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Life form influences survivorship patterns for 109 herbaceous perennials from six semi-arid ecosystems

Chengjin Chu, Kris M. Havstad, Nicole Kaplan, William K. Lauenroth, Mitchel P. McClaran, Debra P. Peters, Lance T. Vermeire & Peter B. Adler

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Chu, C. (corresponding author, chengjin.chu@usu.edu) &
Adler, P.B. (peter.adler@usu.edu): Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, 84322, USA
Havstad, K.M. (Kris.Havstad@ars.usda.gov) &
Peters, D.P. (debpeter@ad.nmsu.edu): USDA, ARS, Jornada Experimental Range, and Jornada Basin Long Term Ecological Research, New Mexico State University, Las Cruces, NM, 88003, USA
Kaplan, N. (Nicole.Kaplan@colostate.edu): Shortgrass Steppe – LTER, Colorado State University, 1499 Campus Delivery, Fort Collins, CO, 80523, USA
Lauenroth, W.K. (wlauenro@uwyo.edu): Department of Botany, University of Wyoming, Laramie, WY, 82070, USA
McClaran, M.P. (mcclaran@email.arizona.edu): School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, 85721, USA
Vermeire, L.T. (lance.vermeire@ars.usda.gov): Fort Keogh Livestock and Range Research Laboratory, USDA-ARS, Miles City, MT, 59301, USA

Abstract

Questions: What factors explain the variation in plant survival parameters across species and ecosystems?

Location: Western North America.

Methods: We compiled six long-term data sets from western North America to test for ecosystem-dependent demographic responses for forbs and grasses. Based on these data, we characterized 123 survivorship curves for 109 species. Three demographic parameters were extracted from these survivorship curves: survival rate at age 1, life expectancy at age 1, and a parameter describing the shape of the survivorship curve. We used a mixed effects model to compare the differences in demographic parameters between life forms (forbs or grasses) and among ecosystems, incorporating 'ecosystem' as a random factor, with life form treated as a categorical factor, and mean annual precipitation and mean annual temperature treated as continuous variables.

Results: Grasses had higher survival and longer life expectancy than forbs at 1 yr of age. Both forbs and grasses followed Type III survivorship curves, although forbs were closer to Type II compared to the grasses. Averaging across species, hazard ratios for whole survivorship curves differed among most ecosystems. While mean annual precipitation had no effect on any demographic parameter, mean annual temperature had a significantly negative effect on both first year survival rates and life expectancy for forbs.

Conclusions: Our results demonstrate that life form exerts a strong influence on demographic parameters and their response to temperature variation among ecosystems. This unprecedented information on the age-specific demography of herbaceous plants has implications for population modelling and research on life-history evolution and senescence.

Introduction

Demographic parameters, such as life span and survival rate, are the key to understanding life history evolution (Weiher et al. 1999) and population dynamics (García et al. 2008; Salguero-Gómez & de Kroon 2010). For example, survivorship curves provide valuable information about senescence (Pinder et al. 1978), which has been defined as the decreasing performance of individuals with age and may be manifested by an increase in the age-specific mortality rate (Partridge & Barton 1993; Vaupel et al. 2004; Baudisch 2005, 2008). Large changes in age-specific

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mortality would also raise questions about the common assumption that plant populations are structured only by size or stage, not age (Roach 2003; Roach & Gampe 2004). However, due to the difficulty of collecting long-term demographic observations, data on demography in perennial herbaceous plants is currently limited (Silvertown et al. 2001; Jongejans et al. 2010; García et al. 2011). While many studies have demonstrated the influence of demographic parameters on population dynamics (Sarukhán & Harper 1973; Caswell 2001), few have explored the potential factors explaining variation across species and ecosystem types in the demographic parameters themselves.

