

Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals

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Summary

1 We analysed a data set containing the locations and sizes of individual plants from five 1-m² permanent quadrats that had been mapped annually from 1934 to 1972. We digitized each map and used geographical information software to evaluate annual recruitment and mortality, age structure, survivorship and longevity of genets and individuals of *Bouteloua gracilis*.

2 Ninety-one per cent of the years between 1938 and 1972 had at least one seedling recruited. An average of 10.3 genets died annually, although the variability among years was high (CV = 70%). The number of seedlings recruited each year was significantly correlated with the number of genets dying. Most genets died before age 10 and the average life span was 3.7 years, although some genets were much longer lived (> 38 years).

3 The average number of individuals per genet was 1.3. Excluding seedlings, 56% of the genets were represented by a single individual. The annual number of individuals in the 5 m² ranged from 29 to 278. Average mortality of individuals was 25.8 per year and the variability among years was high (CV = 91%).

4 The plant community appeared to be relatively stable and openings created by mortality were recolonized by recruitment. Climatic variability did not have a large influence on demography.

Keywords: clonal fragmentation, grassland, mortality, plants, recruitment

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Introduction

Studies that document the recruitment, growth and death of plant genets through time and space require long-term monitoring of individual plants. Because collection and analyses of such data are time-consuming, detailed demographic data sets are rare and published analyses are even rarer (Harper 1977; White 1985). This is especially true for herbaceous perennial plants where individuals may either be genets started from seed or genetically identical ramets that resulted from fragmentation (Harper 1977; White 1985). The differentiation of genets from ramets is difficult if not impossible to do in the field, yet is critical to understanding population dynamics and the ability of a species to respond to change in the environment. Demographic studies that consider the dynamics of both genets and ramets are extremely valuable to our understanding of plant population dynamics, and can help define the underlying evolutionary mechanisms

that determine the structure and succession of plant communities (Harper 1977, 1982; Hartnett & Bazazz 1985).

Demographic studies on plant populations are relevant to evolution because they reveal patterns in population size, genetic variability and vulnerability to selection pressures (Harper 1977; Hartnett & Bazazz 1985). Information about genet survivorship and age structure can distinguish between even-aged and multiple-aged populations, with important consequences for our understanding of natural selection (Harper 1977). For instance, a population consisting of genets of various ages that have survived slightly different selective processes may be more tolerant of environmental variation or disturbance than a population consisting of clones that are all of a similar age (Demetrius 1975; Harper 1977).

In field studies of herbaceous plants, the type of individual plants most often sampled are autonomous individuals that are fragments from genets (Coffin & Lauenroth 1988). The number and size of these fragments, as well as their mortality rates, determine the size and fitness of particular genets (Harper 1977;

Harper & Bell 1979; Hartnett & Bazazz 1985). Comparing the dynamics of genets and individual plants can be useful in characterizing the genetic variability in a population as well as evaluating how well field studies represent the gene pool.

Demographic studies of plant populations also have relevance to gap-phase dynamics. In this case, the spatial and temporal dynamics of a plant community can be assessed by correlating the demography of genets and individual plants of the dominant species with the corresponding successional phases of the associated microsites (Watt 1947). The demography of mature genets and their associated individual plants can thus be related with the gap, building, mature and degenerate phases of microsites within the community. Quantifying these phases can allow the prediction of important community dynamics, such as in the use of annual mortality rates to predict the frequency of creation of gap openings.

Bouteloua gracilis [H.B.K.] Lag ex. Griffiths (blue grama) is a C₄ perennial bunchgrass that is widely distributed throughout the central grassland region of North America (nomenclature follows Great Plains Flora Association 1986). It dominates shortgrass communities and is a codominant in the southern mixed grass prairie (Weaver & Albertson 1956; Albertson & Tomanek 1965; Lauenroth & Milchunas 1992). Its relative importance increases with grazing by cattle and decreases as annual precipitation increases (Weaver & Albertson 1956; Milchunas *et al.* 1989; Epstein *et al.* 1996). Although *B. gracilis* is recognized as a key species in these grasslands, its ability to maintain dominance in the presence of disturbance is a controversial issue.

The shortgrass steppe and southern mixed grass prairie are subject to a number of types of disturbances, each with its characteristic size and frequency of occurrence (Coffin & Lauenroth 1988; Umbanhowar 1992). Because *B. gracilis* tillers slowly (Samuel 1985) and reproduces by seed infrequently (Lauenroth *et al.* 1994), the ability of this species to recover after disturbance has been questioned (Costello 1944; Hyder & Everson 1968; Hyder *et al.* 1971). Recent experimental studies and simulation analyses of different disturbance types and sizes have indicated the importance of knowledge about life-history traits of *B. gracilis* in understanding recovery rates and patterns (Coffin *et al.* 1993, 1996; Coffin & Lauenroth 1994).

Despite the value of demographic studies that focus on genets and individual plants, they are very infrequently encountered in the literature (van der Maarel 1996; Bakker *et al.* 1996). Our overall objective was to evaluate the demography of genets and individual plants of *B. gracilis* in a southern mixed prairie. Our specific objectives were to: (i) quantify the demography of *B. gracilis* genets in terms of annual recruitment and mortality, age structure and survivorship, and longevity; (ii) determine temporal

trends in the relative importance of sexual reproduction vs. fragmentation by comparing number of genets to number of individuals for each year, and by calculating the number of individuals per genet; and (iii) determine annual mortality of individual plants to assess the potential for gap dynamics in this community.

