

Demography of perennial grassland plants: survival, life expectancy and life span

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Summary

1. Survival, life expectancy and life span are key demographic parameters that are essential for understanding life-history evolution and forecasting population dynamics, but empirical data on these parameters is extremely limited for herbaceous species.

2. We used long-term data from annually mapped permanent quadrats in a Kansas, USA, grassland to estimate survival, life expectancy and life span for 29 perennial forbs (herbaceous dicots) and 11 perennial grasses. In the cases of both forbs and grasses, they were the most common species at the research site.

3. We developed computer programs to track the identity of individual genets based on their spatial locations in the permanent quadrats. The programs distinguished between new recruits and surviving individuals, and calculated the ages and life spans of the survivors.

4. Most herbaceous perennials die young; life expectancy at age 1 year ranged from 0.6 to 6.5. However, forbs are more likely to die young than grasses. Survival from age 1 to 2 years for forbs ranged from 0.11 to 0.49 with an average of 0.30, whereas for grasses it ranged from 0.30 to 0.63 with an average of 0.44. Maximum observed life spans ranged from 3 to 25 years for forbs and 5 to 39 years for grasses.

5. All species tended towards Type III survivorship curves, but grasses were more strongly Type III while many forbs had relatively constant survival rates with age. Therefore, population models must account for increasing survival with age, especially for grasses.

6. Age was a better predictor of grass survival than size, raising questions about the use of size-based methods to indirectly estimate survival and life span.

7. Maximum observed life span was positively and significantly related with species importance.

8. *Synthesis.* The higher survival, life expectancy and life span of grasses compared to forbs may provide a demographic explanation for community-level differences in the dominance and turnover of these two functional groups in grassland plant communities.

Key-words: age-based demographic parameters, forb, grass, Great Plains, herbaceous perennial, Type II survivorship, Type III survivorship

Introduction

Knowledge of survival, life expectancy and life span is fundamental for understanding population dynamics (Harper 1977; Silvertown & Lovett Doust 1993) and evolutionary fitness (Silvertown 1991). Unfortunately, relatively few data on these three key demographic traits are available for plant species (Wright & Van Dyne 1976; West *et al.* 1979; van der Maarel 1996; Silvertown *et al.* 2001; Roach 2003) due to the complications associated with the demography of plants (Harper 1967, 1977). The lack of empirical demographic data has constrained our ability to predict plant population dynamics

or understand the evolution of life-history strategies (Silvertown *et al.* 2001). Extensive empirical data on demographic parameters for species with different life-history strategies and habitat affinities could make generalization possible. For example, evidence that survival is constant with age for many herbaceous perennial forbs – a Type II survivorship curve (Deevey 1947; Harper 1967) – would greatly simplify estimation and modelling of survival for all species in this group.

One of the few ways to determine demographic parameters for populations of herbaceous plants is by long-term mapping of individuals in permanent plots (Weaver & Clements 1938; Dittberner 1971; Harper 1977; West *et al.* 1979; Silvertown & Lovett Doust 1993). The difficulty of the data collection and analysis are reasons why such analyses are rare. In the perennial

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grasslands of the North American Great Plains, Frederic Clements, John Weaver and their students left behind a valuable legacy: decades of annual maps of all individual plants in 1-m² quadrats at a number of locations throughout the grasslands (Albertson & Tomanek 1965; Wright & Van Dyne 1976). These data have been available for much of the past century, but it is only with the recent development of geographic information systems that it has been feasible to extract the richness of the demographic information they contain (Fair *et al.* 1999).

The limited age-specific demographic data for herbaceous perennials has motivated the development of size and stage-specific methods (Lefkovitch 1965; Werner & Caswell 1977; Kirkpatrick 1984). Many authors have argued that size is a more important predictor of plant life-history attributes than age (Kirkpatrick 1984; Caswell 1989; Menges *et al.* 2000). Marba *et al.* (2007) applied allometric theory to the relationship between size and important life-history parameters and reported that mortality and birth rates scaled as the -0.25 power and life span as the 0.25 power of plant mass from phytoplankton to trees. However, testing the assumption that size may serve as a proxy for age requires both age and size-specific data.

Our objective was to evaluate survival, life expectancy and life span for 11 of the most common native grasses and 29 of the most common native forbs in the central Great Plains of North America. For each of these species, we estimated survival rates and life expectancy as a function of plant age, and constructed full life tables. Our estimates of survival, life expectancy and life span allowed us to make generalizations across species and functional groups for important Great Plains plant communities and to explain patterns of dominance within these communities. Additionally, we used general linear models to test relationships between age and size for 11 grass species and to compare the potential of age and size to explain variation in survival. We used these results to comment on a trend to use size-based analyses to estimate age-related parameters in comparative demographic analyses (Cochran & Ellner 1992; Silvertown *et al.* 1993, 2001).