Life form (e.g. forbs, grasses, shrubs and trees) is a key intrinsic property of plants, and may be one factor that explains variation in survivorship curves and parameters. Many demographic studies of herbaceous perennials have focused on forbs alone (Silvertown et al. 2001; Jongejans & de Kroon 2005; Jongejans et al. 2010; Salguero-Gómez & de Kroon 2010; but see Cheplick 1998).

Silvertown et al. (1993) compared woody and herbaceous perennials, although only three of the 45 herbaceous species are grasses. In another study, Salguero-Gómez & Casper (2010) compiled demographic information for 80 herbaceous species, including only six grasses. Lauenroth & Adler (2008) conducted survival analyses for 29 forbs and 11 grasses from a southern mixed prairie in Kansas and found that grasses tended toward Type III survivorship curves more strongly than forbs, and grasses had higher survival and longer life expectancy than forbs. In general, however, comparisons of grasses and forbs are rare, despite the fact that these life forms dominate grassland ecosystems. The lack of long-term demographic data for grasses (but see Canfield 1957; Wright & van Dyne 1976) is unfortunate, given forbs and grasses differ in many ways, including litter decomposition rates (Thurow 1989), their role in community compositional turnover (Adler 2004) and invasiveness (Firn et al. 2011).

Demographic parameters could also vary among ecosystems in response to differences in environmental drivers such as precipitation and temperature. For example, Jongejans et al. (2010) chose three similar forb species in different European countries, and found considerable demographic variation among them. An understanding of the underlying causes of variation in demographic parameters across ecosystems, such as precipitation and temperature, might help us anticipate species' responses to ongoing climate change (Thuiller et al. 2008; Jongejans et al. 2010). However, to our knowledge, few studies have compared ecosystem-level variation in demographic parameters for groups of species or explored the environmental factors that might explain such variation.

Our objective was to use an unprecedented data set on age-specific survival for herbaceous species to describe the influence of life forms and ecosystem types on survivorship. Based on long-term mapped quadrats from six grassland ecosystems in western North America, we constructed 123 life tables and corresponding survivorship curves for 109 herbaceous perennials (i.e. forbs and grasses). Using this multiple ecosystem data set, we explored variation in demographic parameters between life forms and among ecosystems. We focused on three demographic parameters: (1) the survival rate at age 1, which is simply the probability that a plant survives from age 1 to age 2, a measure of early life survival; (2) life expectancy at age 1, which is the expected number of years of life (i.e. life span) remaining at age 1, and represents an integrated measure of survival across age; and (3) a parameter that describes the shape of the survivorship curve and distinguishes between Type I, Type II and Type III survival patterns (Lauenroth & Adler 2008). Second, we complemented this comparison of univariate descriptors of survivorship curves with hazard ratio analyses that consider the entire survivorship curve when comparing species from different life forms and ecosystems. We also investigated environmental correlates of demographic parameters. Finally, we discuss the potential implications of our work for structured population modelling and research on senescence.

Methods

Study ecosystems and data sets

Chart quadrats are permanent 1-m^2 locations in which all individual plants are identified and mapped each year using a pantograph (Hill 1920). Due primarily to Clements's (1907) influence, many range experiment stations in the western US began mapping quadrats in the 1910s–1930s, and continued annual censuses for decades. In the present paper, we focus on six of the richest chart quadrat data sets (Adler et al. 2007; Zachmann et al. 2010; Anderson et al. 2011, 2012; Chu et al. 2013; Table 1).

Extracting demographic data

During the mapping of quadrats, plants were depicted by different markings according to their life forms. Usually, forbs were mapped as points, and grasses and sedges appeared as polygons with indeterminate shape. We tracked individual plants based on their spatial locations within each mapped quadrat. Due to mapping error, and the ability of herbaceous perennials to 'move' short distances via re-sprouting, our tracking algorithm imposed a buffer around each individual. We chose 5 cm as the

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Table 1. Information on the six ecosystems.

