BELOWGROUND BUD BANKS AS REGULATORS OF GRASSLAND DYNAMICS

by

HARMONY J. DALGLEISH

B. A., Grinnell College, 2000

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2007

Abstract

In perennial grasslands, the belowground population of meristems (the bud bank) plays a fundamental role in local plant population structure and dynamics. I tested the “meristem limitation hypothesis” prediction that bud banks increase along an increasing precipitation/productivity gradient in North American grasslands. I sampled bud populations quarterly at six sites across a 1,100 km gradient in central North America. Bud banks increased with average annual precipitation, which explained 80% of variability in bud banks among sites. Seasonal changes in grass bud banks were surprisingly similar across a 2.5-fold range in precipitation and a 4-fold range of aboveground net primary productivity (ANPP). Secondly, I tested the hypothesis that tallgrass prairie plants respond to increases in a limiting resource (nitrogen) through demographic effects on the bud bank. I parameterized matrix models for individual genets, considering each genet as a population of plant parts (buds and stems). Nitrogen addition significantly impacted bud bank demography of both *Sporobolus heterolepis* and *Koeleria macrantha*. In 2005, emergence from the bud bank and growth rates (λ) of the tiller population were significantly higher in *S. heterolepis* genets that received nitrogen. In contrast, nitrogen addition decreased λ in *K. macrantha*. Both prospective and retrospective analyses indicated that bud bank dynamics are the key demographic processes driving genet responses to nutrient availability. Lastly, I tested the hypothesis that the effects of fire and grazing on plant species composition and ANPP are mediated principally through demographic effects on bud banks. I found that plants respond to fire and grazing with altered rates of belowground bud natality, bud emergence, and both short-term (fire cycle) and long-term changes in bud density. The size of the bud bank is an excellent predictor of long-term ANPP, supporting my hypothesis that ANPP is strongly regulated by belowground demographic processes. Meristem limitation due to water or nutrient availability or management practices such as fire and grazing may constrain grassland responses to inter-annual changes in resource availability. An important consequence is that grasslands with a large bud bank may be the most responsive to future climatic change or other phenomena such as nutrient enrichment, and may be most resistant to exotic species invasions.

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In perennial grasslands, the belowground population of meristems (the bud bank) plays a fundamental role in local plant population structure and dynamics. I tested the “meristem limitation hypothesis” prediction that bud banks increase along an increasing precipitation/productivity gradient in North American grasslands. I sampled bud populations quarterly at six sites across a 1,100 km gradient in central North America. Bud banks increased with average annual precipitation, which explained 80% of variability among sites. Seasonal changes in grass bud banks were surprisingly similar across a 2.5-fold range in precipitation and a 4-fold range of productivity. Secondly, I tested the hypothesis that tallgrass prairie plants respond to increases in limiting resources (N) through demographic effects on the bud bank. I parameterized matrix models for individual genets considering each genet as a population of plant parts (buds and stems). Nitrogen addition had significant impacts on bud bank demography in both *Sporobolus heterolepis* and *Koeleria macrantha*. In 2005, emergence from the bud bank and λ of the tiller population were significantly higher in *S. heterolepis* genets that received N. Nitrogen addition decreased λ in *K. macrantha*. Both prospective and retrospective analyses indicated that bud bank dynamics are the important demographic process driving genet responses to nutrient availability. Lastly, I tested the hypothesis that the effects of fire and grazing on plant species composition and ANPP are mediated principally through demographic effects on bud banks. My data indicate that plants respond to fire and grazing with altered rates of belowground bud natality, bud emergence, and both short-term (fire cycle) and long-term changes in bud density. The size of the bud bank is an excellent predictor of long-term ANPP, supporting my hypothesis that ANPP is strongly regulated by belowground demographic processes. Meristem limitation due to water or nutrient availability or management practices such as fire and grazing may constrain grassland responses to inter-annual changes in resource availability. An important consequence is that grasslands with a large bud bank may be the most responsive to future climatic change or other phenomena such as nutrient enrichment, and may be most resistant to phenomena such as exotic species invasions.

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Acknowledgements

I thank my advisor, David Hartnett, and my supervisory committee, John Blair, Carolyn Ferguson, Jeff Pontius, Brett Sandercock, and Anita Dille. They have challenged me to do my best and have each taught me a great deal. I deeply appreciate their willingness to discuss ideas and questions throughout my time at K-State.

I thank the many people who assisted me with fieldwork and their names are acknowledged at the end of each chapter. I want to single out three people who made my fieldwork and the long drives that it entailed most enjoyable: Abby Kula, Jayne Jonas and Jon Dalgleish. Each of them did field work in the snow, which elevates them to the rank of 'extraordinary bud collector.'

My graduate experience has been greatly enhanced by the graduate students, faculty, and staff at K-State, particularly the members of the Hartnett, Joern and Ferguson labs. These students and faculty were always willing to discuss research problems, listen to preliminary results and involve me in their research. Although she was one of those "fish people" my discussions with Katie Bertrand were always stimulating and she was great at helping me talk though analysis questions and study design on my daily drive to Bushnell.

I thank the staff at each of my field sites for their assistance: Jim Larkin and Tom VanSlyke at Konza Prairie, Renee Robichaud of the USFWS at Sevilleta, Mark Lundquist at the Short Grass Steppe, Tracey Vodehnal at the Niobrara, and Galen Pittman and Dean Kettle at the Rockefeller Native Prairie of the University of Kansas. Lastly, I thank Tim Todd for allowing me to store my buds in his cold room. My research was supported by NSF grant DEB-0234159, the Konza Prairie LTER, and the Kansas State University Division of Biology.

Dedication

I dedicate this dissertation to four special teachers. Firstly, to Mr. Johnson, my eighth grade gym teacher, who was the first person to instill in me the idea of pursuing a doctorate degree. He used to call me Dr. King when he'd see me in the hall. I finally told him that I had no desire to go to medical school, and, in fact, I hated the idea. That just made him smile more and say, "There's more than one kind of Dr., you know." Secondly, to Vince Eckhart, Jackie Brown, and Kathy Jacobson, whose classes and interactions at Grinnell saved me from my naïve thoughts of becoming a geneticist and made me recall Mr. Johnson's words. I hope to emulate their example of combining quality research with inspiring teaching.

Lastly, I dedicate this work to my husband, Jon. He believes in me when my own faith falters and is one of the finest people I have ever known.

Chapter 1 — Introduction

In perennial grasslands and many other herbaceous communities, the belowground population of meristems associated with rhizomes or other perennating organs (the “bud bank” *sensu* Harper, 1977) plays a fundamental role in local plant population persistence, structure and dynamics. For example, in North American tallgrass prairie, recent studies indicate that regeneration and maintenance of plant populations is regulated principally by vegetative reproduction and belowground bud bank dynamics (Benson et al. 2004, Benson and Hartnett 2006). Almost all plant species maintain some dormant buds below ground, above ground or both, but the size of the bud bank can vary both within and among species (Lehtila 2000). Just as communities vary in the size of their seed banks, bud banks may vary among communities as well.

Plants can be studied at the level of populations of genets or populations of ramets (Harper and White 1974, Harper 1977). My approach in this research was to study the grassland as a population of parts: ramets and their propagules, namely stems and buds as shown by the model in Figure 1.1. My goal was to characterize the different nodes and transitions in the model and then to understand both community (species composition) and ecosystem (productivity) consequences of bud bank dynamics. In the following paragraphs, I introduce the objectives of each chapter. Figure 1.1 illustrates how the objectives for each chapter are related to my overarching goal.

Bud banks have the potential to strongly influence patterns of net primary production (NPP) in ecosystems such as grasslands, where meristem limitation may constrain primary production and its inherent temporal variability. Understanding differences in bud banks among geographically distributed grassland communities may be important for understanding regional patterns, such as gradients of aboveground net primary production (ANPP). The first objective in Chapter 1 was to test this “meristem limitation hypothesis” using the natural gradient of precipitation and productivity across the Great Plains grasslands of the central United States. If meristem limitation does constrain production potential in drier grasslands, then sites with low average annual precipitation should have a small belowground bud bank compared to more mesic sites. I tested the hypothesis that there is a direct linear relationship between average annual precipitation and belowground bud bank density and expected to see an increase in belowground bud bank densities along the increasing precipitation/productivity gradient among grasslands in North America (desert grasslands < short grass prairie< mixed-grass prairie < tallgrass prairie). My second objective in Chapter 1 was to test the hypothesis that the seasonal dynamics of bud banks for two plant functional groups, grasses and forbs, would be similar among sites across the gradient, regardless of average annual precipitation or community composition. I hypothesized that bud bank densities would peak at the end of the growing season, remain constant over the dormant season (i.e., there would be low bud mortality or natality over the dormant season) and be lowest just after the start of the growing season for both plant functional groups.

