

Vegetative Reproduction and Bud Bank Dynamics of the Perennial Grass *Andropogon gerardii* in Mixedgrass and Tallgrass Prairie

Authors: Ott, Jacqueline P., and Hartnett, David C.

Source: The American Midland Naturalist, 174(1) : 14-32

Published By: University of Notre Dame

URL: <https://doi.org/10.1674/0003-0031-174.1.14>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Vegetative Reproduction and Bud Bank Dynamics of the Perennial Grass *Andropogon gerardii* in Mixedgrass and Tallgrass Prairie

JACQUELINE P. OTT¹ AND DAVID C. HARTNETT

Division of Biology, Kansas State University, 104 Ackert Hall, Manhattan 66506

ABSTRACT.—Plant species with wide distributions may differ in their population dynamics across their range, especially in contrasting habitats. Most tiller recruitment of perennial grasses occurs vegetatively from the belowground bud bank rather than from seed. Seed reproduction often occurs under a narrower range of environmental conditions than vegetative reproduction. As a result flowering and seedling recruitment patterns of a species often differ between contrasting habitats and across its range. How vegetative reproduction and bud bank dynamics of a species vary between contrasting habitats has not been well studied and could explain the differences in its persistence and productivity between habitats. Therefore, the vegetative reproduction and dynamics of *Andropogon gerardii*, a dominant C₄ perennial grass of the Great Plains of North America, were compared between tallgrass and northern mixedgrass prairie habitats. Bud production and tiller recruitment in 10 populations were examined throughout an annual growing cycle in the northern mixedgrass prairie of South Dakota. Bud bank characteristics, and individual and population performance were compared with previous work conducted in Kansas tallgrass prairie. Stage-structured matrix models examined population growth rates. *Andropogon gerardii* tillers produced lower numbers of buds and had lower flowering rates in mixedgrass prairie populations. The annual phenology of bud and tiller development was also contracted to fit within the shorter growing season in northern mixedgrass prairie. However, bud longevity and bud bank age structure were similar between habitats, both having buds that lived for > 2 y and multi-aged bud banks. Similar population growth rates occurred in both habitats despite lower individual performance of both flowering and vegetative reproductive capacity (*i.e.*, bud production) in mixedgrass prairie populations. Lower regional productivity of *A. gerardii* in northern mixedgrass prairie than in tallgrass prairie does not appear to be due to differences in bud and tiller population growth. Instead, sparse or patchy suitable habitat and/or reduction in tiller size may explain its reduced productivity. Lower population growth rates may be observed in other habitats or in years with harsher environmental conditions that further lower individual performance.

INTRODUCTION

The dominant grasses of the North American Great Plains primarily reproduce vegetatively rather than sexually. Although these grasses can put forth a sizable flowering effort (*e.g.*, Fay *et al.*, 2003), seedling recruitment of these perennial grasses in undisturbed habitat is rare (Fair *et al.*, 1999; Peters, 2000; Benson and Hartnett, 2006). Therefore, most tiller recruitment occurs via vegetative reproduction from belowground axillary buds (*i.e.*, the bud bank *sensu* Harper, 1977; Benson and Hartnett, 2006). Dominant and subdominant perennial grasses within the same grassland can vary in their timing of annual bud production and in their bud bank size and age structure (Ott and Hartnett,

¹ Corresponding author present address: US Forest Service-Rocky Mountain Research Station, Forest and Grassland Research Laboratory, 8221 South Highway 16, Rapid City, South Dakota 57702 : e-mail: jacquelinepott@fs.fed.us

2012). Although bud bank characteristics vary locally among species, regional intraspecific variation in bud bank characteristics is unknown.

The life history and population traits of a plant species, such as vegetative reproduction, may vary significantly among habitat types, among years, or between the center and periphery of its range (*e.g.*, Wellstein *et al.*, 2013). Successful sexual reproduction of a plant species generally occurs under a narrower range of environmental conditions than its vegetative growth and reproduction (Baker's Law, Baker, 1959; Hengeveld, 1990; Philbrick and Les, 1996). Vegetative reproduction of a perennial grass could change near its range limit similar to changes observed in the flowering effort and seed production of some annual species near their range limits. Vegetative reproduction could also change across habitats due to differences in resource availability, competition, or disturbance regime.

Regional productivity distributions of the dominant perennial grasses of the Great Plains are determined by their response to the north-south gradient in mean annual temperature and east-west gradient in mean annual precipitation (Epstein *et al.*, 1998). Because of these gradients, C₃ grasses (*i.e.*, cool-season phenology) dominate in the northwest and C₄ grasses (*i.e.*, warm season phenology) dominate in the south and east (Teeri and Stowe, 1976; Epstein *et al.*, 1997). *Andropogon gerardii* (Vitman) is most abundant in areas of high mean annual precipitation and intermediate mean annual temperature, which are found geographically in the tallgrass prairies of eastern Kansas and Oklahoma (Epstein *et al.*, 1998). Although *A. gerardii* has the C₄ photosynthetic pathway, one edge of its range extends into the northern mixedgrass prairie where C₃ perennial grasses dominate and *A. gerardii* has reduced productivity (Epstein *et al.*, 1998). Populations of *A. gerardii* in this northern mixedgrass prairie experience lower temperatures and 60% of the average annual precipitation normally received in its optimal tallgrass prairie habitat. Therefore, the life history patterns, phenology, and/or the demographic rates of *A. gerardii* could be altered due to the contracted and cooler growing season and lower water availability.

To provide insights into the mechanisms driving regional variation in grass population dynamics and productivity, the general objective of this study was to determine if and how vegetative reproduction and the bud bank characteristics and dynamics of a perennial grass, differed between contrasting habitats. Replicate populations of *A. gerardii* in tallgrass and northern mixedgrass prairie were assessed. Our specific objectives were to compare: (1) phenology of bud and tiller development and bud bank age structure, (2) individual tiller performance (*e.g.*, bud production, daughter tiller initiation and establishment, and flowering), (3) vital rates within the vegetative life cycle, and (4) retrospective and prospective population performance based on the finite population growth rate (λ). Bud bank characteristics and vital rates that are conserved (*i.e.* similar) between habitats will be considered important to species persistence. Because bud bank and tiller dynamics strongly drive the population dynamics of many grasses, our findings will provide a valuable basis for addressing general questions about the role of bud bank dynamics in determining differences in plant population dynamics and/or productivity across a species' range. Additionally, our findings will help identify which aspects of bud bank structure or dynamics are most important to grass population viability and species persistence in the Great Plains.

METHODS

SITE DESCRIPTION AND FIELD SAMPLING

Demographic data for *A. gerardii* were collected from populations in northern mixedgrass prairie at Wind Cave National Park and compared with previous published demographic data for *A. gerardii* in tallgrass prairie from Ott and Hartnett (2012) and Ott

(2009). Wind Cave National Park (WCNP) is a 13,699 ha mixedgrass prairie interspersed with ponderosa pine forest with hilly topography (elevation ranging from 1113 m to 1527 m) located at the southeastern edge of the Black Hills in western South Dakota (43°33'N, 103°29'W). The vegetation is dominated by cool-season grasses such as *Hesperostipa comata*, *Pascopyrum smithii* and *Nassella viridula*, with discrete patches of less abundant warm-season grasses including *A. gerardii*, *Bouteloua curtipendula* and *Bouteloua gracilis*. Bison (*Bison bison*), elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) are the major large herbivores. However, bison and elk are the primary consumers of grass due to their grazing habits and population sizes. For this study the northern prairie portion of the 42 ha Elk Mountain enclosure within the park, which excludes bison but no other herbivores, was used. Prescribed fire occurs every 5 to 7 y. The Elk Mountain enclosure was last burned in the fall of 2008. The region's semi-arid climate has cool winters (average Jan. temp: -2.3 C) and warm summers (average Jul. temp: 22.9 C) with moderate rainfall (499 mm) primarily occurring Apr. through Oct., especially in May and Jun.

In Oct. 2010 ten populations were located within the grassland portion of the enclosure. The sampled populations were discrete, separated by an average distance of 74 ± 7 m with intervening stands of cool-season grasses between them. Populations occurred at an approximate elevation of 1310 m with primarily loamy-skeletal soils (Typic Argiustolls) with the exception of one population on fine-loamy soil (Fluventic Haplustolls; Soil Survey Staff, NRCS, USDA).