Location	Jornada experiment range, New Mexico	Fort Keough, Montana	US Sheep experiment station, Idaho	Santa Rita experiment range, Arizona	SGS, Long-term ecological research, Colorado	Hays, Kansas
Vegetation	CD	NMP	SBS	SD	SGS	SMP
Elevation (m)	1260	720	1650	1150	1653	650
Lat/Long	32.6 °N/106.6 °W	46.3 °N/105.8 °W	44.2 °N/112.1 °W	31.8 °N/110.8 °W	40.8 °N/104.7 °W	38.8 °N/99.3 °W
Temp. (annual mean; °C)	14	8	6	16	8	13
Precip. (annual total; mm)	246	343	325	350	340	585
Quadrats	70	44	26	178	24	51
Annual census period	1915–1950	1932–1945	1923–1957	1915–1935	1997–2010	1932–1972
Forbs	39/13	24/9	60/20	9/2	36/2	63/29
Grasses	20/9	13/8	10/7	15/6	13/7	22/11

CD, Chihuahuan Desert in New Mexico; NMP, Northern mixed prairie in Montana; SBS, Sagebrush steppe in Idaho; SD, Sonoran Desert in Arizona; SGS, Shortgrass steppe in Colorado; and SMP, Southern mixed prairie in Kansas.

The last two rows show the total number (x) of perennial herbaceous species mapped in each ecosystem, relative to the number of species included (y) into the current analysis, for forbs and grasses, respectively (x/y).

buffer distance, based on previous analyses (Fair et al. 1999; Lauenroth & Adler 2008).

For forbs, the tracking programme was based on two rules: (1) a new recruit was defined as an individual that appears in a location >5 cm from any conspecific in the previous year, and (2) a survivor was an individual <5 cm from the location of a conspecific in the previous year, from which it inherits its identity. For grasses, we first added a 5-cm buffer area to all polygons of the focal species in year $t - 1$. We then calculated the overlap of each of these polygons with each individual plant occurring at year t. If the year t individual did not overlap any polygon from the previous year, it was labelled as a new recruit. Otherwise, the individual inherited the identity of the polygon with which it shared the greatest overlap. We also allowed plants to 'miss' 1 yr in our data sets. In other words, if a genet was observed at similar coordinates in year t and year $t + 2$, but did not appear in year $t + 1$ or the quadrat was not mapped in year $t + 1$, the genet observed in year $t + 2$ inherits the identity of the genet observed in year t. This approach allowed plants to grow and coalesce, or to shrink and fragment, from year to year.

Statistical analyses

Life table and Weibull survivorship curve

Censoring is a form of missing data management common in survival analysis (Kaplan & Meier 1958; Lauenroth & Adler 2008). In our analysis, new recruits appearing in the first observed year for each quadrat, or appearing after a year without mapping, were marked as left-censored observations; individuals still alive in the last year of the data set, or disappearing during a missing year, were treated as right-censored observations. We also treated genet disappearance due to coalescence (i.e. many small polygons merge into one large polygon) as right-censored. Our survival analysis excluded left-censored individuals but accounted for right censoring. We constructed the full life table for each species based on the Kaplan–Meier estimate (Kaplan & Meier 1958) using the function *survfit* in the 'survival' package in R (R Foundation for Statistical Computing, Vienna, AT).

In order to classify each species' survivorship curve (Type I, Type II or Type III), we fitted the survival data (i.e. the probability of surviving to a given age T) with the two-parameter Weibull model (Pinder et al. 1978):

$$S(T) = \exp\left[-\left(\frac{T}{a}\right)^{b}\right]$$

where a (>0) and b (>0) are the scale and shape parameters of the Weibull frequency distribution, respectively. Based on the above equation, Pinder et al. (1978) derived that the age-specific mortality rate in the interval T_i to T_{i+1} as

$$M(T_i, T_{i+1}) = 1 - \exp\left[\left(\frac{T_i}{a}\right)^{b} - \left(\frac{T_{i+1}}{a}\right)^{b}\right]$$

Furthermore, Pinder et al. (1978) found that the form of the survivorship curve is entirely determined by the shape parameter b: (1) $M(T_i, T_{i+1})$ is an increasing function of age for $b > 1$, corresponding to the Type I survivorship curve; (2) $M(T_i, T_{i+1})$ is constant when $b = 1$ corresponding to the Type II survivorship curve; and (3) $M(T_i, T_{i+1})$ is a decreasing function of age for $b < 1$, which indicates that species could escape senescence, i.e. individual performance remains constant or improves with age.