Site description

This study took place in a southern mixed prairie near Hays, Kansas, USA (38°52'N latitude, 98°23'W longitude), in pastures owned by Fort Hays State University. Long-term mean annual precipitation is 588 mm (Sims *et al.* 1978), with 77% occurring between April and September as irregularly spaced thunderstorms (Albertson & Tomanek 1965). Mean annual air temperature is 12.1 °C, mean growing season air temperature is 18.4 °C, and the thermal potential growing season is 226 days (Sims *et al.* 1978). The region has a history of being grazed by bison and antelope over the past 8000–10 000 years (Stebbins 1981) and the pastures have been grazed by domestic cattle for the past 100 years (R.A. Nicholson, personal communication).

Three plant communities are common in the area: a shortgrass community dominated by *B. gracilis* and *Buchloë dactyloides* (Nutt.) Engelm. (buffalo grass); a little bluestem community dominated by *Schizachyrium scoparium* (Michx.) Nash with small amounts of *Andropogon gerardii* Vitman; and a little bluestem–big bluestem community that supports varying amounts of *S. scoparium*, *A. gerardii*, *Bouteloua curtipendula* (Michx.) Torr., and *B. gracilis* (Albertson & Tomanek 1965). The focus of our study was the shortgrass communities in which *B. gracilis* is the dominant species. Shortgrass communities are most often located in uplands on silty clay to silty clay loam soils (Albertson & Tomanek 1965; Heitschmidt *et al.* 1970).

Methods

DATA DESCRIPTION AND DIGITIZATION

Over 70 chart quadrats (1 m²) were established in 1932 by F.W. Albertson and mapped annually from 1932 to 1972. Cattle exclosures were built around a portion of the quadrats, to protect them from grazing. Within each quadrat, the perimeter of each plant was traced onto paper using a pantograph, and labelled by species (Hill 1920). Charts were planimeted to document changes in total basal cover of species through time (Albertson & Tomanek 1965), but these data have not been used previously to document demography of individual plants or genets. Because the quadrats were mapped by different individuals over the 40 years of data collection, a portion of the variability among years is certainly due to differences in recorders.

Five 1-m² quadrats, all located within the same enclosure and in a shortgrass community, were selected for this study. Either or both of *B. gracilis* and its codominant, *B. dactyloides*, had been recorded in each year in each selected quadrat. All individual plants in each chart quadrat in each year were manually digitized using ARC/INFO software (ESRI, Redlands, CA). We did not digitize quadrats from 1932 and 1933 because no distinction was made between *B. gracilis* and *B. dactyloides* plants in these years. Analysis for one quadrat therefore started in 1934, two in 1935, and two in 1938; maps were available for all five quadrats for all years between their start and 1972. Annual recruitment and mortality of genets, total numbers of genets and individuals per year, and annual mortality of individuals were estimated starting in 1938, the first year that contained data from every quadrat. Genet survivorship and longevity were estimated using all of the digitized quadrats, including those before 1938, because the objective was to discover the longest living genets and not to compare data between specific years.

ANALYSIS PROCEDURE

We used a geographical information system (ARC/INFO) to analyse the temporal dynamics of each *B. gracilis* genet and its associated individuals. Seedlings were followed through growth stages, including fragmentation and merging of plants, until all plants from a particular genet either died or the data ended. A genet was defined as all of the individuals that derived from a single seedling. An individual *B. gracilis* plant was defined as all tillers connected by a single crown, regardless of genetic origin (Coffin & Lauenroth 1988).

Individuals were identified and aged by overlaying digitized chart quadrats from consecutive years. Any individual that completely overlapped or was within 5 cm of a conspecific individual from the previous year was recorded as the same plant, and its life span was incremented 1 year. The 5-cm buffer between concurrent years accounted for inconsistencies in mapping of quadrats and in the overlaying process (Wright & Van Dyne 1976; West *et al.* 1979). When individuals merged, all were incremented in age every year, regardless of genetic identity, until the space occupied when they merged was free of *B. gracilis* individuals.

Recruitment of *B. gracilis* by seedlings occurs infrequently in the shortgrass steppe (Hyder *et al.* 1971; Lauenroth *et al.* 1994) and a similar situation has been suggested for the southern mixed prairie (Savage 1937; Weaver & Mueller 1942). Therefore, throughout our analysis we assumed that clonal spread of *B. gracilis* plants prevailed over seedling recruitment, and the most conservative approach to adding seedlings was employed (Albertson *et al.* 1966). A seedling was assigned a genet identification

number if it did not overlap with and was at least 5 cm away from individuals present in the previous 2 years. The 5-cm buffer minimized the possibility that vegetative spread would be confused with seedling recruitment. The establishment of *B. gracilis* seedlings within 5 cm of a conspecific adult plant is unlikely (Aguilera & Lauenroth 1993), especially since at least 75% of the roots of an adult *B. gracilis* plant are found within 5 cm of the crown (Coffin & Lauenroth 1991; Hook *et al.* 1994). Thus new plants found at distances equal to or greater than 5 cm from established plants were likely to be seedlings. The 2-year leeway required between old individuals and new seedlings provided a conservative estimate of seedling recruitment. The number of new genets recruited annually was estimated by summing the number of new genets recorded for each year.