Andropogon gerardii (big bluestem) is a short-rhizomatous C₄ perennial grass that produces annual tillers and flowers in the Great Plains from Jul. to Sep. Due to the rhizomatous growth form and intermingling of different genets of *A. gerardii*, genets are very difficult to identify in the field. Therefore, an "individual" of *A. gerardii* consisted of all interconnected tillers and associated belowground parts within an 8.0 cm radius. Ten individuals of *A. gerardii* were randomly selected within a 2m² plot of each population and marked using a metal tag and a wire ring. Each individual was at least 10cm away from a neighboring individual.

From Mar. 16, 2011 until Nov. 4, 2011, an individual from each population was harvested approximately every 3 wk during the growing season (*i.e.*, while soil temperatures remained consistently above freezing; 10 sample dates; Ott, 2014). Plants were harvested by excavating to a 15 cm depth and were washed to remove soil.

Although the demographic data from tallgrass and northern mixedgrass prairie were collected in different years, both examined *A. gerardii* under similar field conditions. At both sites large grazers were excluded and it had been 2 to 3 y since fire. Although Konza Prairie Biological Station (KPBS, tallgrass prairie site) has a higher average annual precipitation (835 mm) than WCNP (499 mm), precipitation was between 115 and 138% of the site-specific long-term average in both the year of (KPBS: 1012 mm, WCNP: 646 mm) and the year preceding (KPBS: 1153 mm, WCNP: 575 mm) the study at each site.

LAB ANALYSIS AND BUD, TILLER AND RHIZOME CLASSIFICATION

Two bud developmental stages (developing and mature) were characterized by their prophyll development. Collectively, developing and mature buds are referred to as "buds". A bud transitions to a tiller when the bud apex emerges and elongates past its protective prophyll. Two developmental stages of tillers (juvenile and adult) were identified. Adult tillers were also classified according to annual cohort: (1) current year, (2) 1 y old (RT₁), and (3) ≥ 2 y old (RT₂). Current year adult tillers were identified by the presence of expanded aboveground leaves and were further classified as vegetative (V) or flowering (F). Senesced aboveground tillers which had lost all aboveground tissue were classified as

residual tillers (RT). RT₁ were distinguishable from RT₂ by their color and leaf remains. Juvenile tillers were classified as activated buds in previous work (Ott and Hartnett, 2012). See Ott (2014) and Ott and Hartnett (2012) for more detailed descriptions of buds and tiller classifications. These bud and tiller developmental stages enabled examination of changes occurring within the bud bank during the year while the demographic stages (*see below*) considered changes occurring within the bud bank from year to year.

The length of each rhizome was measured and each was classified by developmental stage. Rhizomes were defined by having at least two elongated internodes and a horizontal trajectory in the soil. Two rhizome developmental stages (mature and aged) were identified. Mature rhizomes included those that were currently elongating with actively growing scales and those with yellow hardened stem tissue and senesced scales that were associated with actively growing tillers. Aged rhizomes (> 1 y old) had browned senesced internodes and scales.

Buds, tillers, and rhizomes from each plant were examined using a dissecting scope with magnifications between 7 and 40 x. Tillers, rhizomes, and basal/belowground buds were counted, assessed to be living or dead, and classified by developmental stage. Although tillers and rhizomes of the entire plant were measured and counted, a random subsample of 10 tillers was chosen for assessing bud numbers and development for each annual tiller cohort and flowering status (exception: 25 tillers were used to assess buds on RT₂).

DATA ANALYSIS

Individual performance.—The effects of habitat and tiller cohort on initial spring bud production per tiller, peak new tiller initiation per tiller, end-of-year bud production per tiller, and end-of-year tiller production per tiller were each tested using a two-way factorial treatment structure with habitat and tiller cohort as fixed factors in a split-plot design (PROC MIXED, SAS 9.2). Because one individual was harvested from each population on each sample date, there were ten replicate individuals from each habitat for each response variable. The habitat factor was applied to the whole-plot experimental unit of individual plant and the tiller cohort factor was applied to the sub-plot experimental unit of tiller. Because of the variance-covariance structure, Satterthwaite's approximation of the denominator degrees of freedom was used. For the two response variables (spring bud production and end-of-year tiller production), the variance of individual within habitat was zero and the containment method was used to give proper denominator degrees of freedom. For additional comparisons within each overall test, appropriate contrasts were used.

Population performance - matrix model parameterization and assumptions.—Bud and tiller demography were examined using a stage-structured matrix population model of a plant's population of ramets (*i.e.*, buds and tillers) over an annual time step from Feb. to Feb. (*see* Caswell 2001 for a general description of matrix models). The model included four discrete life stages including buds younger than 1 y old (b1), buds older than 1 y old (b2), live vegetative tillers (v) and live flowering tillers (f) (Fig. 1). The developed projection matrix:

$$A = \begin{bmatrix} 0 & 0 & V_v & V_f \\ G_{b1} & S_{b2} & 0 & 0 \\ G_{b1-v} & G_{b2-v} & 0 & 0 \\ G_{b1-f} & G_{b2-f} & 0 & 0 \end{bmatrix}$$

included stage-specific transition rates for axillary bud survival (S), belowground axillary bud production (*i.e.*, vegetative reproduction, V) and tiller growth (G). The projection

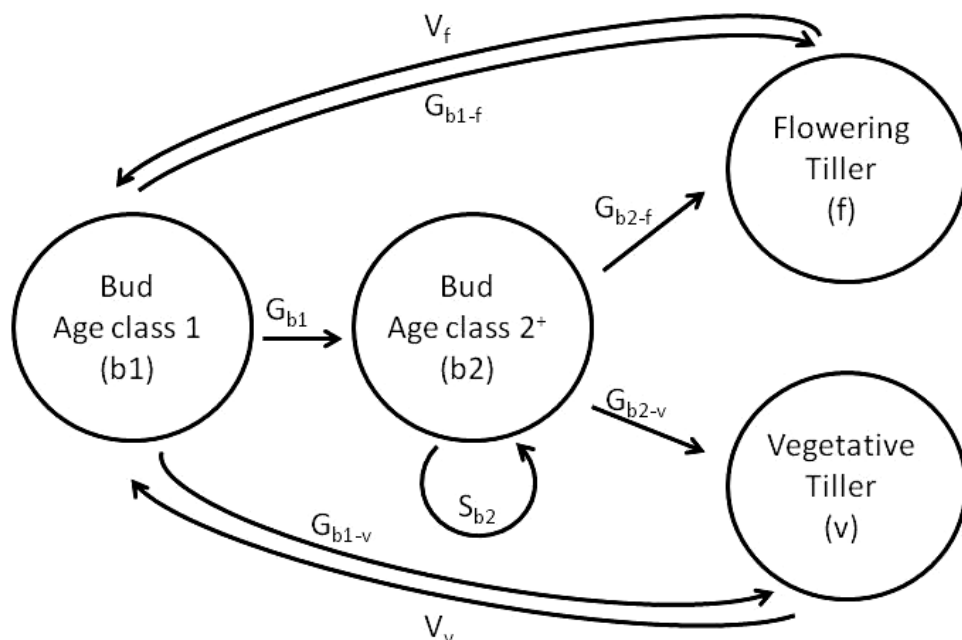


FIG. 1.—Vegetative reproduction life cycle diagram of *A. gerardii*. Collectively, buds from both age classes form the bud bank

matrix assumed no density dependence and was linear and deterministic. Because the projection matrix is based on an annual time step and focuses on live buds and tillers, not all of the bud and tiller developmental stages described above (*e.g.* juvenile tillers, RT_1 , and RT_2) are included as life stages in the matrix.

Projection matrices, one for each population within each habitat (*i.e.*, tallgrass or mixedgrass prairie), were parameterized to determine population growth rates and to use in retrospective and prospective analyses. Vital rates were calculated using per tiller estimates of buds and current year tillers of three tiller cohorts (current year (V and F), 1 y old (RT_1) and ≥ 2 y old (RT_2); Table 1). ‘Per tiller’ estimates were used because transitions between stages are controlled at the tiller level (*i.e.*, apical dominance). ‘Per tiller’ estimates also help control for differences, such as tiller number, between individuals (genets) within a population. Vital rate calculations often involved two different individuals within a population that were destructively harvested on different sample dates. Fecundity and growth transition rates included both the production or growth and the subsequent survival at that stage over the annual time step. Therefore, buds in age class 1 (b1) occur on RT_1 and buds in age class 2+ (b2) occur on RT_2 . The incoming b1 cohort occurs on current year vegetative and flowering tillers (v and f). Estimates of V_f were unavailable for seven of the WCNP populations. The WCNP average V_f was used in the projection matrices of these populations.