Nonlinear least squares regression (*nls* function in the 'stats' package in R) was used to obtain the scale and shape parameters for each species. We excluded very short-lived species (maximum age <3 yr) for this analysis (Lauenroth & Adler 2008). Ultimately, we obtained 123 survivorship curves for 109 species from six ecosystems (11 species occurred in more than one ecosystem; Appendix S1). We included two sedges, *Carex douglasii* of the Sagebrush steppe ecosystem and *Carex duriuscula* of the Northern mixed prairie ecosystem, in the 'grass' life-form category (Appendix S1). Three critical demographic parameters were extracted from life tables: both the survival rate and life expectancy at age 1, and the shape parameter of the survivorship curve.

Relationships between climatic variables and demographic parameters

For each ecosystem, we calculated the mean annual precipitation (MAP) and mean annual temperature (MAT) from historical data (Table 1). To compare the differences in demographic parameters between life forms and among ecosystems, we used mixed effects models incorporating 'ecosystem' as a random factor, with life form treated as a categorical factor, and MAP and MAT treated as continuous variables. After preliminary analyses demonstrated that the interactions between MAP and MAT were not significant, we excluded them from the final analyses. We fitted the models using *lmer* in R package 'lme4'. In addition, due to the unbalanced nature of our data (Table 1, Appendix S1), we used the function ANOVA in the 'car' package in R to conduct the analysis of deviance for each model.

Hazard ratio analysis for survivorship curves

Although the metrics described above provide valuable information on individual demographic rates, an approach that takes into account the whole survivorship curve may be more sensitive to differences between life forms and among ecosystems. We chose the Cox model to determine how much the life forms differed in hazard ratio (HR). Here, hazard means the probability of dying given that individuals have survived up to a given time point, or the risk of death at that moment. Note that a hazard ratio of one implies no difference between life forms. We conducted a weighted estimate for Cox regressions, as proposed by Schemper et al. (2009), which provides unbiased estimates of average hazard ratios for non-proportional hazards.

To compare forbs and grasses for pooled data from all ecosystems, the following formula was used: $hazard = h_0(t) \times \exp(c \times x_L)$, where $h_0(t)$ is defined as the baseline hazard when all explanatory variables are zero, $\exp(c)$ is the hazard ratio indicating the probability of death for grasses relative to forbs (in the present paper, forb is the reference category), and x_L is a categorical variable for life form. To explore differences in survivorship curves among ecosystems, either treating forbs and grasses separately or pooling all data together, each ecosystem in turn was treated as the reference for the weighted Cox regression. The function *coxphw* in the 'coxphw' package in R was utilized (Schemper et al. 2009), where life forms and ecosystems were both considered as categorical variables.

Results

Forbs and grasses significantly differed in survival ($P = 0.004$; Fig. 1) and life expectancy ($P < 0.0001$) at 1 yr of age, and in the shape of survivorship curves ($P = 0.028$; Fig. 2). Tests of the shape parameters showed that values for pooled data (0.64 ± 0.025), for forbs (0.69 ± 0.032) and for grasses (0.56 ± 0.039) were <1, indicating that, on average, these species followed Type III survivorship curves. For pooled data, ecosystems SGS and SMP had lower first-year survival rates (0.39 and 0.35) and shorter first-year life expectancy (1.99 and 1.97) than other ecosystems. Among the six ecosystems, SBS had the highest shape parameter (0.73).