Tallgrass prairie plants can be limited by three key resources: water, nitrogen, and light. (Seastedt and Knapp 1993, Knapp and Seastedt 1998). The relative importance of these resources for limiting plant growth varies considerably both in space and in time (Seastedt and Knapp 1993, Knapp and Seastedt 1998). In the second chapter, I test the role of the bud bank in determining plant responses to manipulation of one of these three key limiting resources, nitrogen. Nitrogen is not only limiting to plant growth, but recent theory also suggests that N may play a direct role as a proximal cue for bud dormancy and emergence (Tomlinson and

O'Connor 2004). I addressed the question of how tallgrass prairie bud banks respond to altered resource availability and hypothesized that tallgrass prairie plant responses to changing resource availability are mediated principally through demographic effects on the bud bank. I experimentally manipulated nitrogen availability at the genet level for two representative tallgrass prairie caespitose grass species: *Sporobolus heterolepis* (prairie dropseed) and *Koeleria macrantha* (Junegrass) at Konza Prairie Biological Station. My objectives were to test the effect of a pulsed addition of a limiting nutrient on (1) bud bank demography (2) plant reproductive allocation between flowering and vegetative bud production, and (3) ramet (tiller) size.

Both ungulate grazing and fire have shaped the evolution of plant populations within the tallgrass prairie of central North America (Axelrod 1985). Along with a variable continental climate, fire and grazing are considered the most important drivers of tallgrass prairie ecosystem dynamics and both have large impacts on net primary productivity (NPP), plant population dynamics, and plant community composition (Briggs and Knapp 1995, Hartnett et al. 1996, Collins and Steinauer 1998). Annually burned tallgrass prairie generally has higher NPP, reduced plant species richness and evenness, and lower woody plant cover compared to infrequently burned tallgrass prairie (Collins and Steinauer 1998, Knapp et al. 1998). Grazing by bison, *Bos bison*, or cattle, *B. taurus*, increases plant species diversity by increasing richness and evenness (Hartnett et al. 1996, Towne et al. 2005). Though the patterns of change in community composition and productivity in response to fire and grazing in grasslands have been well described, the underlying demographic mechanisms responsible are largely unexplored (Benson et al. 2004). The few studies that have examined soil seed banks in tallgrass prairie have shown that the seed bank is a poor predictor of aboveground community composition (Rabinowitz and Rapp 1980, Abrams 1988).

In grasslands dominated by clonal plant growth forms, such as the tallgrass prairie, the size of the bud bank available for tiller (ramet) recruitment, the patterns of bud dormancy and activity, and the rate of tiller emergence from the bud bank may determine both the population dynamics of individual species as well as species composition changes in response to fire frequency, grazing, and climate variability (Olson and Richards 1988). In addition, population processes such as the demography of buds and tillers may strongly regulate temporal and spatial variability in aboveground net primary productivity seen in response to fire and grazing. Previous studies have examined aboveground tiller population dynamics in response to plant density, nutrient availability, and/or grazing intensity (Kays and Harper 1974, Noble et al. 1979, Coughenour et al. 1985, Olson and Richards 1988, Briske and Butler 1989, Vinton and Hartnett 1992, Hartnett 1993, Wikberg and Svensson 2003), but few studies have examined the consequences of these factors, and of variation in tillering rates, on the ultimate recruitment source for tillers: the belowground bud bank (Benson et al. 2004). My objectives in chapter 3 were to examine the effects of fire frequency and the effects of large ungulate grazers (bison) and their interaction on belowground bud and aboveground stem demography. An additional objective was to examine the relationship between bud and stem demography and ANPP under different fire frequencies in order to assess the contribution of bud banks to variation in ANPP.

The belowground bud bank is the primary source of recruitment for new tillers in tallgrass prairie (Benson and Hartnett 2005). Most of the variation in ANPP in tallgrass prairie can be accounted for by differences in tiller density, rather than differences in tiller size (Hartnett and Fay 1998). Therefore, population processes such as the demography of buds and tillers have the capacity to explain temporal and spatial variability in ANPP and plant responses to different levels of resource availability (Chapter 3) and represent a crucial link between organismal and ecosystem level processes. Meristem limitation, either along a regional gradient (Chapter 2) or due to management practices (Chapter 4), may constrain responses to inter-annual changes in resource availability. An important consequence is that grasslands with high bud bank densities may be the most responsive to future environmental change such as altered precipitation regimes and nutrient enrichment, and they may be most resistant to phenomena such as exotic species invasions. If meristem limitation is an important constraint on potential ANPP responses to environmental variability, then bud bank populations must be considered in the development of predictive models for grassland and savanna ecosystem dynamics, and their responses to environmental change. In my dissertation, I present research that enhances my understanding of the local and regional patterns and dynamics of these belowground populations of plant parts. This work is a vital step to obtaining a better mechanistic and predictive understanding of the dynamics of grasslands and their projected responses to environmental change.

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Figures and tables

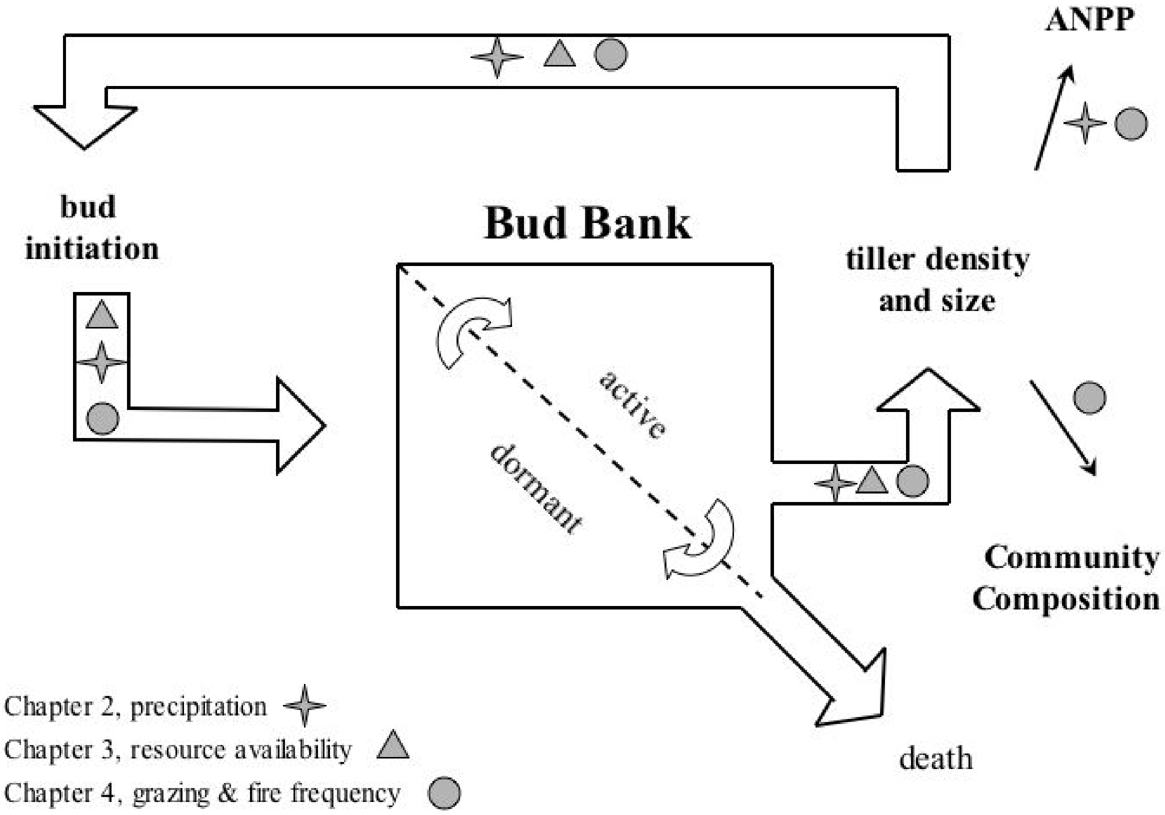

Figure 1.1 Conceptual model of bud bank demography and its potential community and ecosystem consequences.

Chapter 2 — Belowground bud banks increase along a precipitation gradient of the North American Great Plains: a test of the meristem limitation hypothesis[1]

Abstract

In perennial grasslands, the belowground population of meristems (bud bank) plays a fundamental role in plant population dynamics. I tested the "meristem limitation hypothesis" prediction that bud banks increase along an increasing precipitation/productivity gradient in North American grasslands and assessed seasonal dynamics of bud banks. I sampled bud and stem populations quarterly at six sites across a 1,100 km gradient in central North America. Bud banks increased with average annual precipitation, which explained 80% of variability among sites. Additionally, seasonal changes in grass bud banks were surprisingly similar across a 2.5-fold range in precipitation and a 4-fold range of productivity: densities peaked in March, decreased in June and increased slightly in September. Increasing meristem limitation may constrain vegetation responses to inter-annual changes in resources. An important consequence is that biomes with large bud banks may be the most responsive to environmental change. If meristem limitation represents an important constraint on productivity responses to environmental variability, then bud banks must be considered in developing predictive models for grassland responses to environmental change.