In order to calculate each of the eight transition rates for each habitat, several assumptions were made, each of which we deemed reasonable based on field observations and/or our previous studies: (1) no buds produced in the current year recruit to tiller before the end of the growing season. Tiller recruitment from current year buds is rare and is mainly observed in years of extreme drought (J.P. Ott, pers. obs.); (2) axillary buds

TABLE 1.—Matrix element parameterization of the projection matrices. B = buds, V = vegetative tiller, F = flowering tiller, RT = residual tiller; Subscripts indicate from which sampling date data were used. If only a season is listed, then the average of all sampling dates from that season was used. If “peak” or “base” is listed, the sampling date within the season with the highest or lowest average value was used respectively. For example, $(B/RT_1)_{fall\ base}$ refers to the lowest value of buds on RT_1 per RT_1 for sample dates from Sep. to Nov. Estimates for V_f in peripheral populations at WCNP were based on data from both 2010 and 2011 as only one 2011 tiller flowered

Matrix element	Definition	Equation
G_{b1}	Survival probability of a 1 year old bud	$\frac{(B/RT_1)_{fall\ base}}{(B/RT_1)_{spring\ peak}}$
G_{b1-v}	Outgrowth probability of a 1 year old bud to vegetative tiller	$\frac{(V/RT_1)_{fall}}{(B/RT_1)_{spring\ peak}}$
G_{b2-v}	Outgrowth probability of a 2 ⁺ year old bud to vegetative tiller	$\frac{(V/RT_2)_{fall}}{(B/RT_2)_{spring\ peak}}$
G_{b1-f}	Outgrowth probability of a 1 year old bud to a flowering tiller	$\frac{(F/RT_1)_{fall}}{(B/RT_1)_{spring\ peak}}$
G_{b2-f}	Outgrowth probability of a 2 ⁺ year old bud to a flowering tiller	$\frac{(F/RT_2)_{fall}}{(B/RT_2)_{spring\ peak}}$
S_{b2}	Survival probability of a 2 ⁺ year old bud	$\frac{(B/RT_2)_{fall\ base}}{(B/RT_2)_{spring\ peak}}$
V_v	Axillary bud production of a vegetative tiller	$\left(\frac{B}{V}\right)_{fall}$
V_f	Axillary bud production of a flowering tiller	$\left(\frac{B}{F}\right)_{fall}$

produced by flowering and vegetative tillers have equivalent outgrowth probabilities; (3) bud death is minimal over the winter months. For each *A. gerardii* tiller cohort, bud numbers per tiller did not change over the winter at KPBS (Ott and Hartnett, 2012); (4) neither rhizomes nor tillers that fail to successfully establish contribute to the bud bank. Buds borne on rhizomes of *A. gerardii* were low in number and never transitioned to tillers (Ott and Hartnett, 2012). Tillers that do not survive to the end of the growing season due to causes such as herbivory or drought produce low numbers of buds (Ott, 2009); (5) residual tiller density does not change during the growing season. Residual tiller density was variable but there was no notable change in its density over time at WCNP; and (6) successful recruitment from seed is rare and does not influence tiller population dynamics (Benson and Hartnett, 2006).

Population performance - matrix parameter analyses.—Habitat effect on each matrix element was evaluated using either a one-way treatment structure or contrasts within a two-way factorial treatment structure. G_{b1} and S_{b2} were individually analyzed using a one-way treatment structure with the fixed factor of habitat in a completely randomized design structure (CRD) with Kenward-Rogers degrees of freedom (PROC MIXED, SAS 9.2). Based on the Brown-Forsythe test, homogeneous variances and heterogenous variances were necessary for G_{b1} and S_{b2} respectively. Habitat and bud age effects on bud to vegetative tiller transitions and bud to flowering tiller transitions were each tested with a two-way factorial treatment structure with the fixed factors of habitat and bud age class in a split-plot design. The habitat factor was applied to the whole-plot experimental unit of individual plant and the bud age factor was applied to the sub-plot experimental unit of tiller. Because of the variance-covariance structure, Satterthwaite’s approximation of the denominator degrees of freedom was used. Due to nonnormality data were aligned rank-transformed (PROC

MIXED, SAS 9.2; Higgins, 2004). Contrasts were conducted using rank-transformed data controlling for the family-wise error rate (FWER) by using the permutation min-p adjustment (PROC MULTTEST, SAS 9.2). Bud production matrix elements were evaluated using a two-way factorial treatment structure with the fixed factors of habitat and tiller developmental status in a split-plot design (PROC MIXED, SAS 9.2). The habitat factor was applied to the whole-plot experimental unit of individual plant and the tiller developmental status factor was applied to the sub-plot experimental unit of tiller. Satterthwaite's approximation of the denominator degrees of freedom was used.

Population performance - matrix model analyses.—Both retrospective (*i.e.*, Life table response experiment (LTRE)) and prospective (*e.g.*, elasticities) analyses were used to analyze the population models (Caswell, 2001). A fixed effect LTRE determined which demographic parameters made the greatest contributions to the difference between the finite rate of ramet population growth (λ) of the mean habitat matrices. Even if λ is similar between the two habitats, each habitat can have a separate set of parameters determining its λ (*e.g.*, Brault and Caswell, 1993) as contribution values take into account differences between habitats and the sensitivity of each parameter. Elasticities, sensitivities, stable stage distribution, and λ of the mean habitat matrices were calculated. For each habitat a random effect LTRE of its 10 populations quantified the habitat variance of λ and examined which matrix element's variance and covariances contributed the most to the habitat variance of λ .

Estimates of the variance around the fixed effect LTRE contribution values and habitat element elasticities, loop elasticities, stable stage distributions and λ s were obtained using a bootstrap approach. Appropriate distributions were fitted to each habitat vital rate to obtain bootstrapped distributions of these values. Normal distributions were fitted to fecundity vital rates and beta distributions were fitted to all other vital rates (Appendix Table A1). Every distribution was assessed for goodness-of-fit (GOF; Shapiro-Wilks or Kolmogorov-Smirnov at $\alpha = 0.05$; PROC UNIVARIATE, SAS 9.2). If fitted distributions were rejected due to GOF tests or fitted beta distributions were U-shaped due to one observational value being greatly different from the rest of the observations in the data, distributions were not assigned to these matrix elements. Instead, the values of these matrix elements were resampled with replacement from among the values of the 10 populations of the given habitat in the following bootstrapping analysis (Appendix Table A1). Growth and survival rates transitioning from the same node were constrained to $\text{sum} \leq 1$ but otherwise transition elements were allowed to vary independently. From the bootstrapped distributions (10,000 iterations) of habitat matrix element elasticities, loop elasticities, stable stage distribution elements, and λ s, 95% bootstrapped confidence intervals were extracted and randomization tests were conducted to obtain P-values comparing each of these parameters between habitats (Brault and Caswell, 1993; Gotelli and Ellison, 2004). P-values were insensitive to using either the vital rates of the habitat mean matrices or the bootstrapped means as the observed value (Gotelli and Ellison, 2004). Bootstrapped 95% confidence intervals were also obtained for the contribution values produced in the fixed effect LTRE comparing habitats. LTRE analyses and bootstrapping were conducted in R utilizing some functions from the *popbio* library (R Foundation for Statistical Computing, 2013).