Hazard ratios, based on comparisons of full survivorship curves, differed in most pair-wise comparisons of ecosystem types (Table 2). When pooling data across ecosystems, grasses had lower hazard (HR = 0.80) compared to forbs, meaning that grasses on average had a lower probability of dying.

The MAP had no significant effects on any demographic parameters ($P > 0.05$), whether we treated life forms separately or pooled the data for forbs and grasses. For forbs, MAT had significantly negative effects on both first year survival rates (regression coefficient −0.019; $P = 0.012$) and life expectancy (regression coefficient −0.14; $P = 0.014$) (Fig. 3), but had no effect on the shape parameters. MAT had no effect on the demographic parameters of grasses or on the pooled parameters.

Discussion

The effect of life form

Life form plays a critical role in explaining the variation of demographic parameters. We found that grasses had higher survival and longer life expectancy at age 1, and lower hazard ratio than forbs. Both forbs and grasses followed Type III survivorship curves, but forbs were closer to Type II than grasses. While similar results were previously reported for the Southern mixed prairie ecosystem (Lauen-

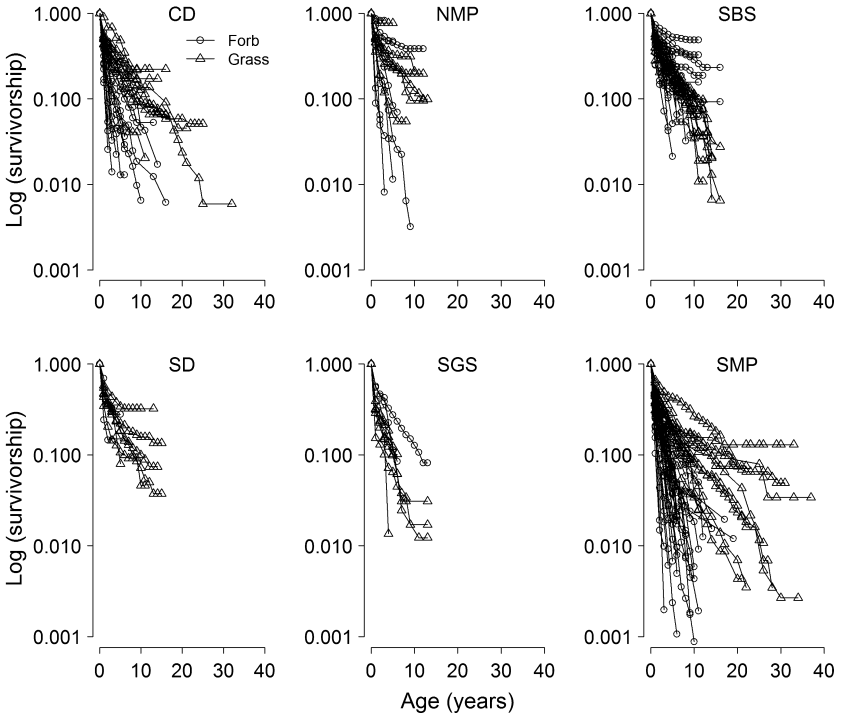

Fig. 1. 123 survivorship curves for 109 species from six ecosystems. Note that the *y*-axis has a logarithmic scale. See Table 1 for the abbreviation of ecosystem types.

roth & Adler 2008), our analysis, spanning six ecosystems, demonstrates that these patterns are general across arid to sub-humid plant communities in North America. Demographic parameters link physiological differences between grasses and forbs with differences in their population sizes and dynamics (Thurow 1989; Adler 2004; Firn et al. 2011). For example, Lauenroth & Adler (2008) demonstrated that demographic variation between life forms (i.e. forbs and grasses) could explain patterns of dominance (i.e. relative abundance).