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[1] This chapter is published in *New Phytologist*, volume 171, pages 81-89

Introduction

In perennial grasslands and many other herbaceous communities, the belowground population of meristems associated with rhizomes or other perennating organs (the “bud bank” *sensu* Harper 1977) plays a fundamental role in local plant population persistence, structure and dynamics. For example, in North American tallgrass prairie, recent studies indicate that regeneration and maintenance of plant populations is regulated principally by vegetative reproduction and belowground bud bank dynamics (Benson, et al. 2004; Benson and Hartnett 2006). Almost all plant species maintain some dormant buds belowground, above ground or both, but the size of the bud bank can vary both within and among species (Lehtila 2000). Just as communities vary in the size of their seed banks, bud banks may vary among communities as well. Bud banks have the potential to strongly influence patterns of net primary production (NPP) in ecosystems such as grasslands, where meristem limitation may constrain primary production and its inherent temporal variability. Understanding differences in bud banks among communities may be important for understanding regional patterns, such as gradients of aboveground net primary production (ANPP).

Recently, Knapp and Smith (2001) compared patterns of inter-annual variability in ANPP (range and CV) across 11 Long-Term Ecological Research (LTER) sites in North America. Their objective was to quantify the inherent variability in ANPP among major biomes as a crucial prerequisite for accurately detecting directional changes in ANPP in response to global environmental change phenomena. Contrary to their predictions that biomes with the most temporally variable precipitation patterns (deserts) would also have the greatest inter-annual variability in ANPP, they found that ANPP was most variable in grassland biomes that were intermediate in mean annual precipitation and productivity. Low inter-annual variability in

ANPP in forest biomes can be attributed to low precipitation variability. At the other end of the gradient, Knapp and Smith (2001) hypothesized that low ANPP variability in desert and arid grassland biomes could be explained by meristem limitation, which constrains their production potential and their ability to respond to pulses of high resource availability. While annuals constitute a larger portion of the flora in desert grasslands compared to tallgrass prairie, the annual seed banks did not confer the ability to track variability in precipitation in the desert grasslands surveyed by Knapp and Smith (2001). Intermediate biomes such as mesic grasslands have the capacity for large ANPP responses to increases in water or other resources, and it is hypothesized that this capacity is due to their maintenance of large reserves of belowground meristems.

My first objective was to test this meristem limitation hypothesis using the natural gradient of precipitation and productivity across the Great Plains grasslands of the central United States. If meristem limitation does constrain production potential in drier grasslands, then sites with low average annual precipitation should have a small belowground bud bank compared to more mesic sites. I test the hypothesis that there is a direct linear relationship between average annual precipitation and belowground bud banks and expected to see an increase in belowground bud bank densities along the increasing precipitation/productivity gradient among grasslands in North America (desert grasslands < short grass prairie< mixed-grass prairie < tallgrass prairie). The phenology of belowground bud production is largely unknown, but the timing of bud production and the size of bud banks available at different times during the growing season is important for understanding tiller and ANPP dynamics. Work on perennial forbs such as *Solidago canadensis* indicates that bud production commences following flowering at the end of the growing season (Hartnett and Bazzaz, 1985). My second objective was to test the hypothesis that the seasonal dynamics of bud banks for two plant growth forms, grasses and forbs, would be similar among sites across the gradient, regardless of average annual precipitation or community composition. I hypothesized that bud bank densities would peak at the end of the growing season, remain constant over the dormant season (i.e. there would be low bud mortality or natality over the dormant season) and be lowest just after the start of the growing season for both growth forms.

Materials and methods

The six study sites span a 1,100 km gradient across the central grasslands of the U. S. and vary 3-fold in mean annual precipitation and 4.5-fold in mean annual productivity and include the following vegetation types: tallgrass prairie, mixed-grass prairie, short grass steppe, and desert grassland (Table 2.1).

Site Descriptions

Tallgrass Prairie

Rockefeller Native Prairie, University of Kansas Field Station and Ecological Reserves. The Rockefeller Native Prairie is a four hectare tallgrass prairie research tract located in eastern Kansas (38^{o} 97’ N, 95^{o} 23’ W). The land has never been plowed, but was hayed from the 1870s until 1956. Since 1957, this prairie has been burned in the spring on a 1-3 year return interval (Kettle, et al., 2000). The soils are Pawnee and Grundy silty clay loams (fine montmorillonitic, mesic Aquic Argiudolls) (Kindscher and Tieszen, 1998). Mean annual precipitation (MAP) is 948 mm/yr. Mean January temperature is –2^{o}C and the mean July temperature is 27^{o}C.

Konza Prairie Biological Station and Long-Term Ecological Research (LTER) Site. The Konza Prairie Biological Station is 3,487 hectare tallgrass prairie located in the Flint Hills of northeastern Kansas (39^{o} 05’ N, 96^{o} 35’ W). Vegetation is dominated by perennial, warm-season grasses such as *Andropogon gerardii*, *Sorghastrum nutans,* and *Schizachyrium scoparium.* Spring (April) burning treatments (burned at 1, 2, 4, 10, and 20 year intervals) have been maintained on replicate watershed units since the 1970s. Transects for this study were established in grazed and ungrazed, annually burned watersheds (1D, SpB, N1A, N1B), within the upland prairie vegetation growing on shallow, cherty, silty clay loam soil overlying limestone and shale layers (Udic Argiustolls, Florence series). Mean annual precipitation is 834 mm/yr. Mean January temperature is –3^{o}C and mean July temperature is 27^{o}C.

Mixed-Grass Prairie

Kanopolis State Park. Kanopolis State Park is located in the Smokey Hills region of central Kansas (38^{o} 42’ N, 98^{o} 09’W). The park is 648 hectares in size and encompasses both mixed-grass prairie and woodland vegetation. The dominant grassland species include *S. scoparium,* and *Stipa comata*. This mixed grass prairie is protected from both grazing and fire. MAP is 664 mm/yr. Mean January temperature is –3^{o}C and mean July temperature is 27^{o}C.

Niobrara Valley Preserve. The Niobrara Valley Preserve is a 21,000 hectare mixed-grass prairie that lies within the Sandhills Prairie region of north central Nebraska (42^{o} 55’N, 99^{o} 86’W). Dominant grasses include *A. hallii, S. scoparium,* and *S. comata,* (Churchill, et al., 1988). Bison were reintroduced in fall of 1985, stocked year-round at 0.2 animal unit months ha-1 y-1, resulting in 25% consumption of annual ANPP (Fay, 2003). Average fire return interval is prescribed at 7.5 yr. MAP is 534 mm/yr. Mean January temperature is –4^{o}C and mean July temperature is 24^{o}C.

Short Grass Steppe

Short Grass Steppe LTER Site. The Short Grass Steppe LTER Site is located at the western edge of the high plains region of northeast Colorado (40^{o} 49'N, 104^{o} 46'W). The vegetation is composed of short grasses (64%), forbs (7%), succulents (21%). The key species of these groups are *Bouteloua gracilis* and *Buchloe dactyloides; Sphaeralcea coccinea; Opuntia polyacantha,* respectively. Soils in the study area are fine sandy loams in the Remmit series (Ustollic camborthids). MAP is 322 mm/yr. Mean winter temperature is 0.6 °C with maximum July temperatures averaging 30.6 °C.

Desert Grassland

Sevilleta LTER Site. The Sevilleta LTER site is located in central New Mexico at the Sevilleta National Wildlife Refuge (34^{o} 21' N, 106^{o} 41' W). Transects for this study were established in the McKenzie Flats area near the Deep Well Meteorological station. The vegetation is Chihuahuan Desert Grassland, dominated by *B. eriopoda* and *B. gracilis*. The refuge is protected from cattle grazing and a prescribed burn was conducted in the study area in 2001. MAP is 250 mm/yr. Mean annual temperature is 13.2° C, with a low of 1.6°C in January and a high of 25.1°C in July.

Above and Belowground Sampling

Replicate 50 m transects were established at each site within similar soil and vegetation types. The number of transects per site was dependent upon the size of the available sampling area: 2, Rockefeller Native Prairie; 8 Konza Prairie; 3 Kanopolis State Park; 4 Niobrara Valley Preserve;

4 Short Grass Steppe; 8 Sevilleta. Six random points along each transect were chosen for destructive stem and belowground bud sampling. At each random point, all live (defined as greater than 50% green, potentially photosynthetic tissue) above ground stems within a sampling frame were counted, clipped and sorted as grass or forb. Because sedges are indistinguishable from grasses belowground, and because true grasses constitute the majority within a sample, all graminoids were combined as ‘grass’ both above and belowground. The soil within the frame was excavated to a 10 cm depth using a shovel and all belowground perennating organs (rhizomes, etc.) were collected in a plastic bag and stored in a cooler for transport. The sampling frame was 25 cm x 25 cm for all sites except Rockefeller Native Prairie. Due to the small size of this reserve and the desire to minimize soil disturbance, a 10 cm diameter circular frame was used. Before the study began, I sampled belowground buds and aboveground stems at Konza Prairie using the same number of replicates of both sample frame sizes. Both methods yielded average values of buds and stems per square meter that were not statistically significant (a = 0.05) from each other. However, the smaller frame size did have higher variability (Dalgleish, unpublished). Due to logistical constraints, only four sites were sampled between 18 November 2003 and 6 December 2003 (Konza Prairie, Niobrara Valley Preserve, Short Grass Steppe, and Sevilleta) and all six sites were sampled between 6 March 2004 and 3 April 2004; 1-14 June 2004; and 1-26 September 2004. Thus, there were approximately three months between each sampling period.