RESULTS

BUD BANK CHARACTERISTICS AND VEGETATIVE REPRODUCTION PHENOLOGY

In mixedgrass prairie populations, both bud development and transition to tiller were synchronous across all bud cohorts (Fig. 2). Bud longevity exceeded 2 y creating a multi-age bud bank primarily composed of buds ≤ 1 y old (Fig. 3). These characteristics were similar

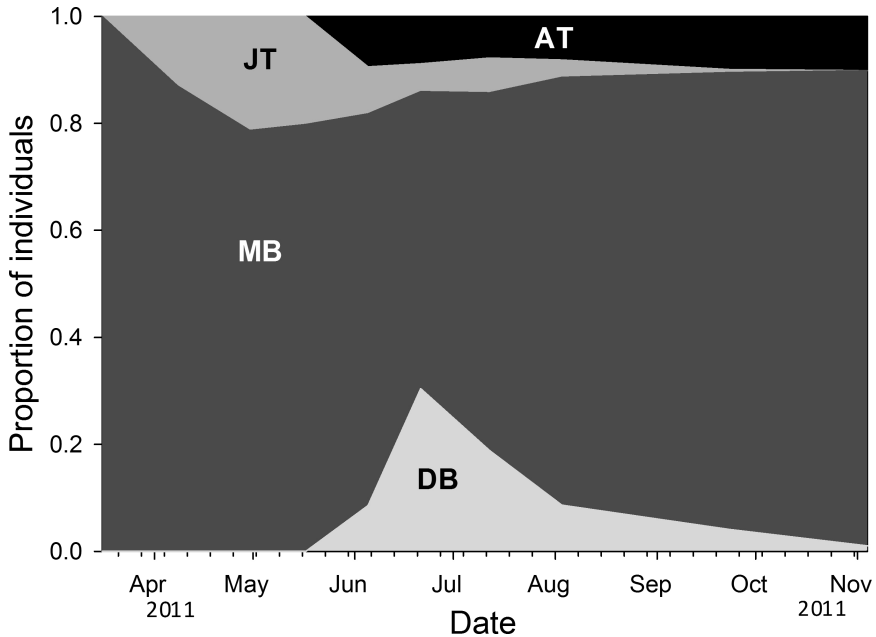


FIG. 2.—Overall proportion of live ramets according to developmental stage in mixedgrass prairie. Developing (DB) and mature (MB) buds comprised the majority of individuals throughout the annual cycle. Juvenile tillers (JT) were synchronously recruited from MB in the early spring. JT transitioned synchronously to adult tillers (AT) in late spring

to those of *A. gerardii* populations in tallgrass prairie (Ott and Hartnett, 2012). In the spring mature buds began transitioning to juvenile tillers at a similar time but more slowly in mixedgrass than in tallgrass prairie (Fig. 4B). Although adult tiller production was delayed 5–6 w in mixedgrass prairie (Fig. 4C), bud production on these adult tillers began in both habitats within 2 wk of each other (Fig. 4A). Bud production was completed within 12 wk in mixedgrass prairie and 8 wk in tallgrass prairie.

INDIVIDUAL TILLER PERFORMANCE

Individual tiller performance varied by habitat and tiller cohort. In the spring tillers from mixedgrass prairie had significantly fewer buds than those from tallgrass prairie and 2 y old tillers (RT_2) had significantly fewer buds than 1 y old tillers (RT_1 ; Fig. 4A). Peak tiller initiation was significantly lower in mixedgrass RT_1 than tallgrass RT_1 (contrast, $F_{1,33} = 56.81$, $P < 0.0001$) but did not differ by habitat on RT_2 (contrast, $F_{1,33.4} = 0.16$, $P = 0.69$, Fig. 4B). Overall RT_1 had a significantly greater peak bud outgrowth than RT_2 (Fig. 4B). Buds of RT_1 produced $89 \pm 2\%$ of current year tillers in mixedgrass prairie, compared to $65 \pm 3\%$ of current year tillers in tallgrass prairie. Final current year tiller production was significantly greater on RT_1 than RT_2 but did not significantly differ between habitats (Fig. 4C). By the end of the growing season, current year tillers had significantly more buds than RT_1 (contrast, $F_{1,35.2} = 185.73$, $P < 0.0001$) and RT_1 had significantly more buds than RT_2 (contrast, $F_{1,35.2} = 49.17$, $P < 0.0001$). At that time mixedgrass prairie had significantly fewer buds than tallgrass prairie only on current year tillers (contrast, $F_{1,51.7} = 25.41$,

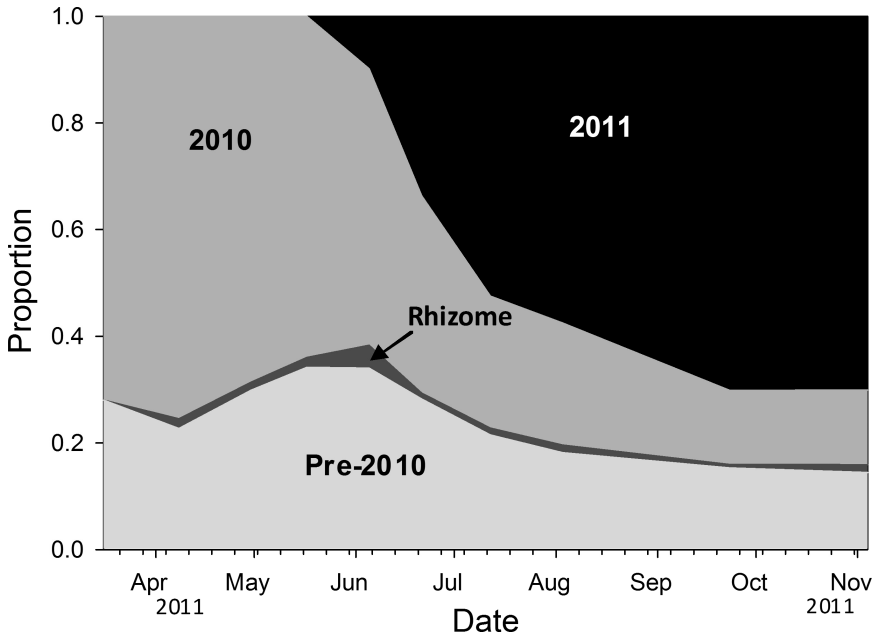


FIG. 3.—Overall proportion of total buds and juvenile tillers according to cohort in mixedgrass prairie. Pre-2010, 2010, and 2011 buds and juvenile tillers were on RT_2 , RT_1 , and current year tillers respectively. Rhizome buds were either from pre-2010 or 2010. Rhizome buds from 2011 were included with the 2011 tiller cohort. At any given point in an annual cycle, multiple ages of buds were present

$P < 0.0001$) but not on older tiller cohorts (contrast for RT_1 , $F_{1, 51.9} = 1.11$, $P = 0.30$; contrast for RT_2 , $F_{1, 51.7} = 0.09$, $P = 0.76$). Although fewer buds were maintained on RT_2 than on RT_1 , RT_2 were more abundant than RT_1 over the entire time of the study in each habitat (mixedgrass: $4.2 \pm 0.4SE$ RT_2/RT_1 , tallgrass: $5.3 \pm 0.4SE$ RT_2/RT_1). In summary on a per tiller basis, *A. gerardii* in mixedgrass prairie produced fewer buds and initiated fewer tillers than in tallgrass prairie. Adult tiller production and the amount of buds on older tiller cohorts (RT_1 and RT_2) in the fall were similar in both habitats. Younger tillers (RT_1) maintained more buds and produced more new tillers than did older tillers (RT_2).

Rhizome buds made small contributions to the bud bank and no buds borne on rhizomes transitioned to tiller in either habitat (Fig. 3, Ott & Hartnett 2012). Rhizomes in mixedgrass prairie averaged 2.00 ± 0.05 cm in length and maintained 0.13 ± 0.02 and 0.17 ± 0.04 buds per cm of rhizome for aged and mature rhizomes respectively. Rhizomes were formed when axillary buds elongated and became the apical meristem of the rhizome. The apical meristem of the rhizome always rapidly transitioned into an aboveground tiller or died.

