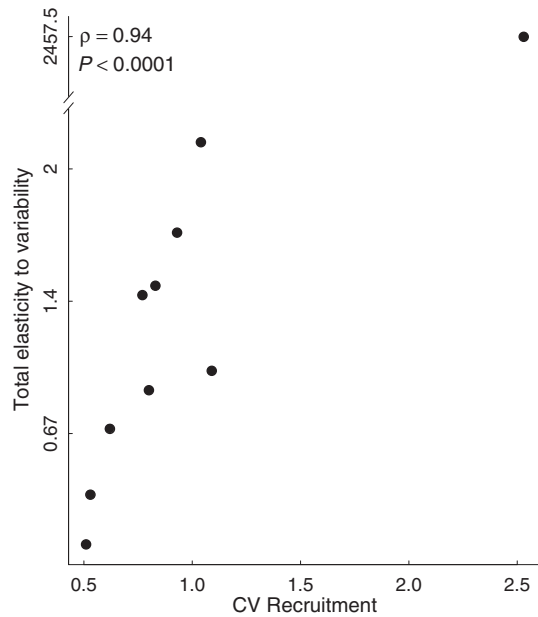
Fig. 2. Relationship between the total elasticity to variability (summed over the entire life cycle) and the coefficient of variation in recruitment. Each point represents a different species.
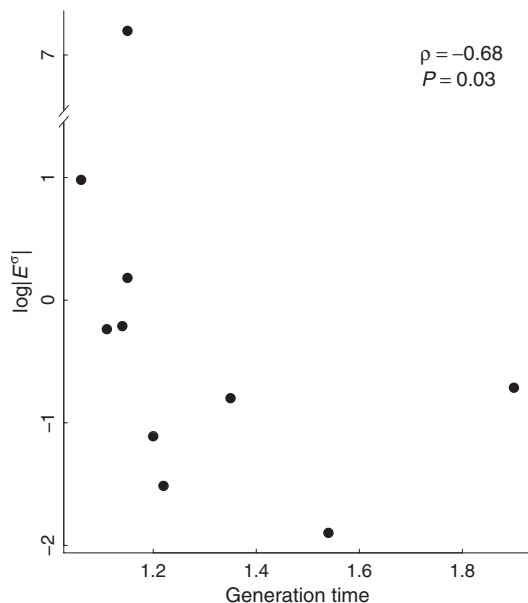
Fig. 3. Relationship between generation time and the total elasticity to variability (summed over the entire life cycle). Each point represents a different species.

though the correlation was not statistically significant ($\rho = -0.42$, $P = 0.22$).

The pattern of species responses to changes in the mean of survival and recruitment was similar to that observed for changes in the variance. Species with longer generation times had larger elasticities to changes in mean survival ($\rho = 0.66$, $P = 0.04$) and lower elasticities to changes in mean recruitment ($\rho = -0.83$, $P = 0.003$). Over all life stages, the total elasticity to changes in the mean of vital rates was higher in

species with longer generation times ($\rho = -0.68$, $P = 0.04$). As with the elasticity to the variance, a similar pattern was observed between expected life span and total elasticity to the mean, but the relationship was not statistically significant ($\rho = -0.57$, $P = 0.08$). There was no relationship between seed size and any of the elasticities we measured.

Discussion

For all 10 forb species, recruitment consistently had higher contribution and elasticity values than survival. Although all 10 of our study species are perennials, their expected life span and generation times are all < 2 years, and it is not surprising that, like annuals, recruitment was the dominant influence on population growth rates. We found support for our first hypothesis that the relative importance of recruitment and survival to these species' population growth was related to life-history traits, especially generation time. As generation time increased, contribution and elasticity values for survival increased, although they always remained lower than contribution and elasticity values for recruitment. An implication of this result is that for short-lived species such as our forbs, the potential impacts of climate change should be largest at the recruitment stage.