Sample Processing

Belowground samples were washed free of soil and examined under a dissecting scope. Belowground buds (rhizome meristems) were counted and scored as either grass or forb based on bud morphology and the morphology of the attached root systems. Only developed meristems that formed a distinct stem tissue bud were counted. Questionable structures that may have developed into a root were not counted. Different grass growth forms have different morphology and therefore require different counting techniques: rhizomatous grass and forb buds can be found at the rhizome nodes, sometimes covered with a bud scale, but are quite visible without much dissection; caespoitose (bunch or tufted growth form) grass buds can be found at the base of each stem and oftentimes dissection of the base of the tiller is required in order to count the buds. Many samples included both growth forms and the appropriate technique was used for each growth form within a sample.

Analysis

The mean of each response variable was calculated using the six sub-samples taken along each transect at each sampling time. Means were then analyzed with a nested ANOVA design (transects nested within a site) within a repeated measures framework with a heterogeneous compound symmetry covariance structure using SAS Proc Mixed (SAS, 2003). This covariance structure was selected because it had the lowest value of Akaike Information Criterion (AIC) of ten possible covariance structures fit to the data. The Kenward-Rogers correction was applied. Pair-wise comparisons were performed among sites within a month and among months within a site. The adjust = simulate option was used in Proc Mixed to keep the experiment wise error rate below $\alpha = 0.05$. Two data sets were analyzed separately: one containing only data from four sites sampled from Dec 2003 to Mar 2004 and the other data set containing data on all six sites from March to September 2004. Least squares linear regression was used to examine the relationship between annual bud density and long-term average annual precipitation, using site as the experimental unit.

Results

Bud bank comparisons among sites and relation to precipitation

Regression analysis revealed a significantly increasing linear relationship between average bud bank density and long-term average annual precipitation (Figure 2.1). Long-term average annual precipitation alone explained 80% of the variability among the average annual bud banks of these sites (Regression analysis, $F_{1,4} = 16.46$, $P = 0.0154$, Figure 2.1).

There was a significant interaction between site and month from March 2004 to Sept 2004 (Repeated measures ANOVA, $F_{10,39.8} = 11.91$, $P < 0.0001$). Pair-wise comparisons indicated that tallgrass prairie sites had the largest bud banks with peak (March) belowground meristem densities of 2450 ± 231 and 1835 ± 67 buds/m^2 (mean ± 1 standard error, Konza Prairie and Rockefeller Prairie, respectively). Mixed grass prairie and short grass prairie sites did not differ from each other and had lower peak densities than tallgrass prairie: Niobrara Valley Preserve, 595 ± 87 buds/m^2; Kanopolis State Park, 581 ± 12 buds/m^2; and Short Grass Steppe, 730 ± 118 buds/m^2. The desert grassland site had significantly smaller peak bud banks than all other sites with a mean and standard error of 146 ± 24 buds/m^2. Grasses constitute the vast majority of the bud bank at all sites (from 86%-98%) except for Rockefeller Prairie: only 53% of the Rockefeller bud bank is grasses (Table 2.2).

Growth form differences and seasonal patterns

The seasonal pattern of change from December 2003 to September 2004 in grass bud bank densities was similar at five of the six sites across tallgrass prairie, mixed-grass prairie and short grass steppe (Figure 2.2). Grass bud banks increased over the dormant season from December 2003 to March 2004 at all four sites sampled in 2003 (Figure 2.2). There was a statistically significant interaction between site and month ($F_{3,\,21}$ = 13.62, $P < 0.0001$): while the magnitude of the change (200-250%) was similar at Konza Prairie, Niobrara Valley Preserve, and Short Grass Steppe, grass bud banks at Sevilleta increased approximately 400% from December 2003 to March 2004 (Figure 2.2). All sites except the desert grassland exhibited similar seasonal patterns in grass bud banks during the growing season: densities peaked in March, dramatically decreased in June and then showed a slight increase in September. At Kanopolis State Park, the September increase was larger than observed at the other sites.

Unlike grass bud banks, forb bud banks remained at a constant density over the dormant season in all sites from December 2003 to March 2004 (Repeated measures ANOVA, Month, $F_{1,21}$ = 2.30, P = 0.1438, Figure 2.3). There was significant interaction between month and site for forb bud banks during the growing season from March to September ($F_{10,34.1}$ = 6.83, $P <$ 0.0001). Pair-wise comparisons of forb bud bank values across months within a site show that the tallgrass prairie sites were the only sites with a detectable decrease in forb bud banks from March to June (Figure 2.3a), but they remained low through September, rather than showing the steady increase as the grass bud banks did (Figure 2.3a). While belowground forb bud banks at the Niobrara Valley Preserve, Short Grass Steppe, and Sevilleta exhibited some increasing and decreasing trends over the year, the mean forb bud density was not statistically different among the four sample times ($P < 0.05$ for pair-wise comparisons within a site Figure 2.3b and c). The September sample of Kanopolis State Park, however, exhibited the same increase in the forb bud bank as was seen with the grass bud population (Figure 2.3b).

Relationship between live stem and bud densities

Live grass stem density peaked in June across all sites, which was the opposite pattern observed in belowground meristem densities: when grass bud banks have the lowest density, above ground stem density is highest (Figure 2.4). Peak grass stem density was not statistically different at any site except Rockefeller, which had the lowest peak grass stem density (pair-wise comparisons among sites in June, $P < 0.05$ only for comparisons involving Rockefeller). Forb stem density also showed a June peak in tallgrass prairie, but not in the other grassland sites (Figure 2.5). Peak forb stem density was higher in the tallgrass prairie sites than the other grasslands (pair-wise comparisons among sites in June). The mixed-grass prairie, short grass steppe and desert grasslands showed no clear relationship between above and belowground forb stem and bud populations.

The ratio of belowground buds to aboveground stems can be used as an index of meristem limitation, with values less than one indicating meristem limitation. However, ratios greater than one are a bit harder to interpret: even though the bud bank could replace the aboveground stem population when the meristem limitation index is greater than one, these sites may still be meristem limited. For example, a large portion of the bud bank may be dormant and unavailable for recruitment. I determined that four of the six sites are meristem limited by this index: the mixed-grass prairie and short grass steppe sites have meristem limitation index values around 0.5 and the desert grassland has the lowest meristem limitation index of 0.09 (Table 2.2). Tallgrass prairie sites (Rockefeller and Konza Prairie) are the only sites with meristem limitation index values greater than one (Table 2.2).

Discussion

In their comparison of temporal patterns of productivity and precipitation across North American Biomes, Knapp and Smith (2001) found that ANPP was most variable in biomes that were *intermediate* in mean annual precipitation and productivity, rather than in biomes with the highest variability in precipitation. My study supports the meristem limitation hypothesis: that low temporal variability in ANPP in arid biomes may be explained by meristem limitation, which constrains responses to pulses of high resource availability. While the more arid sites have similar stem densities compared to more mesic sites, my data show that they do not maintain a large population of belowground buds throughout the growing season (a bud bank) compared to the mesic grasslands. Values of the meristem limitation index are less than one in the more arid sites. These sites do not have enough buds present in the bud bank during the growing season to completely replace the aboveground stem population and can be considered meristem limited. Meristem limitation index values greater than one, such as those found in the two tallgrass prairie sites, suggest that these sites are not meristem limited. These data indicate that the ability to increase production in response to resource pulses may be constrained by the availability of meristems in arid grasslands.

My data show that, especially in arid grasslands, the majority of the bud bank is produced just prior to the growing season and these buds quickly emerge into the year’s standing crop of stems, leaving behind the small bud bank populations that I sampled. Not only is the bud bank smaller in more arid grasslands, but previous studies indicate that these buds may not constitute a viable source for continued recruitment. For example, Hendrickson and Briske (1997) found that less than 10% of *Bouteloua curtipendula* and *Helaria belangeri* tillers in the arid grasslands of Texas were recruited from dormant bud banks over two years, indicating that a very small proportion of the bud bank for these two species is able to break dormancy. Unlike arid grasslands, mesic prairies maintain a much larger bud bank and continue to add grass buds to the bud bank throughout the growing season. I hypothesize that the more substantial bud bank in mesic prairies retains the ability to break dormancy and recruit into the aboveground tiller population. Studies are ongoing to test this hypothesis.

A dormant pool of meristems that can be mobilized following damage is one mechanism whereby some plants may tolerate herbivory (Vail 1992; Tuomi *et al.*, 1994; Lehtila and Larsson 2005). Because buds constitute a very small proportion of total plant biomass, a reserve bud bank may have insignificant production and metabolic maintenance costs. However, buds have been hypothesized to incur a high opportunity cost if they remain dormant and do not contribute to seed production (Tuomi, *et al.*, 1994), or if they are unable to break dormancy due to resources, competition, or herbivory (Newton and Hay 1996). Lehtila and Larsson (2005) contend that the loss of bud viability due to environmental factors indicates that buds do indeed incur production and metabolic maintenance costs. The ability to re-sprout rapidly from a pool of dormant meristems may confer some benefits to offset these costs, as plants can capitalize on a newly available resource such as a light gap, significant precipitation or a nutrient flush (Vesk and Westoby 2004). An additional benefit of rapid re-sprouting from a reserve bud population may be the pre-emption of resources from potential exotic invaders, making a resident population more resistant to invasion (Davis, et al. 2000). Gradual and continual activation of buds from the bud bank may serve to protect buds early on in the season from herbivore damage, but avoids the costs associated with maintaining dormancy and foregoing seed production all together (Lehtila 2000).