Data from 1934 to 1937 were used to identify seedling origin, and thus genet identification of individuals present in 1938. Fragmentation of genets recruited before 1938 was followed to determine genet identity. More individuals than genets existed in 1938 because some genets had fragmented prior to 1938. Some individuals present when data collection started were not included in this study because their genet identity could not be determined. Individuals located within 5 cm of the edge of a quadrat were also excluded as their origin and destiny were uncertain.

Mortality of a genet occurred when all fragments (individuals) belonging to that genet died. Mortality of an individual occurred when it was no longer found in the quadrat. Because data collection ended in 1972, we could not follow the fate of genets or individuals after 1971, and therefore mortality estimates ended in 1970.

A survivorship curve for *B. gracilis* genets was obtained by subtracting the number of genets that died in each age class in 1 year from the number of surviving plants of the next age class in the following year (Deevey 1947). Age of death for each genet was determined by subtracting the year each seedling was recruited from the year that the last individual of that genet died. Age class was estimated by the number of years that a genet was mapped.

Since 11% of the original population of genets was still alive when data collection ended, the survivorship curve was calculated using the 374 genets that died during the study. Mean genet longevity was estimated by averaging life spans of the genets that died. Maximum longevity was estimated using the maximum age of the 46 genets alive in 1972.

Growth patterns of individual *B. gracilis* plants were examined by comparing the number of genets to total number of individuals in the same year, and by calculating number of individuals per genet. These comparisons show how genets occupy space in a plant community and address whether the population of individual plants is made up largely of clonal fragments or different genotypes. The total number of

genets from the five quadrats was calculated by summing the number of genets each year. The total number of individuals was calculated from the number of individual plants each year.

Results

CLIMATE

Annual precipitation was variable during the study, with the wettest year occurring in 1951 (1101 mm) and the driest in 1952 (340 mm) (Fig. 1a). Two major droughts occurred (1933–39, 1952–56) during which annual precipitation remained below average. Another, less severe drought occurred between 1964 and 1972, in which annual precipitation was below average in 4 out of 9 years and near average for the remaining 5 years. Mean annual maximum, mean, and minimum temperatures were average to above-average from 1931 to 1955, and average to below-average from 1956 to 1972 (Fig. 1b).

GENET DEMOGRAPHY

Recruitment of *B. gracilis* seedlings occurred frequently between 1938 and 1972; 91% of the years had

at least one seedling recruited in at least one of the five quadrats (Fig. 2). A total of 420 seedlings was recruited during the 35 years, and the average annual number recruited was 10.2 (SD = 7.1). Recruitment was variable in that peak recruitment was 30 seedlings in 1961 and years of minimal recruitment (1963, 1964 and 1969–72) had < 3 seedlings each year. Mean *per capita* recruitment rate was 0.158 per year, with a standard deviation of 0.107 per year. Annual recruitment was not related to current year's annual precipitation or 1 and 2 year's previous precipitation but it was significantly correlated ($r = 0.576$; $P < 0.001$) to mean temperature in that year.

Mortality of *B. gracilis* genets also occurred frequently, as at least one genet died in each year somewhere in the 5-m² area (Fig. 3). From 1938 to 1970 (33 years), a total of 374 genets died, with an average of 10.3 per year (SD = 7.2). High variability in the number of genet deaths was observed through time, with a maximum of 31 in 1938 and a minimum of 2 in 1942, 1952, 1953 and 1970. The average per capita mortality rate was 0.155 (SD = 0.106). No relationship was found between mortality of genets and climatic variables, including current year's annual precipitation, 1 and 2 year's previous precipitation, or maximum, mean or minimum annual temperature.