Methods

STUDY SITE DESCRIPTION

The study site is located 3 km west of Hays, KS, USA (38.8°N, 99.3°W) in native southern mixed grass prairie. Mean annual precipitation is 580 mm, with 75% falling in spring and summer. Mean annual temperature is 12 °C. The permanent quadrats which form the basis of this study were established in 1932 by researchers from Fort Hays State University. The quadrats are distributed across gradients in soil type that produce distinct plant communities (Albertson 1937). Deep soils on the level uplands support a shortgrass community dominated by blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloë dactyloides*). Shallow limestone soils on hill-brows and slopes support a community dominated by little bluestem (*Schizachyrium scoparium*). An ecotone separates the shortgrass and little bluestem areas. Patches of tallgrass prairie, dominated by big bluestem (*Andropogon gerardii*), occur in swales. Nomenclature follows *Flora of the Great Plains* (Great Plains Flora Association 1986).

FIELD METHODS

Long-term mapping of individual herbaceous plants on permanent quadrats was a technique popularized by Fredrick Clements and John Weaver (Clements 1907; Weaver & Clements 1938). Investigators used pantographs, a drafting tool, to create scaled drawings of the identity, location and size (basal area) of all plants occurring in permanently located 1-m² quadrats (Hill 1920). The corners of the permanent quadrats at Hays were marked with iron stakes, minimizing year-to-year error in mapping. In fact, data produced using the pantograph technique can be used the same way as data generated by tagging individual plants, with spatial coordinates substituting for tags. While tagging projects in herbaceous communities typically focus on one species and span a few years (e.g. Kéry & Gregg 2004), the pantograph data set from Hays includes all perennial species in more than 50 quadrats and spanned the period 1932–1972 (Albertson & Tomanek 1965).

The Hays data set has recently been digitized and is now available online (Adler *et al.* 2007). Our analysis here used the 36 quadrats located within livestock enclosures.

QUADRAT ANALYSIS

We developed computer programs to track the identity of individual genets based on their spatial locations in the permanent quadrats. The programs distinguish between new recruits and surviving individuals, and calculate the ages and life spans of the survivors. Because basal, not canopy, cover was mapped, forbs appear as points and grasses appear as polygons with indeterminate shape. The polygons may grow and coalesce, or shrink and fragment from year to year. Therefore, we used different approaches for the forbs and grasses.

The forb tracking program is based on two rules: (i) a new recruit is defined as an individual that appears in a location > 5 cm from any conspecific in the previous year, and (ii) a survivor is an individual < 5 cm from the location of a conspecific in the previous year, from which it inherits its identity. We chose 5 cm as the critical distance after considering both mapping error and the potential for vegetative growth (Fair *et al.* 1999). We also allowed plants to ‘miss’ 1 year. In other words, if a plant is observed at similar coordinates in 1940 and 1942, but does not appear in 1941 or the quadrat was not censused in 1941, we can assign the same identity to both records. We found that while changing the critical distance or number of missed years had some quantitative effect on the results, it did not alter our main conclusions.

Our procedure tracks genets, not individual plants: an individual with one stem can have many stems the following year. For example, if many individuals appear in the current year within 5 cm of a ‘parent,’ all individuals inherit the same identity. We chose to track genets because most forbs and all grasses at our study site have some potential for clonal growth.

We used the same approach to track grasses, but we based the tracking rules on the areas of overlapping polygons rather than distances between points. First, we add a 5-cm buffer to all polygons of the focal species occurring in year $t - 1$. We then calculate the overlap of each of these polygons with one individual plant occurring at time t . If the time t individual does not overlap any polygon from the previous year, it is labelled as a new recruit. Otherwise, the individual inherits the identity of the polygon with which it shares the greatest overlap. These rules are consistent with Fair *et al.* (1999). Note that both fragmentation (one large polygon becoming many small polygons) and coalescence (many small polygons merge into one large one) are possible. In the case of coalescence, only one genet survives. In our statistical analysis of survival, we treated genet disappearance due to coalescence as right-censored observations.

Table 1. Species, family, number of genets for life table analysis, first year survival (years 1 and 2), first year life expectancy, power exponent and maximum observed life span for 29 species of forbs from Hays, KS, USA