In species in which the maintenance of a reserve bud population incurs significant costs, bud production may be a bet hedging strategy (vegetative vs. seed reproduction). Under such circumstances, the probability of disturbance and/or the type of disturbance may be a more important determinant of relative allocation to buds (localized spread and neighborhood competition) versus seed production (longer-distance dispersal and patch colonization). These processes likely vary from arid grasslands where small-scale disturbance and patch dynamics are important (e.g. Coffin and Lauenroth 1988), to relatively productive grasslands such as tallgrass prairie, where the primary result of natural disturbances such as fire is to alter the relative availability of key limiting resources rather than create patches for colonization (Knapp et al. 1998).

My second hypothesis that belowground bud banks would be fully formed by the end of the growing season in the fall was only partially supported as this was the pattern seen for forbs, but not for grasses. While data from this study indicate that the majority of stems, both grass and forb, are recruited from the bud bank by June, the two major plant growth forms differed in the size of their belowground meristem pool, and in the phenology of belowground bud production. Additionally, the patterns and magnitude of changes in grass bud banks were surprisingly similar across a 2.5-fold range in precipitation and a 4-fold range of productivity: grasses have the lowest bud density in June, just after peak shoot emergence, but make gradual and continual deposits to the bud bank until the following growing season, perhaps creating a constantly available propagule pool. Forbs in tallgrass prairie have the lowest bud density in June as well, but then produce all of their belowground buds for the next season in the late fall (November). With their single burst of bud production at the end of the growing season, forbs may have a smaller window for recruitment from the bud population. These differences in timing of bud production could interact with the timing of resource availability during the growing season to drive tiller dynamics, and thus patterns of ANPP, in the following growing season. The costs and benefits of maintaining a bud bank, then, may be quite different for these two types of vegetation. Ongoing collection of longer-term datasets will elucidate the relationship between bud density, stem density, growth form and ANPP.

The belowground bud bank is the primary source of recruitment for new grass and forb stems in tallgrass prairie (Benson and Hartnett 2005). Most of the variation in aboveground net primary production (ANPP) in tallgrass prairie can be accounted for by differences in tiller density, rather than differences in tiller size (Hartnett and Fay 1998). Therefore, population processes such as the demography of buds and tillers have the capacity to explain temporal and spatial variability in ANPP and represent a crucial link between organismal and ecosystem level processes. Meristem limitation along the regional gradient studied here may constrain responses to inter-annual changes in resource availability. An important consequence is that biomes with high bud bank densities may be the most responsive to future climatic change or other global change phenomena such as nutrient enrichment, and they may be most resistant to phenomena such as exotic species invasions. If meristem limitation is an important constraint on potential ANPP responses to environmental variability, then bud bank populations must be considered in the development of predictive models for grassland and savanna ecosystem dynamics, and their responses to environmental change. The clearer understanding of the regional patterns and dynamics of these belowground populations of plant parts presented in this study is a vital step to obtaining a better mechanistic and predictive understanding of the dynamics of grasslands and savannas and their projected responses to environmental change phenomena.

Acknowledgements

I extend gratitude to three anonymous reviewers for helpful comments and insights; Abby Kula, Jon Dalgleish, Janel Sinn and Gail Wilson for field and logistical support; Jeff Pontius and Tom Loughin for help with statistical analysis; Renee Robichaud of the USFWS, the Sevilleta LTER Site, Mark Lundquist and the Short Grass Steppe LTER Site, The Nature Conservancy, the Konza Prairie Biological Station, and Dean Kettle and the Rockefeller Native Prairie of the

University of Kansas. This research was supported by NSF grant DEB-0234159, and the Kansas State University Division of Biology.

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Figures and tables

Table 2.1. The six sites span a regional gradient of precipitation and productivity.

Site	Vegetation Type	Mean annual precip. (mm)	Mean ANPP (g/m^2)
Rockefeller Prairie, KS	Tallgrass prairie	960	480
Konza Prairie, KS	Tallgrass prairie	833.6	450
Niobrara Valley Preserve, NE	Mixed-grass prairie	534	170
Kanopolis State Park, KS	Mixed-grass prairie	644	262
Shortgrass Steppe, CO	Shortgrass Prairie	358.5	116
Sevilleta, NM	Desert grassland	269.1	220

Table 2.2 Comparison of peak bud and stem populations and meristem limitation index at all sites.

Site	Peak Bud Bank * (buds/m^2)	Percent Grass Buds (%)	Peak Stem Density * (stems/m^2)	Percent Grass Stems (%)	Meristem Limitation Index (total buds/total stems)
Rockefeller Prairie	1835 ± 67	53.3	493 ± 8	60.9	3.72
Konza Prairie	2450 ± 231	86.3	1831 ± 167	87.6	1.35
Niobrara Valley Preserve	595 ± 87	96.9	1311 ± 255	98.2	0.45
Kanopolis State Park	581 ± 12	93.6	1162 ± 364	90.8	0.50
Short Grass Steppe	730 ± 118	98.6	2207 ± 81	98.1	0.33
Sevilleta	146 ± 24	93.9	1602 ± 270	96.9	0.09

***** Estimates are means ± one standard error

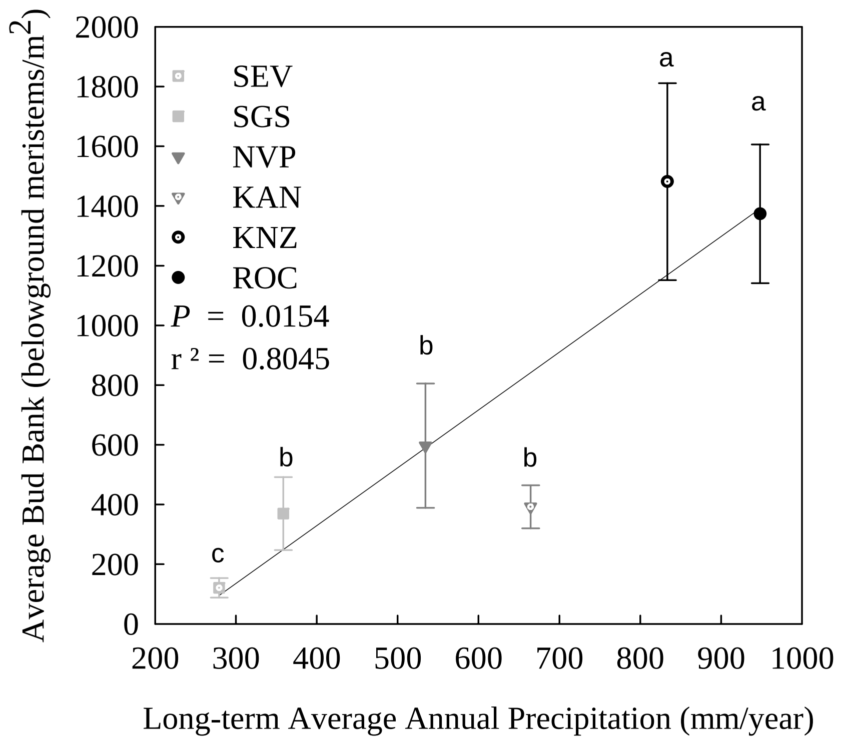

Figure 2.1 Relationship between average bud bank size and long-term average annual precipitation.

Symbols represent annual bud density means, error bars are ± 1 SE. Figure abbreviations: ROC, Rockefeller Prairie; KNZ, Konza Prairie; KAN, Kanopolis State Park; NVP, Niobrara Valley Preserve; SGS, Short Grass Steppe; SEV, Sevilleta.