HABITAT VITAL RATES

Consideration of vital rates offers a broader perspective of the habitat differences in *A. gerardii* ramet demography. Flowering tillers produced significantly more buds than vegetative tillers in each habitat (Habitat: $F_{1, 20.4} = 32.49$, $P < 0.0001$, Tiller Development: $F_{1, 18.1} = 19.16$, $P = 0.0004$, H^*TD : $F_{1, 18.1} = 0.16$, $P = 0.69$). Vegetative fecundity (*i.e.*, bud production) was lower in mixedgrass than tallgrass prairie: both flowering and vegetative

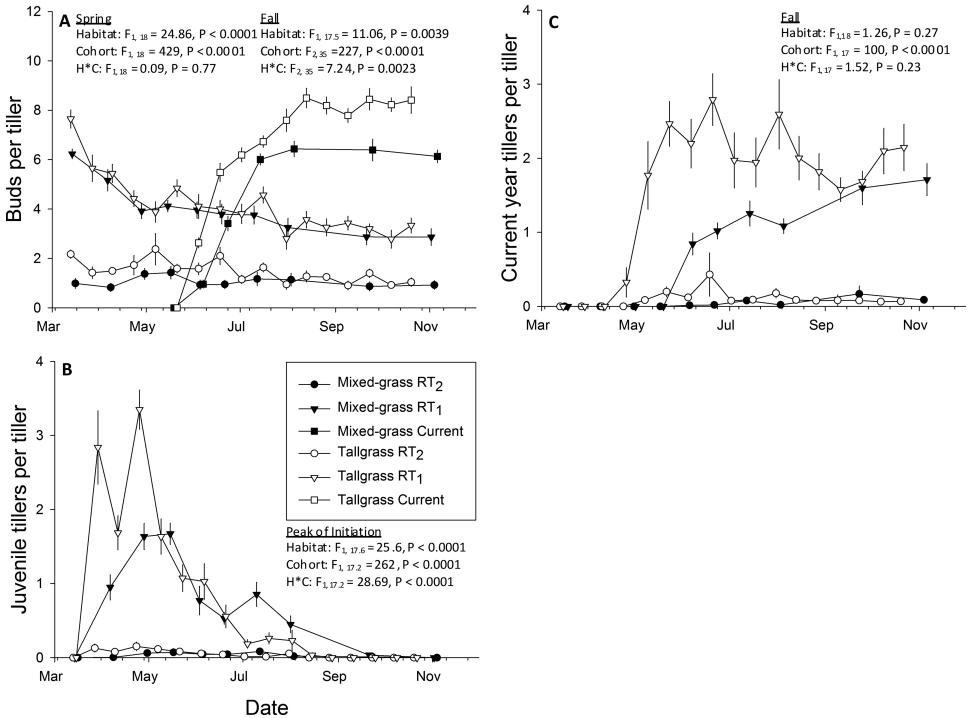


FIG. 4.—Habitat comparison of (A) buds, (B) juvenile tillers, and (C) new adult tillers supported per tiller according to cohort from tallgrass and mixedgrass prairie. Adult tiller cohorts include one year old and two year old residual tillers (RT₁ and RT₂, respectively) and current year tillers. Error bars are ± 1 SE

tillers in mixedgrass prairie had significantly lower bud production than tillers of comparable flowering status in tallgrass prairie (Table 2). Vital rates within the bud bank (bud survival [G_{b1} and S_{b2}]) did not significantly vary between habitats (Table 2).

Tiller recruitment was significantly affected by habitat and bud age class. In general buds in mixedgrass prairie had significantly higher probabilities of transitioning to vegetative tillers than those in tallgrass prairie (Habitat: $F_{1,18} = 10.5$, $P = 0.0045$). Younger buds transitioned to vegetative tiller at higher rates than older buds in both habitats (Bud Age Class: $F_{1,18} = 34.18$, $P < 0.0001$, Habitat*Bud Age Class: $F_{1,18} = 3.96$, $P = 0.062$). Although older bud outgrowth to vegetative tillers did not significantly differ between habitats (Table 2), this difference is primarily responsible for the significance of the habitat main effect on vegetative tiller recruitment. Fewer younger buds transitioned to flowering tillers in mixedgrass than in tallgrass prairie but both habitats transitioned similar amounts of older buds to flowering tillers (Habitat: $F_{1,18} = 69.26$, $P < 0.0001$, Bud Age Class: $F_{1,18} = 91.94$, $P < 0.0001$, Habitat*Bud Age Class: $F_{1,18} = 73.28$, $P < 0.0001$; Table 2).

RETROSPECTIVE POPULATION PERFORMANCE ANALYSIS

Retrospective analyses suggest that *A. gerardii* has relied upon similar vital rates in both habitats to maintain increasing populations. Finite population growth rates did not vary

TABLE 2.—Matrix elements of *A. gerardii* from tallgrass and mixedgrass prairie. Values display the habitat mean $\pm$ 1SE and are boldfaced when there is a significant difference between habitats at $\alpha = 0.05$ with statistical details listed under Habitat Effect. Developmental effect considers either the effect of bud age class or tiller developmental stage within a habitat on the matrix elements. Significant developmental effects at $\alpha = 0.05$ are indicated by gray shading of the statistical details. Perm indicates a permutation contrast was used

Matrix element	Tallgrass	Dev. Effect (Tallgrass)	Mixedgrass	Dev. Effect (Mixedgrass)	Habitat Effect
G _{b1}	0.364 $\pm$ 0.047		0.455 $\pm$ 0.047		P = 0.18, F _{1,18} = 1.9
G _{b1-v}	0.209 $\pm$ 0.018	Perm,	0.266 $\pm$ 0.031	Perm,	P = 0.869, Perm
G _{b2-v}	0.024 $\pm$ 0.007	P = 0.034	0.197 $\pm$ 0.096	P = 0.78	P = 0.056, Perm
G _{b1-f}	0.059 $\pm$ 0.014	Perm,	0.002 $\pm$ 0.002	Perm,	P < 0.0001, Perm
G _{b2-f}	0.008 $\pm$ 0.004	P < 0.0001	0	P = 1.0	P = 0.871, Perm
S _{b2}	0.409 $\pm$ 0.040		0.412 $\pm$ 0.113		P = 0.98, F _{1,11.2} $\approx$ 0
V _v	8.02 $\pm$ 0.30	T_{II} = 3.51,	6.27 $\pm$ 0.22	t₁₁ = 2.90,	P = 0.0002, t₁₁ = 5.43
V _f	8.97 $\pm$ 0.19	P = 0.005	7.54 $\pm$ 0.21	P = 0.014	P = 0.003, t₁₁ = 3.73

significantly by habitat ($\lambda_{\text{mix}} = 1.485$, $\lambda_{\text{tall}} = 1.514$, P = 0.94). Overall, most vital rates provided similar contributions to λ in each habitat (Fig. 5). All contributions of flowering tillers (*i.e.*, V_f, G_{b1-f} and G_{b2-f}) contributed significantly less to λ in mixedgrass than tallgrass prairie but contributions from V_f and G_{b2-f} to the difference were small. Bud production of

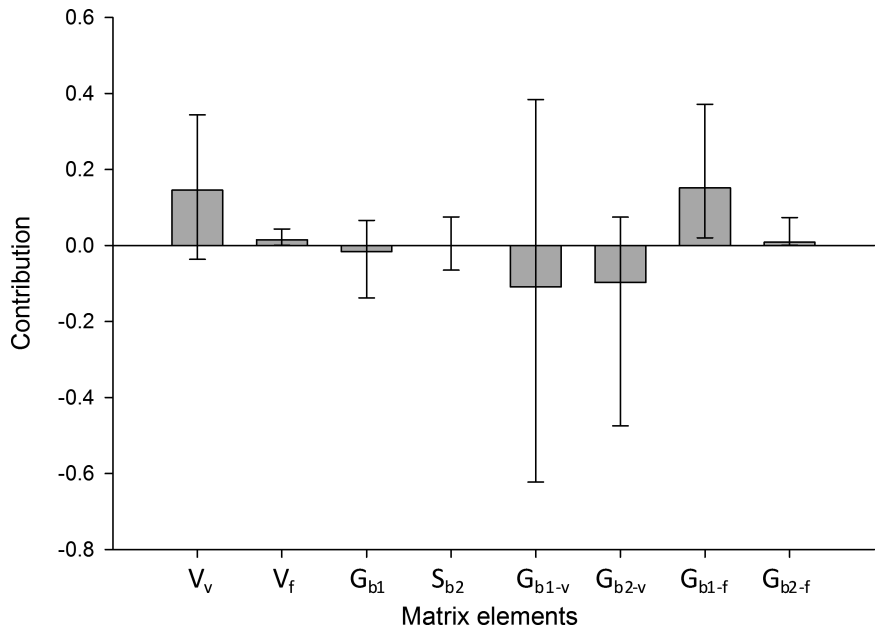


FIG. 5.—Contributions values to the difference in λ between habitats. Positive contributions of demographic parameter indicate that the tallgrass prairie had a greater contribution than mixedgrass prairie and vice versa for negative contributions. Error bars indicate 95% bootstrapped confidence intervals. The lower confidence intervals of V_f and G_{b2-f} are greater than zero

TABLE 3.—Element elasticities according to habitat. No element elasticities varied significantly by habitat. Bootstrapped estimates $\pm$ 1SD and 95% bootstrapped CI