Species	Family/Tribe	N	Survival	Life expectancy	Power exponent	Maximum life span
<i>Ambrosia psilostachya</i>	Asteraceae	5675	0.168	0.79	0.670	7
<i>Amorpha canescens</i>	Fabaceae	63	0.302	1.86	0.578	17
<i>Arenaria stricta</i>	Caryophyllaceae	64	0.266	1.72	0.349	10
<i>Aster ericoides</i>	Asteraceae	351	0.157	0.77	0.664	6
<i>Aster fendleri</i>	Asteraceae	67	0.254	1.32	0.542	11
<i>Aster oblongifolius</i>	Asteraceae	55	0.218	1.10	NA	6
<i>Calylophus serrulatus</i>	Onagraceae	154	0.286	1.28	0.577	10
<i>Cirsium undulatum</i>	Asteraceae	484	0.357	1.33	0.722	9
<i>Dalea purpurea</i>	Fabaceae	142	0.296	1.37	0.512	7
<i>Echinacea angustifolia</i>	Asteraceae	218	0.367	1.65	0.661	11
<i>Evolvulus nuttallianus</i>	Convolvulaceae	55	0.418	2.47	0.544	18
<i>Gaura coccinea</i>	Onagraceae	145	0.193	0.85	0.653	7
<i>Gutierrezia sarothrae</i>	Asteraceae	177	0.282	1.18	0.672	7
<i>Hedyotis nigricans</i>	Rubiaceae	372	0.368	1.45	0.692	7
<i>Hymenoxys scaposa</i>	Asteraceae	89	0.427	2.25	0.618	16
<i>Lesquerella ovalifolia</i>	Brassicaceae	442	0.464	2.27	0.576	14
<i>Leucelene ericoides</i>	Asteraceae	264	0.337	1.51	0.651	11
<i>Liatris punctata</i>	Asteraceae	133	0.256	1.33	0.492	12
<i>Paronychia jamesii</i>	Caryophyllaceae	606	0.348	1.33	0.767	15
<i>Psoralea tenuiflora</i>	Fabaceae	2310	0.271	1.20	0.581	11
<i>Ratibida columnifera</i>	Asteraceae	79	0.253	0.82	NA	3
<i>Schrankia uncinata</i>	Mimosaceae	74	0.338	1.76	0.574	13
<i>Scutellaria resinosa</i>	Lamiaceae	119	0.487	1.88	0.792	13
<i>Solidago glaberrima</i>	Asteraceae	244	0.324	1.38	0.601	8
<i>Solidago mollis</i>	Asteraceae	1370	0.263	1.06	0.701	11
<i>Solidago rigida</i>	Asteraceae	226	0.106	0.62	0.863	3
<i>Sphaeralcea coccinea</i>	Malvaceae	290	0.276	1.03	0.788	6
<i>Thelesperma megapotamicum</i>	Asteraceae	405	0.257	1.01	0.703	7
<i>Tragia ramosa</i>	Euphorbiaceae	147	0.408	2.00	0.604	25

STATISTICAL ANALYSIS

For each species, we calculated the observed life spans and estimated survival curves. These two analyses involved separate subsets of the data. Our analysis of observed life spans used all individuals, whether or not they were present in the first or last year of data collection. These life span estimates are conservative: plants present in year 1 may be more than 1-year-old, and plants present in the final year of data collection may have survived many more years. This negative bias is stronger for longer-lived plants. Therefore, the maximum observed life spans that we report for short-lived species can be used with confidence, whereas the results for long-lived species must be viewed as underestimates.

Our survival analysis was based on a subset of the data used to analyze life spans. First, new recruits appearing in the first observed year for each quadrat, or appearing after a missing year, were removed from the analysis. Second, individuals still alive in the last year of the data set, or disappearing during a missing year, were treated as right-censored data. We calculated Kaplan–Meier estimates (Kaplan & Meier 1958) of each species' survival curve using the 'survival' package in R 2.5.0 (R Development Core Team 2007). Kaplan–Meier estimates are equivalent to the traditional life table approach when data are complete (no censored observations). Based on these estimated survival probabilities, we then constructed full life tables (Anderson 1999). The number of genets used in the calculations ranged from a low of 55 for *Aster oblongifolius* and *Evolvulus nuttallianus* to more than 5000 for *Ambrosia psilostachya* (Table 1).

In order to classify each species' survivorship curve (Types I, II or III), we described each curve using the power function:

$$S_T = aT^b$$

where S_T is the (cumulative) survival at age T , and a and b are free parameters. When the exponent, b , is equal to 1, the annual survival rate is constant with age, corresponding to a Type II curve. When $b > 1$, the survival rate decreases with age, which is a Type I curve. When $b < 1$, the survival rate increases with age, which is a Type III curve. The distribution of b across species, therefore, provides a straight-forward way to characterize the shape of survivorship curves. We fit the power function using nonlinear weighted least squares regression, with the weights given by the sample size of each age class. If fewer than three ages were observed, as in the case of very short-lived species, we could not fit the power function.

For grasses, we used product–moment correlation coefficients to describe relationships between genet age and size, and individual plant age and size. We used generalized linear models, with a logit-link function, to test the relative importance of age and size in explaining variation in genet or individual survival. We compared the regression models using Akaike's Information Criterion (Burnham & Anderson 2002). Genets may be a single polygon or groups of polygons to which our tracking program has assigned a common identity and age. The area of the genet is the sum of all its constituent polygons. Because most field workers do not have information about genets from long-term spatially explicit observations, we repeated these

Table 2. Species, tribe, number of genets for life table analysis, first year survival (years 1 and 2), first year life expectancy, power exponent and maximum observed life span for 11 species of grasses from Hays, KS, USA

Species	Family/Tribe	N	Survival	Life expectancy	Power exponent	Maximum life span
<i>Andropogon gerardii</i>	Andropogoneae	1058	0.499	4.72	0.424	31
<i>Aristida longiseta</i>	Aristideae	82	0.329	2.26	0.355	21
<i>Bouteloua curtipendula</i>	Cynodonteae	1841	0.508	3.16	0.579	39
<i>Bouteloua gracilis</i>	Cynodonteae	914	0.456	3.03	0.509	35
<i>Bouteloua hirsuta</i>	Cynodonteae	265	0.634	6.53	0.590	37
<i>Buchloë dactyloides</i>	Cynodonteae	1040	0.454	2.16	0.675	35
<i>Panicum virgatum</i>	Panicaceae	210	0.481	2.66	0.633	13
<i>Schizachyrium scoparium</i>	Andropogoneae	320	0.381	3.81	0.261	39
<i>Sitanion hystrix</i>	Triticeae	125	0.304	1.03	0.837	5
<i>Sporobolus asper</i>	Eragrosteae	107	0.374	3.51	0.408	26
<i>Sporobolus cryptandrus</i>	Eragrosteae	327	0.431	2.66	0.607	29

analyses at the scale of individual plants (each polygon defined as one plant). Our identity tracking program allows an individual plant to die even if the genet to which it belongs survives.