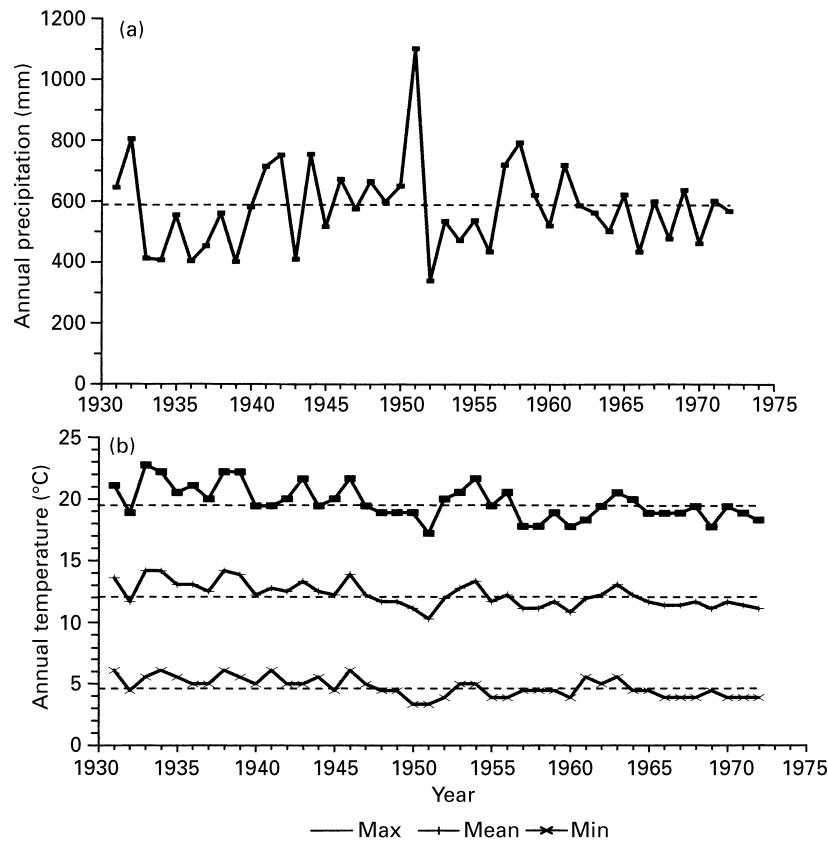


Fig. 1 Climatic variables from data collected at Hays, Kansas (1931–72). (a) Annual precipitation [dashed line is the long-term (93 years) average of 588 (mm)]; (b) annual maximum, mean and minimum temperatures (dashed lines are long-term averages of 19.5 °C, 12.1 °C, and 4.6 °C for maximum, mean and minimum annual temperatures, respectively).

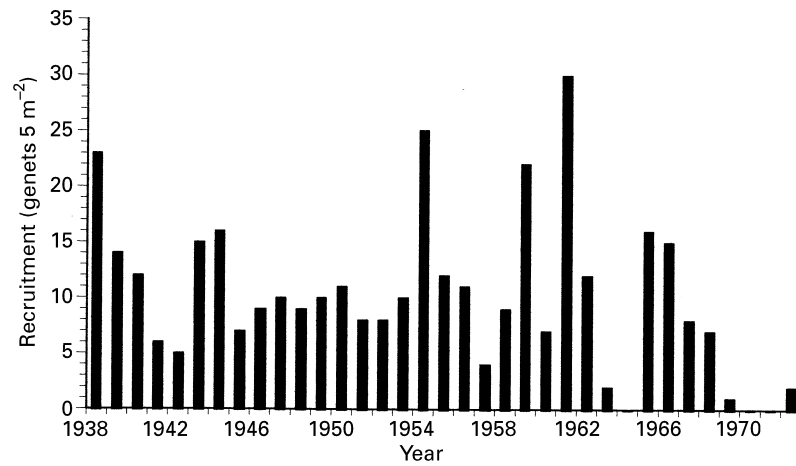


Fig. 2 Number of *Bouteloua gracilis* genets recruited annually in five 1-m² quadrats from 1938 to 1972. Individuals were new recruits if they occurred in a space free of *B. gracilis* for 2 years prior to their establishment.

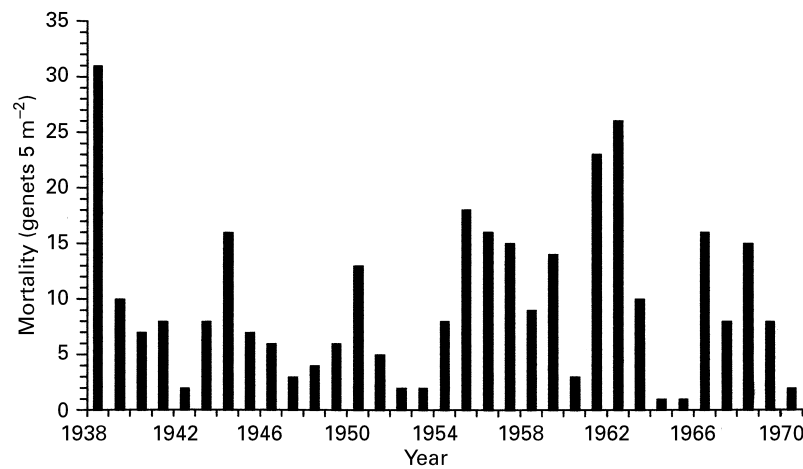


Fig. 3 Number of *B. gracilis* genets that died annually in five 1-m² quadrats from 1938 to 1970. Genets were considered dead in the year that the last remaining individual from a particular genet died.

The number of seedlings recruited each year was significantly correlated to the number of genets dying ($r = 0.53$; $P < 0.01$).

GENET SURVIVORSHIP AND LONGEVITY

Fewer than 50% of all genets reached an age of 2 years and more than 90% died before they reached 10 years (Table 1). Mortality was highest for the first two age classes (Table 1, Fig. 4a). The average life span of a genet was 3.7 years. Life expectancy increased substantially for those genets surviving the first 2 years (Table 1). Because these averages do not include the genets alive in 1972, when data collection ended, they are both underestimates. The maximum life span was estimated using the 46 genets that were alive in 1972 when data collection ended. Of these, more than half had lived at least 20 years (Fig. 4b). From the total population of 420 genets observed during the sample period, only 19 (4.5%) lived longer than 30 years. Maximum longevity of genets is at least

38 years since three genets present at the start of the study were still present when recording ended.