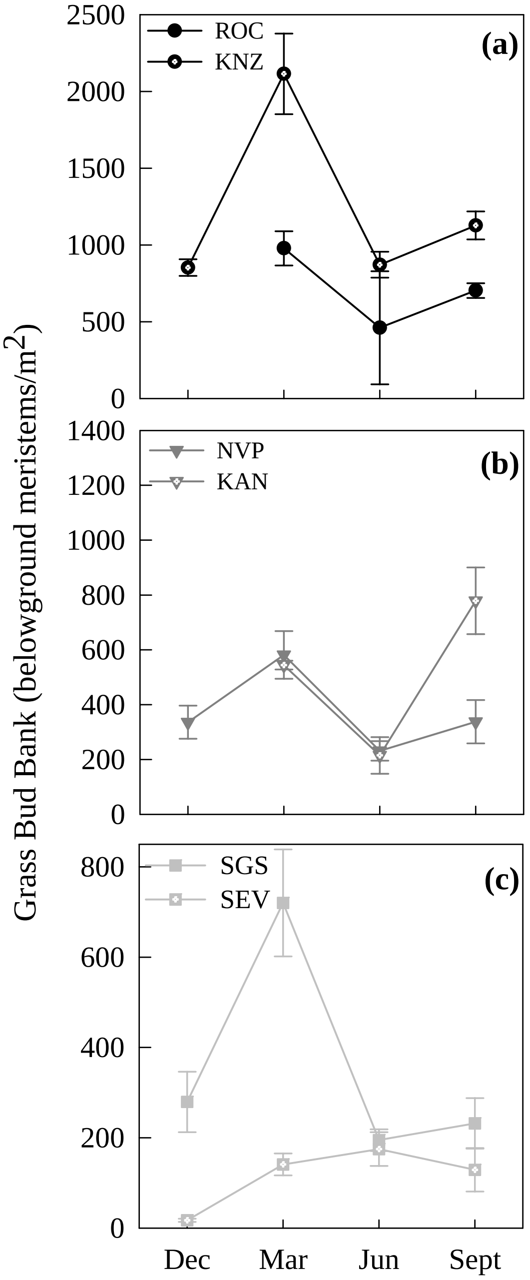

Figure 2.2 Grass bud banks at six sites from December 2003 to September 2004. Points illustrate monthly means ± 1 SE. Panel (a) includes tallgrass prairie sites; Panel (b), mixed-grass sites; Panel (c), arid grasslands. Figure abbreviations: ROC, Rockefeller Prairie; KNZ, Konza Prairie; KAN, Kanopolis State Park; NVP, Niobrara Valley Preserve; SGS, Short Grass Steppe; SEV, Sevilleta

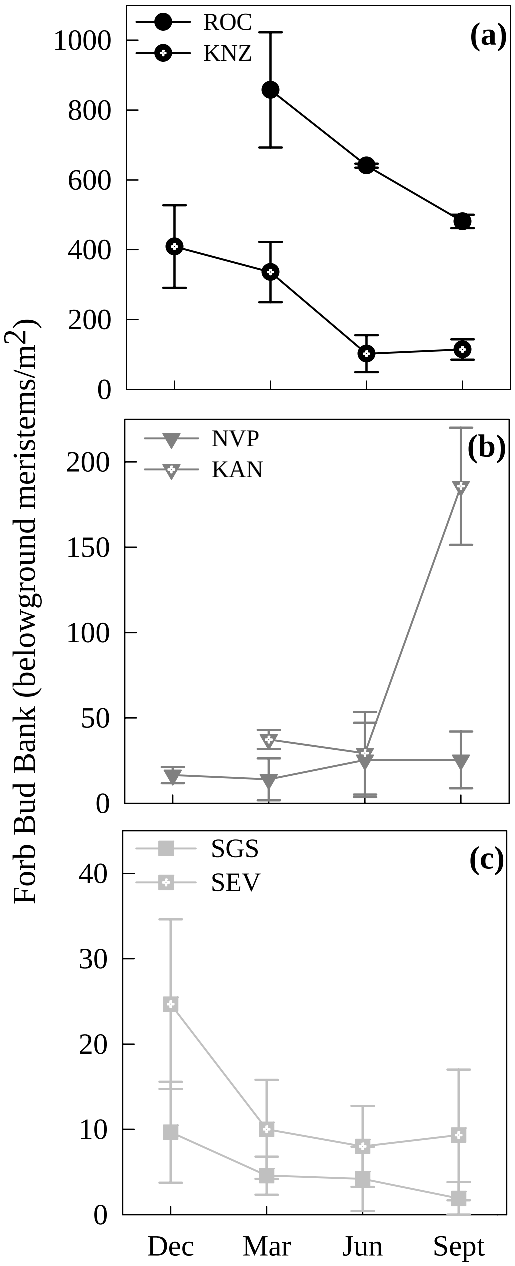

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Figure 2.3 Forb bud banks at six sites from December 2003 to September 2004. Points illustrate monthly means ± 1 SE. Panel (a) includes tallgrass prairie sites; Panel (b), mixed-grass sites; Panel (c), arid grasslands. Figure abbreviations: ROC, Rockefeller Prairie; KNZ, Konza Prairie; KAN, Kanopolis State Park; NVP, Niobrara Valley Preserve; SGS, Short Grass Steppe; SEV, Sevilleta.

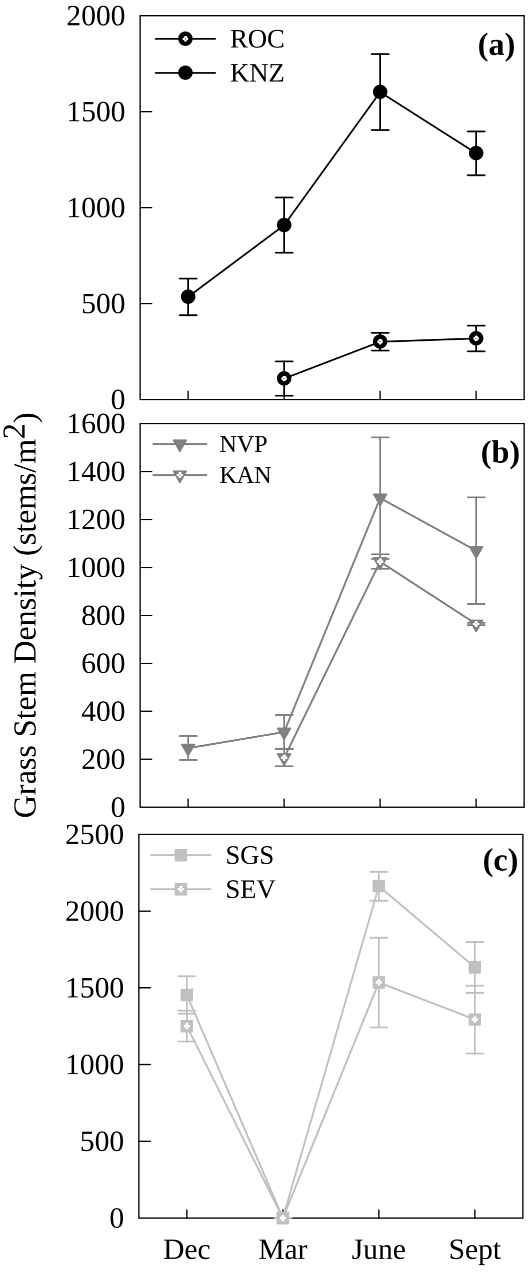

Figure 2.4 Grass stem density at six sites from December 2003 to September 2004. Points illustrate monthly means ± 1 SE. Panel (a) includes tallgrass prairie sites; Panel (b), mixed-grass sites; Panel (c), arid grasslands. Figure abbreviations: ROC, Rockefeller Prairie; KNZ, Konza Prairie; KAN, Kanopolis State Park; NVP, Niobrara Valley Preserve; SGS, Short Grass Steppe; SEV, Sevilleta.

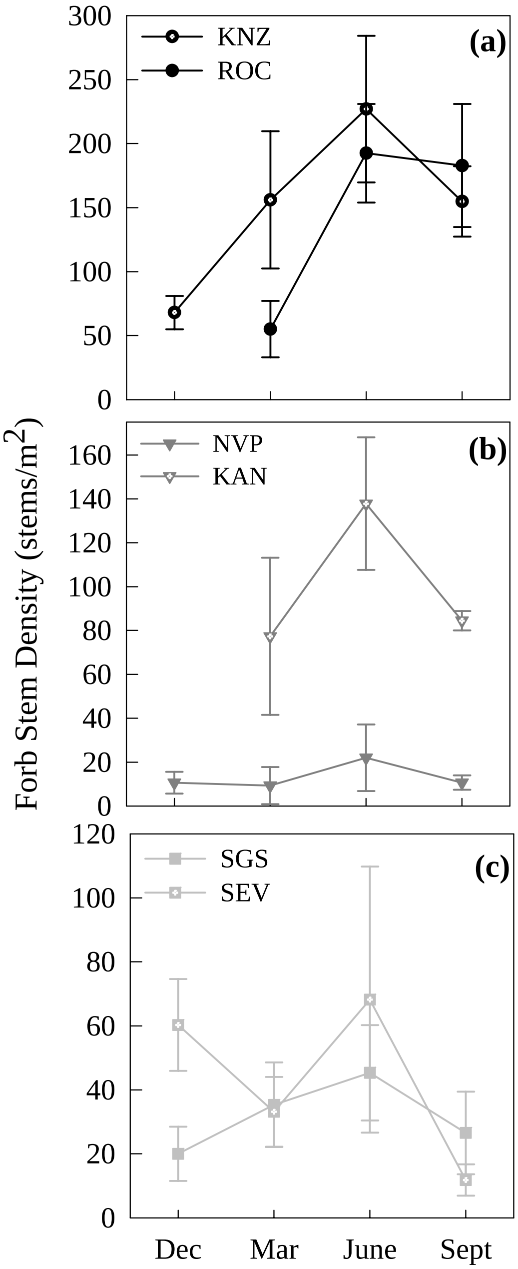

Figure 2.5 Forb stem density at six sites from December 2003 to September 2004. Points illustrate monthly means ± 1 SE. Panel (a) includes tallgrass prairie sites; Panel (b), mixed-grass sites; Panel (c), arid grasslands. Figure abbreviations: ROC, Rockefeller Prairie; KNZ, Konza Prairie; KAN, Kanopolis State Park; NVP, Niobrara Valley Preserve; SGS, Short Grass Steppe; SEV, Sevilleta.