Matrix Element	Tallgrass	Mixedgrass	Bootstrapped P-value
G_{b1}	0.017 $\pm$ 0.024 (0.00009, 0.086)	0.077 $\pm$ 0.059 (0.008, 0.220)	0.31
G_{b1-v}	0.359 $\pm$ 0.063 (0.224, 0.462)	0.355 $\pm$ 0.108 (0.117, 0.487)	0.81
G_{b2-v}	0.012 $\pm$ 0.020 (0.00003, 0.075)	0.077 $\pm$ 0.059 (0.008, 0.220)	0.31
G_{b1-f}	0.112 $\pm$ 0.056 (0.023, 0.237)	0.003 $\pm$ 0.010 (0, 0.036)	0.45
G_{b2-f}	0.005 $\pm$ 0.012 (0.00002, 0.045)	0	0.21
S_{b2}	0.007 $\pm$ 0.012 (0.00003, 0.041)	0.053 $\pm$ 0.086 (0, 0.310)	0.38
V_v	0.371 $\pm$ 0.058 (0.245, 0.465)	0.432 $\pm$ 0.059 (0.279, 0.495)	0.62
V_f	0.117 $\pm$ 0.057 (0.026, 0.243)	0.003 $\pm$ 0.010 (0, 0.036)	0.46

vegetative tillers also tended to contribute less to λ_{mix} than to λ_{tall} . To offset these greater contributions to λ_{tall} , vegetative tiller recruitment from the second bud age class tended to contribute more to λ_{mix} .

Due to a larger variance around λ_{mix} , 95% bootstrapped confidence intervals of λ_{mix} included 1.0 unlike λ_{tall} ($\text{var}(\lambda_{\text{mix}}) = 0.116$, $\text{CI}_{\text{mix}} = [0.930, 1.947]$; $\text{var}(\lambda_{\text{tall}}) = 0.053$, $\text{CI}_{\text{mix}} = [1.140, 1.877]$). Variances and covariances involving the transition of buds to vegetative tillers from either bud age class (G_{b1-v} and G_{b2-v}) in mixedgrass prairie contributed to $\sim 90\%$ of the variance in λ_{mix} . In tallgrass prairie variances and covariances associated with the transition of young buds to vegetative and flowering tillers (G_{b1-v} and G_{b1-f}) contributed to $\sim 85\%$ of the variance in λ_{tall} (Appendix Table A3). Therefore, transitioning of buds to tillers, especially younger buds to vegetative tillers, is responsible for a large portion of the observed variability in each habitat’s λ .

PROSPECTIVE POPULATION PERFORMANCE ANALYSIS

A proportional perturbation of each vital rate would have a similar effect on λ in both habitats (Table 3). A change in the vital rates of vegetative tiller recruitment from young buds or bud production of vegetative tillers would initiate the largest potential change in λ ($\Delta\lambda$). Therefore, perturbations of the cycle of vegetative tillers recruiting from young buds and subsequently producing buds would have a disproportionately large impact on λ (Appendix Table A2). Alterations in vital rates involving older buds and flowering tillers would only create small changes in λ . During the study all known possible biological transitions between stages were observed except for older buds transitioning to flowering tillers in mixedgrass prairie (Table 2). Based on the sensitivities of demographic parameters in mixedgrass prairie (Appendix Fig. A1), adding this transition to this population’s demography would have a moderate to large positive effect on λ . However, increases in tiller recruitment from young buds would have greater effects on λ and would be more biologically feasible.

Predicted stable stage distributions did not differ significantly by habitat and favored maintaining a large bud bank with a large proportion of buds less than one year old (Table 4). Observed stable stage distributions did not differ significantly from predicted stable stage distributions for either habitat implying that these populations are at equilibrium (Table 4).

TABLE 4.—Predicted and observed stable stage distributions according to habitat. Bootstrapped estimates ± 1 SD and 95% bootstrapped CI for predicted stable stage distributions (SSD). Observed SSD are based on fall averages from each habitat and are ± 1 SD. No stable stage proportion varied significantly by habitat. Bootstrapped P-values in the right column compare the predicted proportions of individuals in each stable stage between habitat. Bootstrapped P-values listed underneath the observed SSD of each stage compare the proportion of individuals in the predicted versus observed stable stage distributions for each stage within habitat

Stage	Tallgrass		Mixedgrass		Habitat Predicted SSD P-value
	Predicted	Observed	Predicted	Observed	
B1	0.660 $\pm$ 0.063 (0.530, 0.776)	0.636 $\pm$ 0.074 P = 0.81	0.579 $\pm$ 0.093 (0.357, 0.718)	0.635 $\pm$ 0.071 P = 0.62	0.63
B2	0.219 $\pm$ 0.077 (0.079, 0.382)	0.287 $\pm$ 0.081 P = 0.62	0.289 $\pm$ 0.119 (0.116, 0.573)	0.267 $\pm$ 0.079 P = 0.87	0.78
V	0.094 $\pm$ 0.020 (0.056, 0.133)	0.057 $\pm$ 0.013 P = 0.51	0.131 $\pm$ 0.035 (0.063, 0.198)	0.097 $\pm$ 0.017 P = 0.54	0.41
F	0.027 $\pm$ 0.014 (0.006, 0.059)	0.020 $\pm$ 0.012 P = 0.71	0.0007 $\pm$ 0.002 (0, 0.008)	0.0003 $\pm$ 0.001 P = 0.19	0.45

DISCUSSION

Tiller population dynamics did not differ between mixedgrass and tallgrass prairie populations as mean population growth rates in each habitat were positive and similar to one another. However, individual *A. gerardii* tillers produced lower numbers of buds and had a lower flowering probability in mixedgrass than tallgrass prairie populations. The annual phenology of bud and tiller development in mixedgrass populations was also contracted to fit within the shorter growing season. Mixedgrass prairie *A. gerardii* populations were able to persist locally solely via vegetative reproduction but sexual reproduction may occasionally play an important role under disturbed or harsh environmental conditions. Therefore, the maintenance of both mixedgrass and tallgrass *A. gerardii* populations largely depends on consistent tiller recruitment from the bud bank.

The similar population growth rates of *A. gerardii* in both northern mixedgrass prairie and tallgrass prairie was unexpected given the significant differences in productivity between these two regions. *Andropogon gerardii* has lower biomass production per square meter in northern mixedgrass prairie than in tallgrass prairie (Epstein *et al.*, 1998). Productivity is a function of both tiller density and tiller size. Reduction in tiller size in mixedgrass prairie due to climate, competition, and genotype could reduce regional productivity of *A. gerardii*. Because mixedgrass and tallgrass prairie had similar population growth rates, tiller density within a stand of *A. gerardii* is unlikely to change but the tiller density of an established stand of *A. gerardii* could be habitat-specific and potentially lower in more arid ecosystems such as mixedgrass prairie. The size and extent of *A. gerardii* stands is smaller in C₃-dominated than C₄-dominated grasslands. Assuming that the environmental conditions at the range center reflect the niche center of a species and that these optimal conditions are spatially autocorrelated, overall habitat is expected to decline in its suitability at the edge of its range (Brown, 1984). However, at the edge of its range, habitat may not just decline in suitability but suitable habitat may have a more patchy distribution across the landscape. The cool-season and warm-season elements of northern mixedgrass prairie in South Dakota occur in distinctive topographic positions with warm-season grasses occupying warmer open sites and cool-season grasses occupying cooler more shaded sites (Tiezon, 1970; Teeri, 1979; Barnes

et al., 1983; Steuter, 1987). In the nearby Nebraska sandhills, C₃ and C₄ prairie elements were spatially segregated depending on the seasonal timing of soil moisture (Barnes and Harrison, 1982). Local separation of C₃ and C₄ grasses along environmental gradients would be expected at the latitude of this study due to the difference in temperature effect on C₃ and C₄ quantum yields (Ehleringer, 1978; Barnes *et al.*, 1983). Therefore, reduced productivity of *A. gerardii* in northern mixedgrass prairie could be due to a combination of lowered available area and increased patchiness of suitable habitat, lowered tiller density within stands, and/or reduced tiller size rather than a large difference in vegetative reproductive ability. Because this study and our previous study in tallgrass prairie (Ott and Hartnett, 2012) were short-term studies, it is not possible to fully elucidate the demographic mechanisms contributing to regional productivity differences.