GROWTH AND FRAGMENTATION OF GENETS

The mean numbers of genets and individuals per year in the 5-m² area was 66 (SD = 21) and 95 (SD = 63), respectively. The number of genets was less variable [coefficient of variation (CV) = 32] than that of individuals (CV = 66) and ranged from 34 in 1942 to 110 in 1961, while the number of individuals ranged from 29 in 1942 to 278 in 1961 (Fig. 5a). For both genets and individuals, numbers were average or below-average for the first 14 years, then above-average from 1952 to 1962, followed by average and below-average numbers until 1972. Minimum (1942) and maximum (1961) years for both numbers of genets and individuals were the same.

The number of individuals was similar to the number of genets from 1938 to 1952, and from 1965 to 1972 (Fig. 5a). The average number of individuals per

Table 1 Partial life table for genets of *Bouteloua gracilis* over 38 years in a southern mixed prairie

| Age x | Number N_x | Survival l_x | Mortality d_x | Mortality rate q_x | Survival rate p_x | Life expectancy e_x |
|------------|-----------------|-------------------|--------------------|-------------------------|------------------------|--------------------------|
| 1 | 374 | 1.000 | 0.503 | 0.503 | 0.497 | 3.198 |
| 2 | 186 | 0.497 | 0.144 | 0.290 | 0.710 | 4.925 |
| 3 | 132 | 0.353 | 0.067 | 0.189 | 0.811 | 5.735 |
| 4 | 107 | 0.286 | 0.059 | 0.206 | 0.794 | 5.958 |
| 5 | 85 | 0.227 | 0.043 | 0.188 | 0.812 | 6.371 |
| 6 | 69 | 0.184 | 0.019 | 0.101 | 0.899 | 6.732 |
| 7 | 62 | 0.166 | 0.024 | 0.145 | 0.855 | 6.435 |
| 8 | 53 | 0.142 | 0.024 | 0.170 | 0.830 | 6.443 |
| 9 | 44 | 0.118 | 0.019 | 0.159 | 0.841 | 6.659 |
| 10 | 37 | 0.099 | 0.011 | 0.108 | 0.892 | 6.824 |
| 11 | 33 | 0.088 | 0.013 | 0.152 | 0.848 | 6.591 |
| 12 | 28 | 0.075 | 0.005 | 0.071 | 0.929 | 6.679 |
| 13 | 26 | 0.070 | 0.016 | 0.231 | 0.769 | 6.154 |
| 14 | 20 | 0.053 | 0.003 | 0.050 | 0.950 | 6.850 |
| 15 | 19 | 0.051 | 0.003 | 0.053 | 0.947 | 6.184 |
| 16 | 18 | 0.048 | 0.003 | 0.056 | 0.944 | 5.500 |
| 17 | 17 | 0.045 | 0.011 | 0.235 | 0.765 | 4.794 |
| 18 | 13 | 0.035 | 0.003 | 0.077 | 0.923 | 5.115 |
| 19 | 12 | 0.032 | 0.008 | 0.250 | 0.750 | 4.500 |
| 20 | 9 | 0.024 | 0.008 | 0.333 | 0.667 | 4.833 |
| 21 | 6 | 0.016 | 0.000 | 0.000 | 1.000 | 6.000 |
| 22 | 6 | 0.016 | 0.003 | 0.167 | 0.833 | 5.000 |
| 23 | 5 | 0.013 | 0.003 | 0.200 | 0.800 | 4.900 |
| 24 | 4 | 0.011 | 0.003 | 0.250 | 0.750 | 5.000 |
| 25 | 3 | 0.008 | 0.000 | 0.000 | 1.000 | 5.500 |
| 26 | 3 | 0.008 | 0.000 | 0.000 | 1.000 | 4.500 |
| 27 | 3 | 0.008 | 0.000 | 0.000 | 1.000 | 3.500 |
| 28 | 3 | 0.008 | 0.000 | 0.000 | 1.000 | 2.500 |
| 29 | 3 | 0.008 | 0.003 | 0.333 | 0.667 | 1.500 |
| 30 | 2 | 0.005 | 0.003 | 0.500 | 0.500 | 1.000 |
| 31 | 1 | 0.003 | 0.003 | 1.000 | 0.000 | 0.500 |
| 32 | 0 | 0.000 | — | — | — | — |

genet was 1.33 (SD = 0.45) for the entire period, with number of individuals per genet ranging from approximately 1 in 5 different years to 2.53 in 1961. There were more genets than individuals in some years because genets had merged and were subsequently traced as one individual. The population does not therefore appear to be composed of plants that are clonal fragments of the same genet. There were, however, two periods during which the number of individuals increased more than twofold (80–218 from 1952 to 4, 130–280 from 1960 to 1) without a similar increase in genet number.

Seventy-five per cent of the genets in this population were represented by only one individual (Fig. 5b), and 59% of these were seedlings that lived only 1 year. After excluding seedlings, frequency of genets with only one individual was still high (56% of the population). Fifty-nine genets had between four and 29 associated individuals, and four genets contained > 25 individuals each.

MORTALITY OF INDIVIDUALS

The average number of individuals dying was 25.8 per year (SD = 23.4), with high variability through time

(Fig. 6). Mortality of individuals was below average from 1938 to 1954 and from 1964 to 1970, with a range in deaths from 2 to 28 per year. Two periods of high individual mortality occurred from 1955 to 1957 and 1961 to 1962 immediately following periods of high rates of genet fragmentation (Fig. 5). Annual mortality of individuals was not related to climatic variables, including annual precipitation, 1 and 2 year's previous precipitation, or maximum, mean or minimum annual temperature.