Our 'recruitment' process incorporates many different demographic processes, including vegetative reproduction, fecundity (number of seeds produced per plant), seed survival and dormancy, germination probability and seedling survival probability. We could not use the historical data to compare the importance of these unobserved processes to determine whether, for example, seed survival is more important than fecundity. Because we could not measure survival at the seed or seedling stage, we may be underestimating the importance of survival over the entire life cycle of these species.

We found support for our second hypothesis that life-history traits influence the response of populations to increased variability: as generation time increased, the elasticity to changes in variance decreased. Generation time is a single measure of life-history tempo that encompasses all of the vital rates that describe a population (Gaillard *et al.* 2005), which may explain why it was a better predictor of elasticity patterns than life expectancy. Our analyses support a similar study conducted by Morris *et al.* (2008) showing a negative relationship between life expectancy and the relative elasticity to changes in variability of vital rates on λ_s. Morris *et al.* (2008) analysed taxa representing a large range of life expectancies (two orders of magnitude) and habitat preferences. Our results show that essentially the same pattern emerges within a guild of co-occurring forb species with very similar life expectancies and generation times (1–2 years). If future changes in climate variability lead to increases in the variability of survival and/or recruitment, species with short generation times could experience decreased population growth and abundance relative to competitors with longer generation times.

In mixed-grass prairies, forbs species contribute most of the species diversity while a few species of dominant grasses contribute most of the biomass. Our results suggest that

increases in climate variability could have stronger negative impacts on the short-lived forbs than on the dominant grasses, which tend to be long lived (Lauenroth & Adler 2008). Elasticity analyses of the longer-lived grass species could test this hypothesis. If forbs are in fact more vulnerable to variability, then management strategies that encourage forb population growth and diversity may become more important in the future. Consistent with this intuition, observations from the Great Drought of the 1930s indicate that many forb populations were locally extirpated, while the dominant perennial grasses only decreased in abundance (Weaver & Albertson 1943).

The population influences of changes in climate variability, however, must be considered alongside the influences of changes in mean climate variables. Our results indicate that such influences could have similar magnitudes for some species. While the elasticity to changes in mean matrix elements was larger than the elasticity to changes in variability of matrix elements in all species, the difference between the elasticities was very small in species with the shortest generation times, and was most evident in the recruitment elements. For these species, climate-driven changes in recruitment variability have the potential to significantly amplify or dampen a species' response to climate-driven changes in recruitment means.

The effects of increasing climatic variability will ultimately depend on how environmental variability translates to effects on survival and recruitment. Drake (2005) showed that zooplankton population growth rate is a nonlinear function of temperature, meaning that an increase in temperature variability can actually increase long-term population growth rates. Our elasticity analyses, showing a negative effect of variability on population growth, assume that an increase in climate variability will alter the variability of survival and/or recruitment but not the means. Explicitly modelling nonlinear relationships between climate variables and survival and recruitment would allow changes in climate variability to influence the mean of survival and recruitment, which could potentially change our results (Koons *et al.* 2009). Exploring these relationships by combining our demographic time series with historical climate data available from the site is an important goal of our ongoing research.

Our findings illustrate the potential for applying life-history theory to the current challenges of global change. Despite the apparent life-history similarities of the 10 forbs, we observed a strong negative relationship between generation time and the effect of variability. Our results indicate that the patterns reported by Morris *et al.* (2008) for diverse taxa from many locations also exist within a guild of species from a single community. Data for additional species and life-history traits will enable further testing of life-history theory while also providing valuable information to natural resource managers about which species may be the most vulnerable to climate change.

Acknowledgements

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Supporting Information

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

Appendix S1. Estimation of matrix elements.

Appendix S2. Yearly matrix elements for 10 Kansas forb species.

Appendix S3. Comparison of the different population growth rates for 10 Kansas forb species.

Appendix S4. Sensitivity and elasticity values for 10 Kansas forb species.

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