Both mixedgrass and tallgrass prairie populations of *A. gerardii* were evaluated under high precipitation years. Even with these good growing conditions, a few mixedgrass populations of *A. gerardii* could have declining population growth rates. Probability of population extinction increases as λ decreases and the variance of λ increases (Lande and Orzack, 1988; Lande, 1993). Only further study across several years and habitats will be able to determine whether the variability of the mixedgrass population growth rate is greater than the growth rate of tallgrass populations and is a contributing factor to the range limit and regional productivity of *A. gerardii* (Nantel and Gagnon, 1999).

Changes in vegetative tiller recruitment from young buds and bud production on vegetative tillers will most strongly influence overall changes in λ in both habitats. Even variation in λ among populations within the same habitat was driven by the variability in the annual tiller recruitment rate. Therefore, the response of *A. gerardii* populations to climate (*e.g.*, drought) and disturbances such as grazing are largely dependent on how these disturbances alter the cycle of bud production of vegetative tillers and subsequent vegetative tiller recruitment from young buds.

Tiller recruitment may be more easily altered than bud production per tiller. Grazing has been shown to reduce the number of tillers per plant but not bud production per tiller in perennial C₄ grasses (Hendrickson and Briske, 1997; N'Guessan and Hartnett, 2011). Drought in tallgrass prairie only altered annual bud production per *A. gerardii* tiller by one to two buds (J.P. Ott, unpublished data). *Andropogon gerardii* bud production per tiller may remain relatively unchanged unless a disturbance occurs during the 1 mo period of rapid bud development (VanderWeide, 2013). Insuring adequate population performance of key forage grasses may depend on a minimum level of tiller recruitment if bud production per tiller remains largely unaltered by grazing or climatic shifts. Therefore, the key to understanding how tiller recruitment can influence population performance depends on understanding the environmental and hormonal controls of apical dominance, sustained bud outgrowth, and individual bud characteristics (Tomlinson and O'Connor, 2004; Waldie *et al.*, 2010; Williamson *et al.*, 2012).

Sexual reproduction and seed dispersal still assist in determining the broad scale distribution of perennial grasses (Brown and Gersmehl, 1985). For example two *Bouteloua* species with very low seedling establishment persist and dominate in their respective North American grasslands, desert grassland and shortgrass steppe, via vegetative reproduction (Lauenroth *et al.*, 1994; Peters, 2000). However, spatial patterns in soil water availability and temperature determine seed germination and establishment of each species and the location of the ecotone between desert grassland and shortgrass steppe (Minnick and Coffin, 1999). Tallgrass C₄ perennial grasses have been slowly expanding westward since the 1800's at rates that require seed dispersal, especially in the southern prairies (Brown, 1993).

Vegetative reproduction of tallgrass perennial grasses would be expected to decline and population dependency on seed immigration would increase when these grasses approach their range limit.

Bud bank characteristics did not differ between mixedgrass and tallgrass prairie populations. Bud longevity and vital rates within the bud bank were similar between habitats leading to bud banks with similar age structure. Annual tiller populations were primarily recruited from younger buds. The contributions of older buds to annual tiller production may be small and would be insufficient to offset parent tiller mortality without additional tiller recruitment from younger buds (Hendrickson and Briske, 1997; Ott and Hartnett, 2012). However, older buds contributed to *A. gerardii* population stability as they comprised a large proportion of the bud population and represented a significant storage effect. Older buds are often the most proximal buds of those originally produced on an individual tiller and usually yield tillers with reduced vigor (Mitchell, 1953; McIntyre, 1972; Mueller and Richards, 1986). Therefore, older buds have been proposed to be vestigial organs which have missed their primary outgrowth opportunity and continue to exist due to the developmental constraints of bud abortion and their low maintenance costs (Hendrickson and Briske, 1997). Buds within the bud bank can be used for renewal (*i.e.*, annual tiller recruitment) or regeneration (*i.e.*, recovery following disturbance) and buds destined for each purpose may be indistinguishable from one another (Klimesova and Klimes, 2007). The decreased probability of older bud outgrowth may facilitate their population stabilizing role as regeneration buds and their ability to buffer population dynamics against unfavorable climatic conditions similar to soil seed banks (Ott and Hartnett, 2012; Pake and Venable, 1996).

Successful tiller recruitment via the bud bank is key to population persistence and will vary according to the unique suite of abiotic and biotic conditions of each habitat. Our matrix model analyses and results from previous studies suggest that bud banks and vegetative reproduction are important mediators of grass population responses to climate and disturbance. Therefore, the primary factors that regulate vegetative reproduction and bud bank development in perennial grasses need to be identified and understood to enable better prediction of changes in species abundances and distribution and the vulnerability of different types of grasslands to environmental change.

Acknowledgments.—We thank C. Ferguson, J. Nippert and L. Murray for helpful suggestions on previous drafts of this manuscript. We also thank B. Sandercock for matrix modeling advice, K. Sebes for lab assistance and Wind Cave NP, especially B. Burkhart, for their field site support. Funding for this research came from the Kansas State University Division of Biology, the Konza Prairie NSF Long-Term Ecological Research Program and the USDA Rangeland Research Program (Grant #310306).

LITERATURE CITED

- BAKER, H. G. 1959. The contribution of autecological and genecological studies to our knowledge of the past migrations of plants. *Amer. Nat.*, **93**:255–272.
- BARNES, P. W. AND A. T. HARRISON. 1982. Species distribution and community organization in a Nebraska sandhills mixed prairie as influence by plant soil-water relationships. *Oecologia*, **52**:192–201.
- , L. L. TIESZEN, AND D. J. ODE. 1983. Distribution, production, and diversity of C₃-dominated and C₄-dominated communities in a mixed prairie. *Can. J. Bot.*, **61**:741–751.
- BENSON, E. J. AND D. C. HARTNETT. 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. *Plant Ecol.*, **187**:163–177.
- BRAULT, S. AND H. CASWELL. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecol.*, **74**:1444–1454.

- BROWN, D. A. 1993. Early 19th century grasslands of the midcontinent plains. *Ann. Assoc. Amer. Geographers*, **83**:589–612.
- AND P. J. GERSMEHL. 1985. Migration models for grasses in the American midcontinent. *Ann. Assoc. Amer. Geographers*, **75**:383–394.
- BROWN, J. H. 1984. On the relationship between abundance and distribution of species. *Amer. Nat.*, **124**:255–279.
- CASWELL, H. 2001. Matrix population models: Construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, U.S.A.
- EHLERINGER, J. R. 1978. Implications of quantum yield differences on distributions of C₃ and C₄ grasses. *Oecologia*, **31**:255–267.
- EPSTEIN, H. E., W. K. LAUENROTH, I. C. BURKE, AND D. P. COFFIN. 1997. Productivity patterns of C₃ and C₄ functional types in the US Great Plains. *Ecol.*, **78**:722–731.
- . 1998. Regional productivities of plant species in the Great Plains of the United States. *Plant Ecol.*, **134**:173–195.
- FAIR, J., W. K. LAUENROTH, AND D. P. COFFIN. 1999. Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. *J. Ecol.*, **87**:233–243.
- FAY, P. A., J. D. CARLISLE, A. K. KNAPP, J. M. BLAIR, AND S. L. COLLINS. 2003. Productivity responses to altered rainfall patterns in a C₄-dominated grassland. *Oecologia*, **137**:245–251.
- GOTELLI, N. J. AND A. M. ELLISON. 2004. A primer of ecological statistics. Sinauer Associates, Sunderland, Massachusetts, U.S.A.
- HARPER, J. L. 1977. Population Biology of Plants. Academic Press, London. 892 p.
- HENDRICKSON, J. R. AND D. D. BRISKE. 1997. Axillary bud banks of two semiarid perennial grasses: Occurrence, longevity, and contribution to population persistence. *Oecologia*, **110**:584–591.
- HENGVELD, R. 1990. Dynamic biogeography. Cambridge UP, New York, New York.
- HIGGINS, J. J. 2004. Introduction to modern nonparametric statistics. Brooks/Cole-Thomson, Pacific Grove, California, U.S.A. 366 p.
- KLIMESOVA, J. AND L. KLIMES. 2007. Bud banks and their role in vegetative regeneration - A literature review and proposal for simple classification and assessment. *Perspect. Plant Ecol. Evol. Systematics*, **8**:115–129.
- LANDE, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Amer. Nat.*, **142**:911–927.
- AND S. H. ORZACK. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *PNAS*, **85**:7418–7421.
- LAUENROTH, W. K., O. E. SALA, D. P. COFFIN, AND T. B. KIRCHNER. 1994. The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. *Ecol. App.*, **4**:741–749.
- MCINTYRE, G. I. 1972. Studies on bud development in rhizome of *Agropyron repens*. 2. Effect of nitrogen supply. *Can. J. Bot.*, **50**:393–401.
- MINNICK, T. J. AND D. P. COFFIN. 1999. Geographic patterns of simulated establishment of two *Bouteloua* species: implications for distributions of dominants and ecotones. *J. Veg. Sci.*, **10**:343–356.
- MITCHELL, K. J. 1953. Influence of light and temperature on the growth of ryegrass (*Lolium* spp.). 2. The control of lateral bud development. *Physiol. Plantarum*, **6**, 425–443.
- MUELLER, R. J. AND J. H. RICHARDS. 1986. Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum*. *Ann. Bot.*, **58**:911–921.
- N'GUESSAN, M. AND D. C. HARTNETT. 2011. Differential responses to defoliation frequency in little bluestem (*Schizachyrium scoparium*) in tallgrass prairie: implications for herbivory tolerance and avoidance. *Plant Ecol.*, **212**:1275–1285.
- NANTEL, P. AND D. GAGNON. 1999. Variability in the dynamics of northern peripheral versus southern populations of two clonal plant species, *Helianthus divaricatus* and *Rhus aromatica*. *J. Ecol.*, **87**:748–760.
- OTT, J. P. 2009. Bud bank morphology, dynamics, and production in perennial grasses. M.Sc. thesis, Kansas State University.
- . 2014. Ecological implications of grass bud bank and tiller dynamics in mixed- grass prairie. Ph.D. Dissertation, Kansas State University.