Discussion

GENET RECRUITMENT AND MORTALITY

Seedling recruitment of *B. gracilis* was high and, although genet mortality was frequent, genets were replaced at approximately the same rate as they were lost (Figs 2 and 3). At the start of the study there were 53 genets and at the end there were 41. As the coefficient of variation of the number of genets was high (CV = 32%; Fig. 5a) there is no indication that the number was declining. This implies that genet diversity was maintained during the 38 years of sampling, and vulnerability of the population to

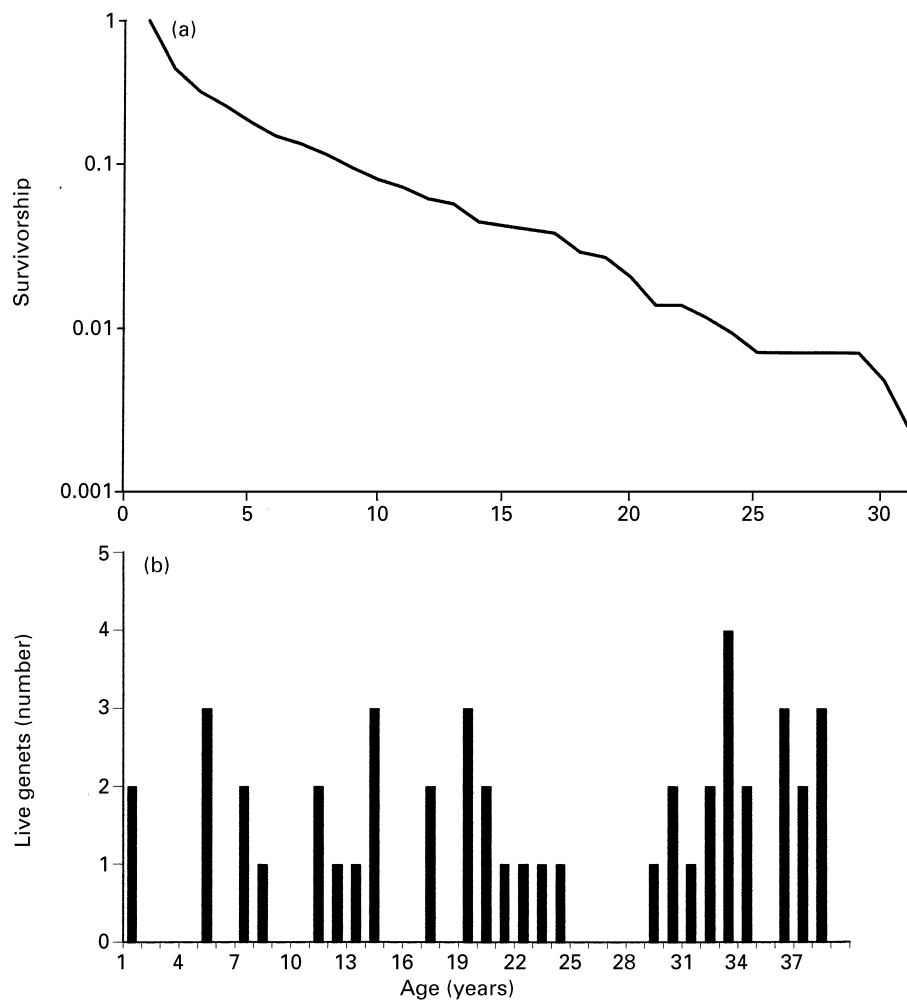


Fig. 4 (a) Survivorship curve of *B. gracilis* genets recruited in five 1-m² quadrats in the years 1934–72. Survivorship shows number of genets that survived in each age class after subtracting the number of genets that died during the previous year. (b) The number and age of *B. gracilis* genets that were still alive in 1972 when data collection ended.

different selective pressures was low (Demetrius 1975; Harper 1977). Because it was not possible to distinguish whether seedlings were from genets in the same vicinity or from genotypes that migrated into the population via wind or faunal transport, we could not quantify trends in genetic diversity. Because seedlings with different genotypes replaced dead genets, some genetic variability was maintained through time (Harper 1977).

The high seedling recruitment observed in this study hints at a difference between the southern mixed grass prairie and the shortgrass steppe. Lauenroth *et al.* (1994) estimated maximum annual probability of recruitment of 0.0344 for a site in the shortgrass steppe. By contrast, seedling recruitment was observed in 30 out of the 33 years of this study and ranged from one to 30 seedlings.

aged genets may be more evolutionarily advanced than those of even-aged genets (Harper 1977; Hartnett & Bazazz 1985). Genets recruited in different years were most probably exposed to different selective pressures. Therefore they may have developed adaptations to a variety of factors, resulting in the ability of the population to withstand large fluctuations in numbers that may have been caused by environmental variability (Demetrius 1975; Harper 1977).