Results

COMMUNITY COMPOSITION

The species for which we have demographic data are important constituents of their communities. We assessed species importance by summing relative density and relative basal cover and scaling the result between 0 and 100. Grasses are the overwhelming dominant life form in all four communities (Fig. 1). The big bluestem community is dominated by *A. gerardii* (big bluestem) and *B. curtipendula* (sideoats grama). Of the 10 most important species, in this community, six are grasses and four are forbs. We have detailed demographic information for all 10 species. The little bluestem community has the least clear dominance structure. Five species of grasses have importance values > 10. Seven of the 10 most important species are grasses and three are forbs. All are represented in our demographic data set. The ecotone community is dominated by *B. gracilis* (blue grama) and *Bu. dactyloides* (buffalograss). It was designated an ecotone because it contains all of the dominants from the other communities within the 10 most important species (six grasses and four forbs). The shortgrass community is dominated by *Bu. dactyloides* and *B. gracilis*. Five of the top 10 species are grasses and five are forbs. All are represented in our demographic data set.

SURVIVAL, LIFE EXPECTANCY AND LIFE SPAN

Survival during the first few years of life was low for all species. First year survival (between years 1 and 2) for grasses ranged from 0.304 for *Sitanion hystrix* to 0.634 for *B. hirsuta* with an average of 0.441 (Table 2). First year survival for forbs ranged from 0.106 for *Solidago rigida* to 0.487 for *Scutellaria resinosa* and averaged 0.302 (Table 2). Such low early survival means that life expectancy at age 1 is also low (Tables 1 and 2). Life expectancy at year 1 ranged from 0.62 to 2.47 years for forbs,

and 1.03 to 6.53 years for grasses. Age-dependent life expectancies were parabolic (opening downward) for all species except three of the forbs with the shortest life spans (Appendices 1 and 2). The correlation between the ages at peak life expectancy and first year survival was significant for all species ($r = 0.53$; $P \leq 0.05$) and forbs ($r = 0.45$; $P \leq 0.05$), but not for grasses alone.

Maximum observed life spans ranged from 3 to 39 years (Tables 1 and 2). Two species of forbs had 3 year maximum life spans and two species of grasses had 39 year life spans. While the uncertainty associated with all of the observed maximum life spans is high because only a single individual achieved that age for each species, the longest life spans are especially uncertain because they were equal to the length of the data set. All of the longest lived species were grasses and the shortest were forbs. Six of the 11 grasses had maximum life spans of > 30 years. The shortest lived grass was *S. hystrix*, with a maximum life span of 5 years. By contrast, 15 forb species had maximum life spans ≤ 10 years. The longest lived forb, *Tragia ramosa* had a maximum life span of 25 years. Maximum observed life spans and estimated life expectancies at year 1 were significantly correlated ($r = 0.85$; $P \leq 0.05$).

Analysis of log survival vs. age suggested that all of our species had Type III survivorship curves, characterized by power exponents ranging from 0.261 to 0.863 (Tables 1 and 2) (Deevey 1947). Type III species have increasing survival (or decreasing mortality) rates throughout their life spans. The highest mortality rates are experienced by the youngest age classes. The species with power exponents approaching 1 arguably had survivorship curves more similar to Type II than Type III. Six forbs and a single grass had power exponents ≥ 0.7 . On average, forbs had larger power exponents than grasses (0.635 vs. 0.534) suggesting that they are closer to Type II species than are the grasses.

We chose three grasses and three forbs to illustrate the range in survivorship curves represented among our species. The distinction between Type II and Type III can be captured by how close to a straight line the curve is (Type II) or how concave the curve is (Type III). The two species with survivorship curves approaching the Type II model are *S. hystrix* and *Paronychia jamesii* with power exponents of 0.832 and 0.767,