- AND D. C. HARTNETT. 2012. Contrasting bud bank dynamics of two co-occurring grasses in tallgrass prairie: implications for grassland dynamics. *Plant Ecol.*, **213**:1437–1448.
- PAKE, C. E. AND D. L. VENABLE. 1996. Seed banks in desert annuals: Implications for persistence and coexistence in variable environments. *Ecol.*, **77**:1427–1435.
- PETERS, D. P. C. 2000. Climatic variation and simulated patterns in seedling establishment of two dominant grasses at a semi-arid-arid grassland ecotone. *J. Veg. Sci.*, **11**:493–504.
- PHILBRICK, C. T. AND D. H. LES. 1996. Evolution of aquatic angiosperm reproductive systems. *Biosci.*, **46**:813–826.
- R DEVELOPMENT CORE TEAM. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- SAS 9.2. 2008. SAS 9.2 help and documentation. SAS Institute, Cary, North Carolina, U.S.A.
- SOIL SURVEY STAFF, NATURAL RESOURCES CONSERVATION SERVICE, USDA [Internet]. 2013. Web soil survey. Available from: <http://websoilsurvey.nrcs.usda.gov/>.
- STEUTER, A. A. 1987. C₃/C₄ production shift on seasonal burns: Northern mixed prairie. *J. Range Manage.*, **40**:27–31.
- TEERI, J. A. 1979. The climatology of the C₄ photosynthetic pathway. p. 356–374. In: O. Sobrig, S. Jain, G. Johnson, and P. Ravens (eds.). Topics in plant population biology. Columbia UP New York.
- AND L. G. STOWE. 1976. Climatic patterns and distribution of C₄ grasses in North America. *Oecologia*, **23**:1–12.
- TIESZEN, L. L. 1970. Photosynthetic properties of some grasses in eastern South Dakota. *Proc. S. D. Acad. Sci.*, **49**.
- TOMLINSON, K. W. AND T. G. O'CONNOR. 2004. Control of tiller recruitment in bunchgrasses: uniting physiology and ecology. *Func. Ecol.*, **18**:489–496.
- VANDERWEIDE, B. L. 2013. Grazing and drought in tallgrass prairie: the role of belowground bud banks in vegetation dynamics. Ph.D. Dissertation, Kansas State University.
- WALDIE, T., A. HAYWARD, AND C. A. BEVERIDGE. 2010. Axillary bud outgrowth in herbaceous shoots: how do strigolactones fit into the picture? *Plant Mol. Biol.*, **73**:27–36.
- WELLSTEIN, C., S. CHELLI, G. CAMPETELLA, S. BARTHA, M. GALIE, F. SPADA, AND R. CANULLO. 2013. Intraspecific phenotypic variability of plant functional traits in contrasting mountain grasslands habitats. *Biodivers. Conserv.*, **22**:2353–2374.
- WILLIAMSON, M. M., G. W. T. WILSON, AND D. C. HARTNETT. 2012. Controls on bud activation and tiller initiation in C₃ and C₄ tallgrass prairie grasses: the role of light and nitrogen. *Bot.*, **90**:1221–1228.

SUBMITTED 8 SEPTEMBER 2014

ACCEPTED 19 MARCH 2015

TABLE A1.—Fitted distributions with location and shape parameters for each matrix element for each habitat separately and for the overall study. N= normal, B = Beta

Matrix Element	Tallgrass	Mixedgrass
G_{b1}	B; $\hat{\alpha} = 3.78, \hat{\beta} = 6.67,$ $\hat{\mu} = 0.3618, \hat{\sigma} = 0.1420$	B; $\hat{\alpha} = 5.51, \hat{\beta} = 6.62,$ $\hat{\mu} = 0.4544, \hat{\sigma} = 0.1374$
G_{b1-v}	B; $\hat{\alpha} = 11.05, \hat{\beta} = 41.90,$ $\hat{\mu} = 0.2087, \hat{\sigma} = 0.0553$	B; $\hat{\alpha} = 4.34, \hat{\beta} = 12.13,$ $\hat{\mu} = 0.2635, \hat{\sigma} = 0.1054$
G_{b2-v}	B; $\hat{\alpha} = 0.283, \hat{\beta} = 11.96,$ $\hat{\mu} = 0.0231, \hat{\sigma} = 0.0413$	Resample from values
G_{b1-f}	B; $\hat{\alpha} = 2.59, \hat{\beta} = 41.32,$ $\hat{\mu} = 0.0591, \hat{\sigma} = 0.0352$	Resample from values
G_{b2-f}	B; $\hat{\alpha} = 0.141, \hat{\beta} = 16.87,$ $\hat{\mu} = 0.00827, \hat{\sigma} = 0.0213$	None
S_{b2}	B; $\hat{\alpha} = 6.71, \hat{\beta} = 9.74,$ $\hat{\mu} = 0.4081, \hat{\sigma} = 0.1176$	Resample from values
V_v	N; $\hat{\mu} = 8.02, \hat{\sigma} = 0.88$	N; $\hat{\mu} = 6.26, \hat{\sigma} = 0.70$
V_f	N; $\hat{\mu} = 8.97, \hat{\sigma} = 0.59$	N; $\hat{\mu} = 7.54, \hat{\sigma} = 0.42$

TABLE A2.—Loop elasticities according to habitat. No loop elasticities varied significantly by habitat. Bootstrapped estimates $\pm$ 1SD and 95% bootstrapped CI

Loop	Tallgrass	Mixedgrass	Bootstrapped P-value
B1-B2-F-B1	0.152 ± 0.0004 (0.00007, 0.135)	Not available	
B1-B2-V-B1	0.036 ± 0.0006 (0.00009, 0.225)	0.231 ± 0.002 (0.023, 0.659)	0.31
B1-F-B1	0.224 ± 0.001 (0.047, 0.475)	0.006 ± 0.0002 (0, 0.072)	0.45
B1-V-B1	0.717 ± 0.001 (0.448, 0.924)	0.710 ± 0.002 (0.234, 0.974)	0.81
B2	0.007 ± 0.012 (0.00003, 0.041)	0.053 ± 0.086 (0, 0.310)	0.38

TABLE A3.—Demographic parameters scaled contributions to the variability of λ within habitat. The sum of the raw contributions approximates the variance in λ . $Var(\lambda)$ of the tallgrass and mixedgrass habitats are 0.053 and 0.116 respectively. Contributions were obtained from the random effect LTRE for each habitat and are scaled by $Var(\lambda)$ to sum to 1

Matrix Element	Tallgrass	Mixedgrass
G_{b1}	-0.018	0.034
G_{b1-v}	0.502	0.342
G_{b2-v}	0.025	0.558
G_{b1-f}	0.359	-0.003
G_{b2-f}	0.028	0
S_{b2}	0.001	-0.023
V_v	0.097	0.092
V_f	0.005	<0.001