Risk of mortality for *B. gracilis* genets was high in age classes 1 and 2, but became low and relatively constant after age class 3. A constant rate of mortality, or a Deevey II curve (Deevey 1947), has been reported previously for herbaceous perennials (Antonovics 1972; Sarukhan & Harper 1973) and is hypothesized to be the general trend (Harper 1977; but see West *et al.* 1979). High risk of mortality early in life, as shown by this population, is typical of a Deevey III curve (Deevey 1947) and is uncommon in plant populations (Harper 1977; but see Williams 1970). It is possible that many populations might tend

GENET SURVIVORSHIP AND LONGEVITY

This population of *B. gracilis* was composed of a wide distribution of ages. Populations made up of different-

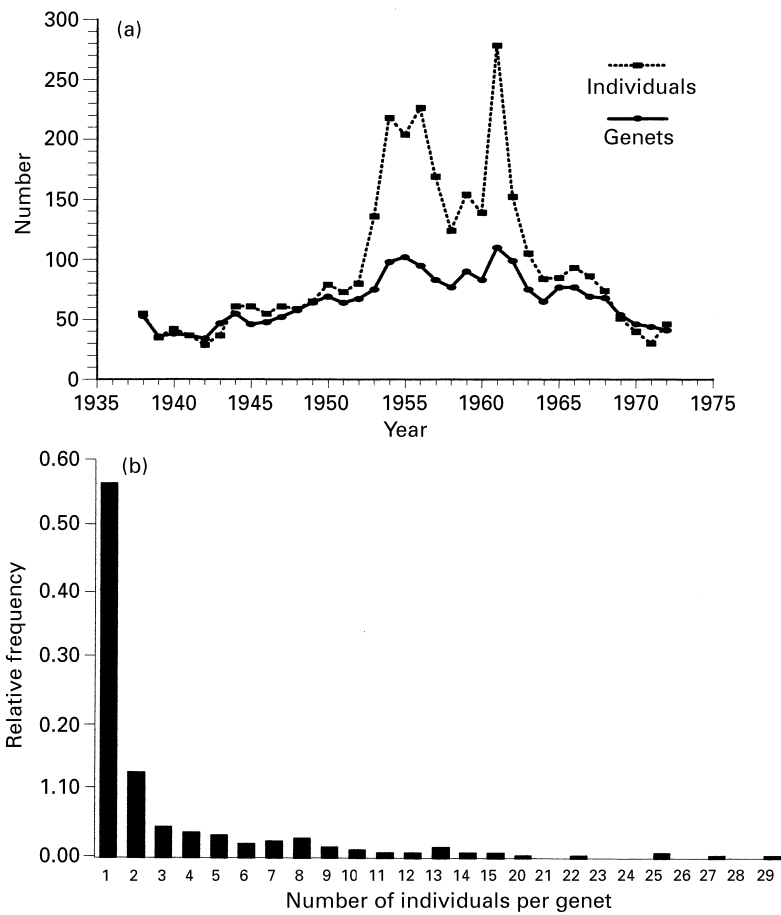


Fig. 5 (a) A comparison of number of *B. gracilis* genets to number of individual plants in five 1-m² quadrats from 1938 to 1972. (b) Relative frequency of number of *B. gracilis* individuals associated with each genet.

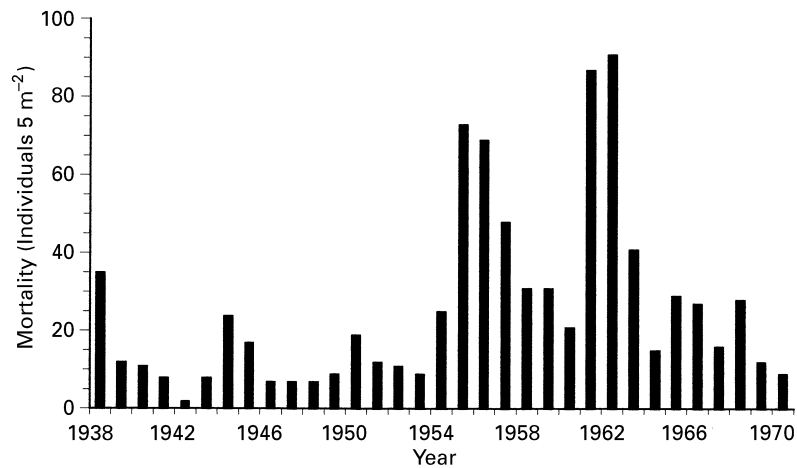


Fig. 6 Number of *B. gracilis* individuals in five 1-m² quadrats that died annually between 1938 and 1970.

toward Deevey III curves, but this trend would not be captured in annually mapped studies if seedlings died before being mapped and were not therefore counted in the recruitment estimate.

The majority of *B. gracilis* genets were not long-lived (3.7 years) but the mean life span was extended

substantially if a genet survived to at least age class 3. Even though the mean life span was low, the potential to live a long time (> 38 years) existed in this population. Typically, the oldest genets were most successful at fragmenting into many individuals and becoming widespread.

COMPARISON OF NUMBER OF GENETS TO
THAT OF INDIVIDUALS

The number of different genets that existed in the population averaged 66 per year, and variability in genets was maintained through time. Variability of individuals with different genet identities was also maintained through time. The number of individuals was similar to the number of genets for most of the study, indicating that the majority of individuals in any given year came from different seedlings. The exception to this trend was between 1953 and 1963 when individuals outnumbered genets consistently due to high fragmentation rates, although there were never more than 2.5 times more individuals than genets. These results imply that, on average, field studies that sample individual *B. gracilis* plants from populations under similar environmental conditions are likely to represent a variable gene pool rather than clonal fragments.