Plant population models typically assume that vital rates are a function of size or phenological stage (Caswell 2001). Although interest in the effect of age on population dynamics is increasing (Childs et al. 2003; Caswell 2012), it is still unclear when we should include age in population models. Type III survivorship curves imply strong changes in survival with age (Pinder et al. 1978). If size and age are not perfectly correlated, age could have an important influence on survival that size-only models would not capture. Our finding that Type III survivorship curves are common for perennial forbs and especially for grasses implies that it may be important to incorporate age structure into population models for these species.

Our results are also relevant to questions about senescence. We found little evidence for demographic senescence, as the shape parameters of Weibull survivorship curves for both forbs and grasses on average were less than 1 (Pinder et al. 1978), meaning that age-specific mortality decreases with age, and implying that these species may escape senescence in late life. Several other studies also have suggested that senescence may not be inevitable in perennial herbaceous plants (Silvertown et al. 2001; Roach 2003; Roach & Gampe 2004; García et al. 2011). Future research could compare patterns of aging between life forms or across species using the recently proposed pace–shape space approach, which provides a tool to identify key determinants of the evolution of aging (Baudisch 2011).

The effect of environmental variables

Attention has focused on how the key demographic parameters underlying population growth vary across large spatial scales (Kaplan & Meier 1958; Jongejans & de Kroon 2005; Angert 2006, 2009; Jongejans et al. 2010). Although hazard ratio analyses showed large differences in survivorship curves among ecosystems (Table 2), mean annual precipitation, which ranged from 246 mm to 585 mm, did not explain variation in survival. However, mean annual temperature, which ranged from 6 °C to 16 °C, had a significantly negative influence on forb survival and life expectancy at age 1 (Fig. 3). In other words,

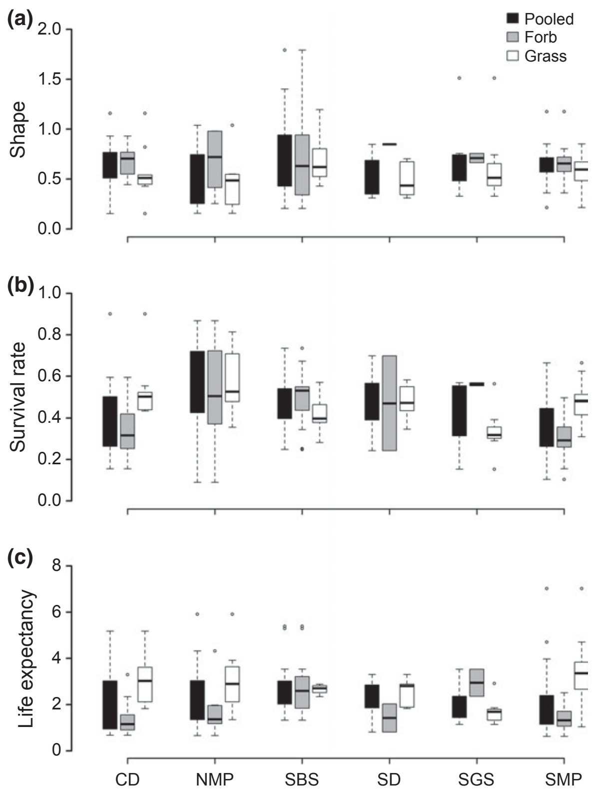

Fig. 2. Comparisons of demographic parameters for pooled data (grey), forbs (red) and grasses (green) from six ecosystems. The box corresponds to the 25th and 75th percentiles, the dark line inside the box represents the median of the data (50% of the individuals), error bars are the minimum and maximum except for outliers (circle points corresponding to values beyond 1.5 times the interquartile range). See Table 1 for the abbreviation of ecosystem types.