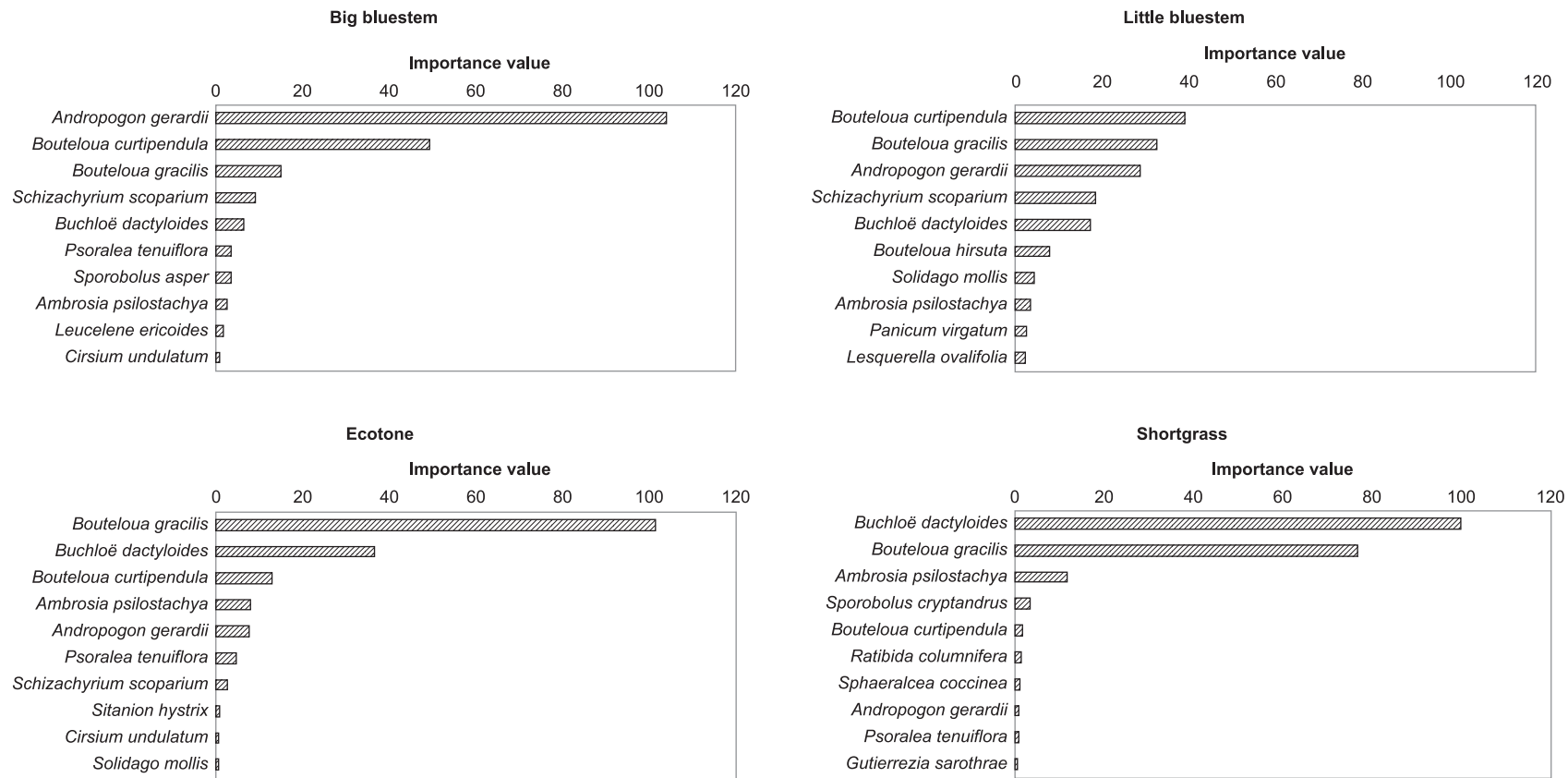


Fig. 1. Importance values for the top 10 species in each of the four plant community types (Big Bluestem, Little Bluestem, Ecotone and Shortgrass) at Hays, KS, USA.

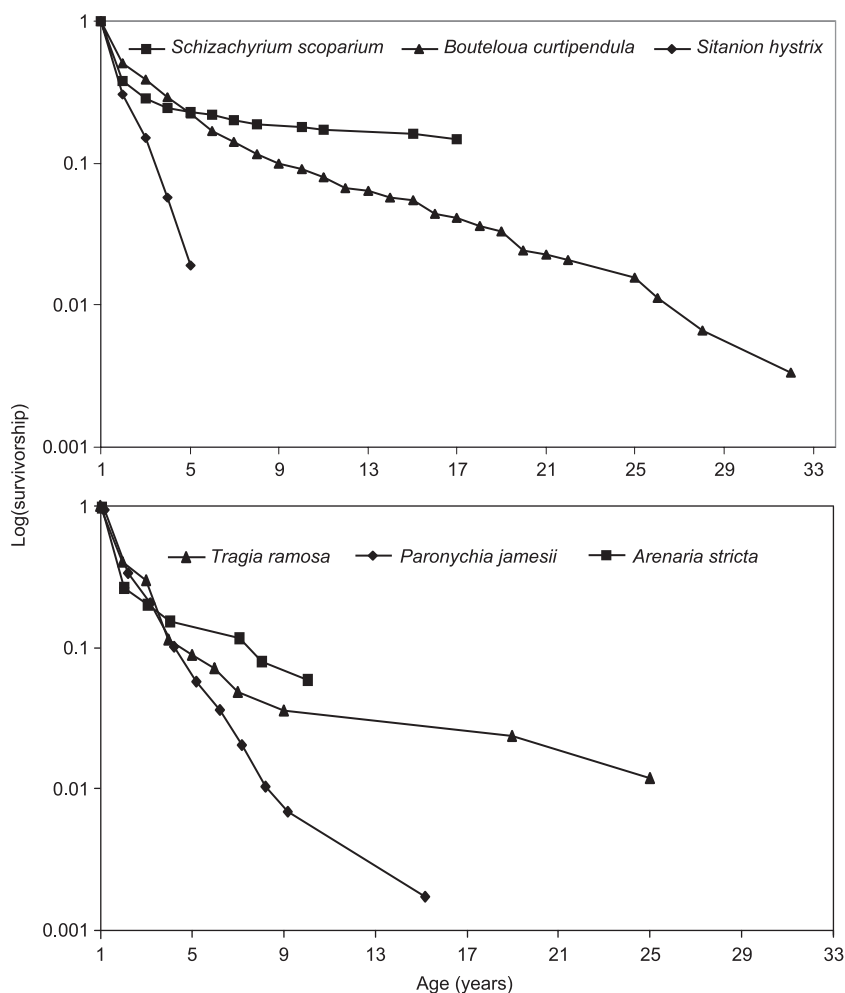


Fig. 2. Log survivorship vs. age curves for three grasses and three forbs representing short, medium and long life spans at Hays, KS, USA.