Chapter 3 — The role of the bud banks in tallgrass prairie plant responses to nitrogen addition

Abstract

In perennial grasslands and many other herbaceous communities, the belowground population of meristems associated with rhizomes or other perennating organs (the bud bank) plays a fundamental role in local plant population persistence, structure, and dynamics. The growth of tallgrass prairie plants, many of which maintain substantial bud banks, can be limited by water, nitrogen (N), and light and the relative importance of these resources varies considerably both in space and in time. I hypothesized that tallgrass prairie plants may respond to increases in a limiting resource (N) through demographic effects on the bud bank. My objective was to test the effect of a pulse of a limiting nutrient on (1) bud bank demography (2) plant reproductive allocation between flowering and vegetative bud production, and (3) ramet (tiller) size. I parameterized matrix models for individual genets considering each genet as a population of plant parts (buds and tillers). Nitrogen addition significantly impacted bud bank demography in both *Sporobolus heterolepis* and *Koeleria macrantha*. In 2005, emergence from the bud bank and ramet population growth rates (λ) were significantly higher in *S. heterolepis* genets that received supplemental N. While N addition also affected the bud demography of *K. macrantha*, N decreased rather than increased λ. Both prospective and retrospective analyses indicated that bud bank dynamics were the important demographic process driving genet responses to nutrient availability in both species. A better understanding of bud bank dynamics in grasslands, may

lead to better predictive models of grassland responses to changes in resource availability, plant invasions, disturbance regimes and other environmental changes.

Introduction

In perennial grasslands and many other herbaceous communities, the belowground population of meristems associated with rhizomes or other perennating organs (the “bud bank” *sensu* Harper, 1977) plays a fundamental role in local plant population persistence, structure, and dynamics. Tallgrass prairie maintains a substantial bud bank that serves as the recruitment source for the vast majority of aboveground tillers (Benson and Hartnett 2006, Dalgleish and Hartnett 2006).

Tallgrass prairie plants may be limited by three key resources: water, nitrogen, and light. (Seastedt and Knapp 1993, Knapp and Seastedt 1998). The relative importance of these resources for limiting plant growth varies considerably both in space and in time (Seastedt and Knapp 1993, Knapp and Seastedt 1998). In this research, I tested the role of the bud bank in plant responses to one of these three key limiting resources, nitrogen. Nitrogen (N) not only can limit plant growth, but recent theory also suggests that N may play a direct role as a proximal cue for bud dormancy and emergence (Tomlinson and O'Connor 2004).

I addressed the question of how tallgrass prairie bud banks will respond to increased resource availability and hypothesized that tallgrass prairie plant responses to changing resource availability are mediated principally through demographic effects on the bud bank. I experimentally manipulated nitrogen availability at the genet level for two representative tallgrass prairie caespitose grass species: *Sporobolus heterolepis* (prairie dropseed) and *Koeleria macrantha* (Junegrass) at Konza Prairie Biological Station in north central Kansas. My objectives were to test the effect of a pulsed increase in a limiting nutrient (nitrogen) on (1) bud bank demography, (2) plant reproductive allocation and a tradeoff between flowering and vegetative bud production, and (3) ramet (tiller) size. I predicted that increased nitrogen would result in

(1) an increased probability of emergence from the bud bank and increased ramet population growth rates (λ). Additionally, we expected that stage transitions involving the bud bank would have the greatest effects on λ.

(2) increased vegetative bud production and an increased probability of flowering. Due to a trade off in sexual and vegetative reproduction, tillers that flower would have decreased bud production;

(3) no change in ramet (tiller) size.

Materials and Methods

Konza Prairie Biological Station (KPBS) is a 3,487 ha tallgrass prairie research site located 10 km south of Manhattan, KS, USA, within the Flint Hills region of northeastern Kansas (39^{o}05’N, 96^{o}35’W). Annual precipitation averages 835 mm. Konza Prairie is representative of the Flint Hills with hard chert- and flint-bearing limestone bedrock. Upland ridges are usually flat with shallow, rocky soils, whereas the lowland valleys have deep permeable soils. KPBS is divided into 52 watershed units (average size = 60 ha) subjected to different combinations of long-term experimental fire frequency, season of fire, and grazing treatments.

My study was conducted in 2004 and 2005, which were above-average years for total rainfall (2004: 987.6 mm, 17% above average; 2005: 891 mm, 7% above average). However, seasonal timing of the precipitation differed between years. March – August precipitation was 148 mm lower in 2005 (666 mm) than 2004 (814 mm). The precipitation deficit accrued from the start of the growing season with March 2005 precipitation having 117 fewer mm of rain than March of 2004. Thus, 2005 was much drier during the critical times of bud emergence, growth, and flower development, and water availability was potentially more limiting to plant growth.

Species and Location

Sporobolus heterolepis is a sub-dominant warm-season, C_4, perennial bunchgrass that is occasional on all Konza prairie sites (Towne 2002). It flowers between August and September. The average basal area of a *S. heterolepis* genet in my study was 953.4 ± 114.0 cm^2 (mean ± 1 SE). *Koeleria macrantha* is a sub-dominant, cool season, C_3 bunchgrass. It is common on the upland areas of Konza Prairie and flowers between late May and June (Towne 2002). The average basal area of a *K. macrantha* genet in my study was 33.9 ± 8.6 cm^2 (mean ± 1 SE). This study was conducted in the uplands on the North side of a 12 ha watershed (FA) burned annually in autumn. I chose this site because the two study species co-occur at sufficient densities in this location.

Nitrogen Treatment

In late April 2004, 220 genets of each study species were flagged and numbered. Genets were then randomly assigned to one of two treatments and either a nondestructive or destructive sampling method (described below). Half of the marked genets (*n* = 110 for each species) received dry ammonium nitrate powder at a rate of 10g-N / m^2 during the week of 5 May 2004 (hereafter, "N addition" plants). Because a bunchgrass genet can uptake nutrients within a circle up to 50% greater than its diameter, I fertilized the entire genet as well as an area 50% greater than its diameter (Derner and Briske 1999). Slow release fertilizer pellets were crushed with a mortar and pestle to create ammonium nitrate powder. Application of powder on calm days ensured an even distribution. Control plants were not treated.

The same nitrogen application methods and rates were used in 2005, although the timing of fertilizer application was six weeks earlier for *K. macrantha* in order to better align with this species' phenology. Fertilizer was applied again to genets that were fertilized, but were not harvested, during the first year of *K. macrantha* on 23 March 2005 and of *S. heterolepis* on 10 May 2005. Thus, the genets sampled in the second year of the study received two applications of nitrogen.

Nondestructive aboveground tiller sampling, 2004

For each N treatment, 30 genets of each species were designated for repeated, aboveground, non-destructive sampling in 2004 ("tiller" plants). These plants were visited every two weeks from 5 May to 2 October 2004 (*n* = eight samples for each plant with sample one used as a baseline). All vegetative and flowering ramets (tillers) of each genet were counted and the heights of ten haphazardly selected tillers were recorded to estimate average tiller size for each genet. One fertilized genet of *S. heterolepis* was mistakenly harvested for bud counts (as described below) mid-way through the season and was removed from the "tiller" plants category. Thus the final sample sizes for "tiller" plants of *S. heterolepis* were 29 fertilized genets and 30 control genets, with 30 of each treatment for *K. macrantha*. The data from these genets were used to parameterize the matrix models in 2004 as described below.

Nondestructive aboveground tiller sampling, 2005

Seven fertilized genets and eight control genets of *S. heterolepis* were designated for repeated, aboveground, non-destructive sampling in 2005. These 15 genets were different from the 60 plants sampled in 2004. Genets were visited every three weeks from 16 May to 11 October 2005 (*n* = 6 sampling occasions for each genet). Due to the high number of tillers within a single genet, it was time-consuming to census all tiller of *S. heterolepis* in 2004. In 2005, I developed a sub-sampling procedure to reduce sampling time and increase counting precision in the field. Five circular, 11.8 cm^2 plots were permanently placed within each genet. Because ramet densities in *S. heterolepis* were higher at the edges of the genet, two of the five plots were placed at the edges: one perpendicular to the shortest diameter and one perpendicular to the longest diameter. One plot was placed at the location with lowest ramet density in the genet, which was always in the interior of the genet, while the remaining two plots were randomly placed elsewhere in the interior of the genet. At each sampling time, all vegetative and flowering tillers were counted within the five plots of each genet. Additionally, the heights of ten tillers were recorded to estimate average tiller size. Before the start of the study in 2005, both tiller counting protocols were applied to 10 *S. heterolepis* genets to determine that they yielded density and total tiller estimates that were not statistically different from each other. Thus, even though the method of determining tiller numbers per genet was different between years, the estimates of tiller population size, survival, and fecundity are directly compareable.