Most genets consisted of only one individual, although a few genets consisted of over 25 individuals. Even though the frequency of genets with one individual was very high (76%), vegetative spread by fragmentation cannot be dismissed as unimportant. Fifty-one out of 420 (12%) genets had more than five individuals per genet and six out of 420 (1.4%) had 20–30 individuals. These few, large genets are likely to have exerted strong competitive effects on smaller or younger individuals. The presence of such neighbours may have limited vegetative spread of young genets and contributed to mortality (Mack & Harper 1977; Harper & Bell 1979; Aguilera & Lauenroth 1993). Although average fragmentation rates were low, fragmentation may be an important strategy in the life history of *B. gracilis* genets. Genets grow and occupy different microenvironments via their fragments, which may live for long periods of time. Genet fitness depends on fragmentation and vegetative spread because the size and number of fragments determine the size of the genet and influence a genet's ability to produce descendants (Harper & Bell 1979; Hartnett & Bazazz 1985).

INDIVIDUAL MORTALITY

Death of mature individual plants of the dominant species theoretically results in gaps in resource space of plant communities. Gaps may initiate succession by facilitating recruitment of new individuals into the community (Watt 1947; Coffin & Lauenroth 1990). In the shortgrass steppe, where *B. gracilis* is the dominant species, resource gaps occur below-ground (Coffin & Lauenroth 1990) because soil water is the most frequent factor controlling plant growth and community structure (Noy-Meir 1973; Lauenroth *et al.* 1978). In southern mixed grass communities, where mean annual precipitation is higher than in shortgrass communities, water may not be the only

limiting factor. Competition with midgrasses for light may also be important (Lane 1995), and the gap opened by the death of a *B. gracilis* plant may be in terms of both above- and below-ground resources.

Death of individual *B. gracilis* plants was frequent at approximately 26 plants year⁻¹ over the 5 m² sampled. Death of mature plants was somewhat lower as 58% of the genets (seedlings that were also counted as single individuals) died before age class 3. Even so, the opportunity for gap dynamics, including establishment of other plants, to occur due to the death of mature plants in this population was high (approximately 10 individuals year⁻¹ over the 5 m² sampled); recruitment of *B. gracilis* genets may have been related to the high mortality rate of mature individuals and genets.

LONGEVITY OF INDIVIDUAL PLANTS

Estimates of the longevity of individuals provides insight into the population dynamics of individual plants such as those commonly sampled in field studies. *Bouteloua gracilis* genets, and therefore individual plants, showed the potential to be long-lived in this community (> 38 years). Estimates of *B. gracilis* plant longevity were also high for the shortgrass steppe (approximately 400 years) (Coffin & Lauenroth 1988, 1990; Lauenroth *et al.* 1997). The ability to produce long-lived genets and individual plants may allow *B. gracilis* to maintain its population size in the community because occupation of resource space for long periods prevents recruitment of other species. A long life span may also increase fitness of genets in terms of increasing their potential to produce descendants (Harper 1977).

COMPARISONS OF DEMOGRAPHICS WITH
CLIMATE

The lack of many relationships between climatic variables and recruitment and mortality patterns of *B. gracilis* genets and plants suggests that other factors are more important. Interactions with other species, in particular *B. dactyloides*, may affect the dynamics of *B. gracilis*. Basal cover of both *B. gracilis* and *B. dactyloides* changed between years in these quadrats and was inversely related at times, especially between 1941 and 1952 (Albertson & Tomanek 1965). Another important factor may be grazing by cattle. Both *B. gracilis* and *B. dactyloides* are well adapted to grazing and may increase in basal cover with grazing intensity (Weaver & Albertson 1956; Milchunas *et al.* 1989). Because grazing had been excluded from these quadrats since 1932, it is very likely that the dynamics of genets and individual plants in this study were affected by lack of grazing, especially when competition with species less tolerant of grazing, such as *S. scoparium* and *A. gerardii*, is considered (Albertson & Tomanek 1965; G. Tomanek, personal communication).

Although annual climatic variables were not important to the demography of *B. gracilis*, periods of extreme climatic conditions (i.e. prolonged drought) may have had important effects. Recruitment of *B. gracilis* was above average in the last 3 years of the two major drought periods (1938–40, 1954–56), below average in the wetter 2–3 years following each of the drought periods, and below average during the variable drought period from 1964 to 1972. Because *B. gracilis* seedlings can survive drought conditions better than any other major species in the southern mixed prairie (Weaver & Mueller 1942), *B. gracilis* may have colonized areas opened by the death of other species during the drought periods. Low recruitment of *B. gracilis* after drought periods may indicate that vegetative growth of established plants, especially *B. dactyloides*, occupied resource gaps during wetter years as basal cover of *B. dactyloides* responds faster to changes in precipitation than *B. gracilis* (Weaver & Albertson 1956; Albertson & Tomanek 1965).

Above-average mortality of both genets and individuals following drought also indicates the importance of extreme climatic conditions to population dynamics of *B. gracilis*. Mortality was above average during and following the three drought periods for both genets and individuals. However, periods of peak mortality in 1961 and 1962 for both genets and individuals were not associated with drought periods.

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