respectively (Fig. 2). The grass *Sc. scoparium* and the relatively short life span forb, *Arenaria stricta* are the clearest representatives of Type III species. They have power exponents of 0.261 and 0.349 respectively. The longest life span forb, *T. ramosa*, and one of the longest life span grasses, *B. curtipendula*, are both examples of species that fall between the Type III and Type II models. The survivorship curve for *Tragia* is slightly more concave than the one for *Bouteloua*. They have power exponents of 0.604 and 0.579 respectively.

Maximum observed life span and year 1–2 survival were significantly positively correlated ($P < 0.01$; $r = 0.74$; Fig. 3). For both the forbs and the grasses, the species with the longest life spans had the highest first year survival. *Ratibida columnifera* and *So. rigida*, the two forb species with the shortest life spans, had first year survival of 0.253 and 0.11 respectively (Table 2). The forb with the longest life span, *T. ramosa*, had a first year survival of 0.408. With their longer maximum life spans, the grasses fall into the upper right hand portion of the relationship (Fig. 3). The grass with the shortest life span, *S. hystrix* overlapped with the forbs with a first year survival of 0.304 (Table 2). The grass with the greatest first year survival, *B. hirsuta*, had a maximum observed life span of 37 years. The grasses with the longest life spans, *B. curtipendula* and *Sc. scoparium*, had first year survivals of 0.508 and 0.381 respectively.

Table 3. Correlation coefficients for the relationship between age and size for 11 species of grasses from Hays, KS, USA. All of the correlation coefficients were significant at $P < 0.05$. See Methods for the distinction between plants and genets

Species	Plant	Genet
<i>Andropogon gerardii</i>	0.06	0.41
<i>Aristida longiseta</i>	0.51	0.68
<i>Bouteloua curtipendula</i>	0.08	0.34
<i>Bouteloua gracilis</i>	0.12	0.45
<i>Bouteloua hirsuta</i>	0.27	0.43
<i>Buchloë dactyloides</i>	0.07	0.30
<i>Panicum virgatum</i>	0.15	0.29
<i>Schizachyrium scoparium</i>	0.48	0.62
<i>Sitanion hystrix</i>	0.36	0.40
<i>Sporobolus asper</i>	0.14	0.54
<i>Sporobolus cryptandrus</i>	0.11	0.30

Size and age were significantly positively correlated ($P < 0.05$) for all 11 grass species (Table 3). The correlations for genets were stronger than for individual plants and in many cases substantially greater. The strength of the relationship between size and age at the plant scale was very low ($r \leq 0.15$) for seven of the nine grasses. At the genet scale, seven of the

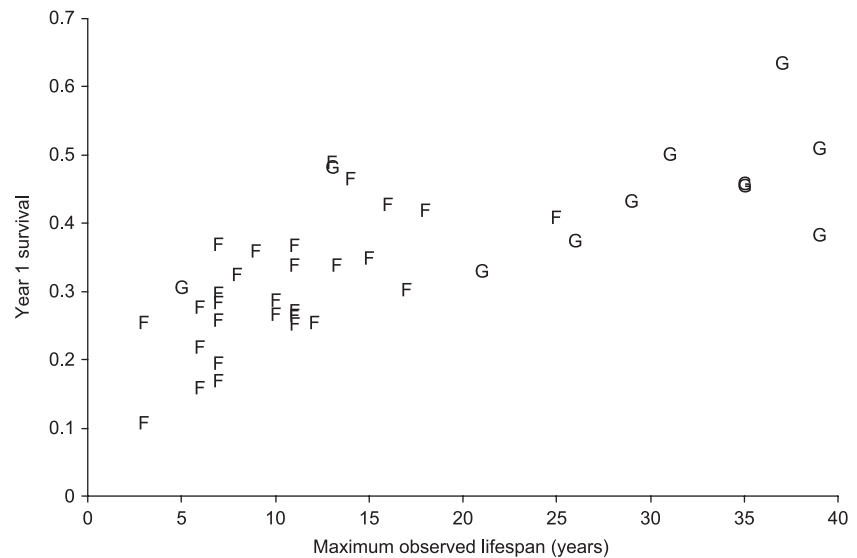


Fig. 3. Relationships between first year survival (from age 1 to 2) and life expectancy at year 1 for 29 species of forbs and 11 species of grasses at Hays, KS, USA.