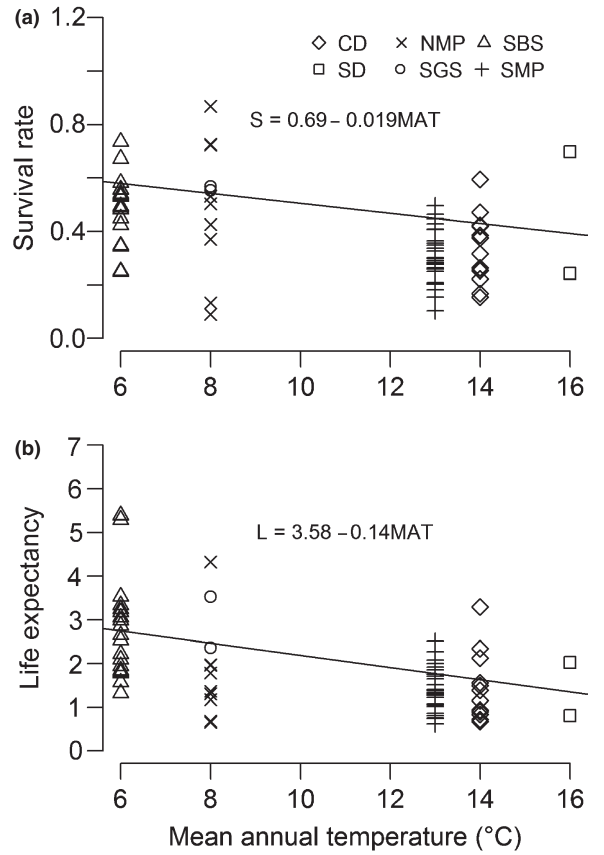

Fig. 3. The significant relationships between mean annual temperature (MAT) and demographic parameters at first year for forbs ($P < 0.05$). 'S' indicates the survival rate, and 'L' indicates the life expectancy. The models also included random effects of ecosystems, which are not shown in the equations. See Table 1 for the abbreviation of ecosystem types.

forbs growing in the Sonoran Desert (16 °C) and Chihuahuan Desert (14 °C) tended to have lower first year survival and shorter first year life expectancy than species in sagebrush steppe (6 °C), although the shape of the survivorship curves was insensitive to MAP and MAT. A more comprehensive synthesis of the effect of climatic variables on demographic parameters will require additional data from wider precipitation and temperature gradients, extending beyond the arid and semi-arid ecosystems that we studied. Future comparisons should account for other environmental factors, such as local edaphic properties and nutrient availability (Gross et al. 1993; Russo et al. 2008), or biotic factors such as plant–plant interactions and herbivory (Bastrante et al. 1995; Mandle & Ticktin 2012),

Table 2. Comparisons of hazard ratios among study ecosystems, with the top right corner with grey cells for the pooled data including both forbs and grasses, the bottom left corner for forbs/grasses, respectively.

Reference	CD	NMP	SBS	SD	SGS	SMP
CD	–	**0.90**	**1.05**	**0.88**	**1.11**	**1.23**
NMP	**1.43**/0.99	–	**1.15**	0.98	**1.23**	**1.39**
SBS	**1.41/0.81**	1.00/**0.81**	–	**0.85**	**1.06**	**1.21**
SD	**1.22**/1.01	**0.85**/1.02	**0.86/1.25**	–	**1.26**	**1.42**
SGS	**1.59/0.68**	**1.10/0.69**	**1.11/0.89**	**1.26/0.68**	–	**1.13**
SMP	**0.88/0.97**	**0.62/0.97**	**0.62/1.20**	**0.72/0.96**	**0.56/1.41**	–

The column 'Reference' indicates that the ecosystem is considered as the reference category. Switching the reference between ecosystems requires taking the inverse of the corresponding hazard ratio. Most pair-wise comparisons are statistically significant ($P < 0.05$), marked in bold type. See Table 1 for the abbreviation of ecosystem types.

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which may also contribute to ecosystem-level variation in demographic parameters.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Summary of demographic parameters of species analysed.

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