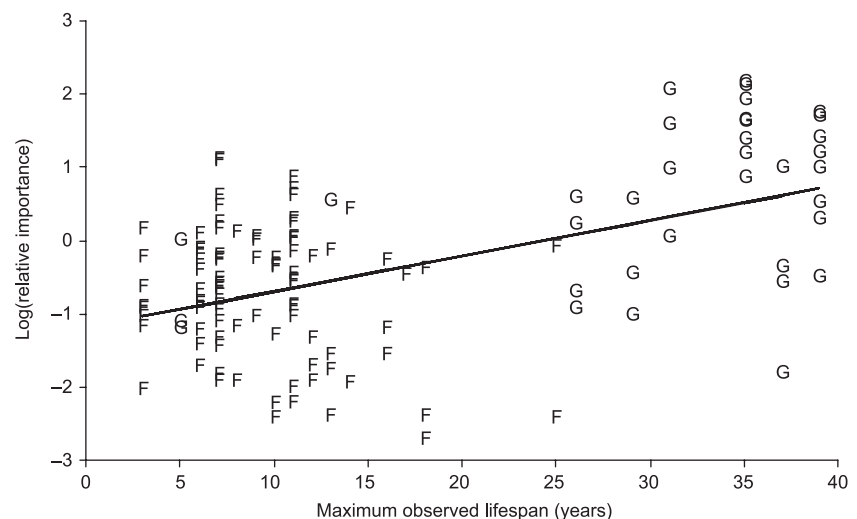


Fig. 4. Log relative importance as a function of maximum observed age for 29 species of forbs and 11 species of grasses in three plant communities and an ecotone at Hays, KS, USA. Each species had just one value for maximum observed life span, but may have had several importance values depending on the number of communities in which it occurred.

nine correlation coefficients were ≥ 0.4 . Models that related first year survival to age alone had the most support for all 11 grasses at the plant scale. At the genet scale, the model for *S. hystris* with size as the sole variable was most supported by the data. For nine of the remaining 10 species, models with age alone received the most support. A model with both age and size was most strongly supported by the data for *Sporobolus cryptandrus*.

DEMOGRAPHY AND COMMUNITY COMPOSITION

The relative importance of our 40 species of grasses and forbs was significantly and positively (exponentially) related to maximum observed life spans ($r^2 = 0.25$; $P < 0.001$; Fig. 4). The longest lived species, most of which were grasses, contributed the largest amounts to community basal area and density. The significant relationships between life span and first year survival, and between life span and life expectancy at age 1 mean that relative importance should also be significantly related to both survival and life expectancy.

Discussion

Our demographic analysis of 40 of the most important plant species in central North American Great Plains grasslands revealed several generalizations about survival, life expectancy and life span. First, much of the variation in survival was explained by life form: forbs had much lower survival rates and life expectancies than grasses. However, most grassland plants die young regardless of life form, with only a few individuals approaching each species' maximum observed life span. Second, we found a relationship among life form, longevity and the shape of survivorship curves. Third, relationships between age and size were very weak at the scale of individual plants, which is the scale commonly observed in the field. These relationships were substantially stronger at the genet scale. Fourth, age was a more useful variable than size in predicting survival from one year to the next. Finally, the relative importance of a species was significantly and positively related to its demographic parameters: first year survival, life expectancy at age 1 and maximum observed life span.

Grasses on average had higher survival rates, longer life expectancies and longer maximum observed life spans than forbs. However, while grasses have the potential to live much longer than forbs, we found that even for the longest lived grasses most individuals die young. For all species (grasses and forbs), the highest life expectancy at age 1 was 6.5 years and the mean was 1.9 years. The average life expectancy at age 1 for grasses was 3.2 years. Only a few individuals escape early death (Appendices 1 and 2). Furthermore, it is almost certain that seedling mortality, occurring early in the growing season before our quadrats were censused, is even higher. Low early survival probabilities are commonly reported for herbs (Dittberner 1971; West *et al.* 1979; Silvertown & Dickie 1980; Mack & Pyke 1983; Ehrlén & Lehtilä 1998; Garrido *et al.* 2007).

The relationship between log survival and age provides us with another set of generalizations about survival across species and plant types (Tables 1 and 2). While strictly speaking all of our species had Type III survivorship curves (power exponents < 1), on average the forbs had larger power exponents than the grasses (0.635 vs. 0.534) suggesting they had closer to constant mortality with age than did the grasses. Both Types II and III survivorship curves have been commonly reported for herbs (West *et al.* 1979; Morris & Doak 1998; Hamann 2001; Silvertown *et al.* 2001).

Longevity and the shape of survivorship curves are related to life form (forbs vs. grasses), suggesting an evolutionary explanation. Reinforcing this finding is that the age at which life expectancy peaked was also correlated to maximum observed life span ($r = 0.71$, $P \leq 0.05$). As demographic data on more species in these communities becomes available, phylogenetic comparisons could shed light on the evolutionary relationship between longevity and the type of survivorship.

Ehrlén & Lehtilä (1998) asked how perennial were perennial plants and suggested that accurate estimates of life span are crucial to our understanding of evolutionary relationships and population and community dynamics. The demographic literature on herbaceous perennial plants makes clear that there are very few field data on life span; most of the estimates are derived from stage-structured demographic analyses (Cochran & Elner 1992; Ehrlén & Lehtilä 1998; Silvertown *et al.* 2001). Further, most of the field data used to estimate matrix elements for stage-structured analyses does not distinguish between ramets and genets and therefore the convention is to assume they are the same even when it is known that a plant or a portion of the plants being analyzed are clonal (Silvertown *et al.* 2001). Our results suggest that the strength of the relationship between age and size is different for ramets than for genets and is much stronger for genets (Table 3). Furthermore, contrary to the assumption that size is a more important predictor of important demographic characteristics, we found that size was an inferior predictor of survival for perennial grasses, many of which are the dominant species in central North American grasslands. At both the plant and genet scales, models including age were more strongly supported by the data in 21 out of 22 cases (Table 4). Models that included both age and size were preferred in only three cases.

Table 4. Akaike's Information Criterion for regression analysis of first year survival for models that included age, size, age², age \times size or age² \times size for 11 species of grasses from Hays, KS, USA. Numbers in bold indicate the model with the most support for each species

Species	Plant scale					Genet scale				
	Age	Size	Age ²	Age \times size	Age ² \times size	Age	Size	Age ²	Age \times size	Age ² \times size
<i>Andropogon gerardii</i>	6830.74	6831.63	6697.30	6829.47	6697.41	2795.79	2851.96	2797.73	2797.49	2799.45
<i>Aristida longiseta</i>	162.43	162.31	161.34	164.22	163.23	144.93	145.26	145.86	145.48	146.96
<i>Bouteloua curtipendula</i>	6413.18	6411.34	6411.19	6411.97	6410.56	3998.81	4044.46	3999.14	4000.72	4000.93
<i>Bouteloua gracilis</i>	3496.59	3541.86	3495.12	3498.03	3496.45	2101.62	2110.76	2102.80	2103.51	2104.32
<i>Bouteloua hirsuta</i>	1206.34	1206.02	1201.34	1205.74	1202.05	904.21	907.88	905.34	906.12	907.34
<i>Buchloe dactyloides</i>	2701.58	2711.20	2703.22	2702.65	2704.41	1904.46	1928.70	1906.39	1906.04	1907.97
<i>Panicum virgatum</i>	573.03	573.55	574.97	574.90	576.87	456.47	458.48	458.22	458.05	459.93
<i>Schizachyrium scoparium</i>	738.52	748.77	735.44	740.52	737.33	642.23	650.89	640.00	644.22	641.99
<i>Sitanion hystrix</i>	181.34	181.50	183.21	183.25	185.15	172.79	172.71	174.46	174.63	176.37
<i>Sporobolus asper</i>	387.88	390.00	389.73	389.29	391.27	293.23	296.77	295.20	293.94	295.85
<i>Sporobolus cryptandrus</i>	1010.35	1010.72	1011.45	1011.38	1012.84	844.48	845.95	845.73	842.88	844.73

Plant communities in central North America that are not dominated by woody plants are dominated by grasses, not forbs. Grasses dominate Great Plains plant communities despite the fact that they often account for fewer than 15% of the herbaceous plant species (Lauenroth 2008). For each of three community types and an ecotone the 10 most important plant species were approximately evenly divided between grasses and forbs (Fig. 1). Yet for all communities, grasses occupied the highest ranks, accounting for an overwhelming portion of total species importance. In addition to their importance, the grasses are more constant in time than the forbs. Adler & Lauenroth (2003) used species–time relationships to show that the high rates of species turnover in these plant communities were driven by the rapid dynamics of the forbs.

Our data suggest that the species with the highest first year survivals, life expectancies at age 1 and maximum observed life spans are the most likely to be the dominant species in the central Great Plains communities we studied. While there is considerable variation around this relationship (Fig. 4), the fact that it exists for 40 species across three plant community types and an ecotone suggests that the pattern is robust. To be sure, a long maximum life span does not guarantee large relative importance. For example, *B. hirsuta* is one of the longest life span species in our data set (Table 2), but ranks in the top ten most important species in only the Little Bluestem community (Fig. 1). From a statistical perspective, however, a long life span increases the probability of dominance. The link between longevity and species turnover is even stronger, as demonstrated by recent work showing that longer life spans are related to greater species persistence through time (Ozinga *et al.* 2007). The higher survival, life expectancy and life span of grasses compared to forbs may provide a demographic explanation for community-level differences in the dominance and turnover of these two functional groups.

The relationship between longevity and dominance may depend on disturbance, an important influence on species composition and dominance in plant communities (Pickett & White 1985). The ability of some forbs to rapidly colonize disturbed sites compared to the slow recovery of perennial grasses (Albertson & Tomanek 1965; Coffin *et al.* 1996) suggests that forbs have much higher recruitment rates and that a survival–recruitment trade-off may exist in these herbaceous perennials. In sites with low disturbance rates such as our permanent plots, the survival–recruitment trade-off would favour the grasses with their high survival rates and long life spans. While survival and life span are commonly considered predictors of dominance in the forest ecology literature (Grime 2001; Lorimer *et al.* 2001), explanations for dominance in herbaceous communities rarely mention life span as an explanatory variable (Tilman 1988; Grime 2001). Evidence of a relationship between longevity and dominance from additional herbaceous plant communities would imply that basic life-history traits can be important in predicting community structure across a wide range of environments.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Life tables for forbs based on Kaplan-Meier survival estimates.

Appendix S2 Life tables for grasses based on Kaplan-Meier survival estimates.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2745.2008.01415.x>
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