There was no change in tiller sampling protocols between 2004 and 2005 for *K. macrantha*. For each treatment, 10 genets per treatment of *K. macrantha* were designated for repeated, aboveground, non-destructive sampling. Genets were visited every three weeks from 23 March to 9 July 2005 (n = 5 sampling times for each genet).

Belowground bud sampling, 2004 and 2005

In 2004, 80 genets of each species in each treatment were used to estimate bud production. Every two weeks, 10 genets of each species per treatment were sub-sampled and then removed from the experiment for a total of eight harvests. All tillers were counted on these plants and 10 tillers were removed and placed in coolers for transport (n = 100 tillers per species per treatment per sampling occasion). In the laboratory, the height of each tiller was measured and each tiller was dissected to count the number of belowground vegetative buds present. Tillers were then dried at 60^{o}C for 48 hours and weighed for biomass estimates.

The protocol remained the same for bud sampling in 2005 but sample sizes were reduced to 49 total genets of *K. macrantha* and 58 total genets of *S. heterolepis*. Every three weeks, approximately 10 genets per species per treatment were sub-sampled with each genet being sampled only once. All tillers on *K. macrantha* genets and five 11.8 cm^2 plots of tillers were counted on *S. heterolepis* (in the same manner as the “tiller” plant sampling described above) to estimate total tiller number on each genet. Twenty tillers were removed per genet and placed in coolers for transport to the lab for measurement and bud counting (n ~ 100 tillers per species per treatment per sampling occasion).

Tiller population model

To synthesize demographic rates of the two species of bunchgrass, I developed a stage-structured matrix population model. Each genet was modeled as a population of tillers and buds over an annual time step. The projection matrix has three nodes representing three discrete life stages: bud, vegetative tiller, and flowering tiller (Figure 3.1).

$$\mathbf{A} = \begin{bmatrix} P_1 & V_v & V_f \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{bmatrix}$$

V, P, and G are stage-specific rates of vegetative bud production, survival, and growth to the next stage, respectively. The projection matrix was linear and deterministic and did not incorporate density-dependence.

Model Parameterization

I created stage-structured projection matrices to determine ramet population growth rates for each genet. I used data from both years for *S. heterolepis* and from only 2005 for *K. macrantha* because 2004 early season data were insufficient. For each matrix, I included six demographic parameters calculated from my bud and tiller censuses (Table 3.1, Figure 3.1).

To create matrix probabilities from the census data, I made three assumptions. First, I assumed no bud mortality within the bud bank. Buds likely persist longer than one growing season and I did not observe any necrotic buds during my sampling. I have no data on bud survival in the bud bank for these two species, but made this assumption in order to calculate P_1, the probability that a bud remains in the bud bank. It is possible, however, that P_1 is an over-estimate. Second, I assumed that all changes in tiller population size leading up to the peak number of tillers were due to emergence of new tillers alone (no tiller mortality before the peak of the growing season). Third, I assumed that all changes in tiller population size after the peak number of tillers were due to mortality.

Analysis

To test for differences in the effects of nitrogen addition between V_v and V_f (the average number of buds produced per tiller) I used a split-plot design with genet as the whole plot factor and flowering as the subplot factor using SAS 9.1 software (Proc Mixed, SAS 2003). Tiller size (g biomass) was used as a continuous covariate. The Kenward-Rogers correction was applied to the degrees of freedom. A repeated measures model was not appropriate because genets were randomly assigned to a destructive sampling time and individual genets were not re-sampled. I used a mixed-model ANOVA design with sampling time and treatment as fixed effects and genet nested within time*treatment as a random effect using SAS 9.1 software (Proc Mixed, SAS 2003) to test for differences in tiller size. The Kenward-Rogers correction was applied to the degrees of freedom. All tests were two-tailed, based on type III sums of squares and considered significant at an α level = 0.05.

Prospective and retrospective analyses were conducted using algorithms of Program Matlab 6.5 following formulae of Caswell (2001) (Matlab 2002). Differences between matrix elements and λ between fertilized and control genets were analyzed with a Kruskal-Wallis test using SAS 9.1 software (Proc Npar1way, SAS 2003). For retrospective analyses, a one-way fixed effect model Life Table Response Experiment (LTRE) was conducted as described by Caswell (2001) on matrices using two levels of fertilizer treatment (for *S. heterolepis* and *K. macrantha*) or two levels of year (for *S. heterolepis* only). The mean N addition matrix or the mean 2005 matrix was used as the reference matrix.

Results

Effects of N addition on transition probabilities

Supplementary N significantly increased the probability of tiller emergence from the bud bank (G_1) for *S. heterolepis* after two N additions in 2005 by two percent (0.23 ± 0.002 SE control; 0.25 ±0.01 +N, $\chi^2_1 = 4.35$, $P = 0.04$). Nitrogen did not affect the probability of emergence in 2004 (Table 3.2). Similarly, N had no effect on the probability of bud outgrowth and tiller emergence in *K. macrantha*.

While the probability of a tiller flowering or the proportion of tillers within a genet that flowered was not a direct measure of resource allocation to sexual reproduction, it still provides a useful estimator that can be used for treatment comparisons. Nitrogen significantly increased the probability of flowering (G_2) by as much as three fold for both species (Table 3.2). In 2004, N addition increased the probability of flowering from 0.03 ± 0.01SE to 0.07 + 0.01SE ($\chi^2_1 = 6.49$, $P = 0.01$) and in 2005 the probability of flowering increased from 0.001 ± 0.001SE in control plants to 0.03 ± 0.01SE in those plants treated with N ($\chi^2_1 = 4.55$, $P = 0.03$). Nitrogen also tended to increase the probability of tillers flowering in *K. macrantha* from 0.05 ± 0.02SE to 0.08 ± 0.02SE, but this was not statistically significant ($\chi^2_1 = 1.76$, $P = 0.18$).

Effects of N addition on bud production

While the absolute number of buds produced per flowering tiller was higher in *S. heterolepis* (Table 3.2), if I take into account the additional biomass accumulated by flowering tillers N addition did not alter the number of buds produced per tiller for either species in either year (Figure 3.2).

Effects of N addition on tiller population λ

In *S. heterolepis,* N addition tended to increase λ (2004: from 1.96 ± 0.02SE to 1.99 ±0.02SE; 2005: from 1.70 ± 0.02SE to 1.82 ± 0.02SE), though the difference was statistically significant only in 2005 (2004; $\chi^2_1 = 0.84$, $P = 0.33$; 2005: $\chi^2_1 = 10.5$, $P = 0.001$). Contrastingly, N addition significantly decreased λ in *K. macrantha* from 1.75 ± 0.02SE to 1.56 ± 0.04SE in 2005 ($\chi^2_1 = 9.6$, $P = 0.002$).

Prospective analysis

Examination of elasticities revealed consistent patterns in both species in both years. The probability of bud outgrowth and tiller emergence from the bud bank (G_1) and the number of buds produced per vegetative tiller (V_v) consistently had the highest elasticity values in both species and in both years and accounted for 52 to 68 percent of the variability in λ (Table 3.3). In 2005, vegetative tiller survival (P_2) had elasticity values greater than 0.25 in both treatments for *K. macrantha* and in the control plants for *S. heterolepis* (Table 3.3). All elasticities associated with flowering stages (P_3, G_2, V_f) were the lowest ranging from 0.001 to 0.2 (Table 3.3).

Retrospective analysis

The difference in λ between the N addition treatment and the control for *K. macrantha* was 0.19 with the control plants having a higher λ on average. The one-way Life Table Response Experiment showed that vegetative bud production by vegetative tillers (V_v) contributed most to the difference in λ (Figure 3.3). In fact, the contribution value for V_v (0.17) was an order of magnitude larger than the contribution value for any other matrix element (Figure 3.3).

The difference in λ between the N addition treatment and the control for *S. heterolepis* in 2004 was only 0.02 with the N addition plants having slightly a higher λ on average. The probability of flowering (G_2) had the highest contribution value (-0.028), nearly double the next largest, which was for vegetative bud production by vegetative tillers (V_v) (Figure 3.4A). In 2005 for *S. heterolepis*, the difference in λ between the N addition and control treatments was 0.13 with the N addition treatment having the higher λ on average. Vegetative bud production by vegetative tillers (V_v) contributed most to the difference in λ with a contribution value (-0.078) double that of the next highest contribution value (-0.036 for the probability of bud emergence (G_1) Figure 3.4B).

A one-way Life Table Response Experiment between years for *S. heterolepis* showed a difference in λ of 0.17 with plants in 2004 having a higher λ on average than those in 2005. Emergence from the bud bank (G_1) had a three times greater contribution to this difference than any other matrix element (-0.45, Figure 3.4C). Survival of buds in the bud bank (P_1) had the next highest contribution value (0.14).

Effects of N addition on tiller size

Nitrogen addition did not affect average tiller size (g biomass) for either species (Figure 3.5). In addition, the average tiller size for *S. heterolepis* (~0.3 g/tiller) was similar between years (Figure 3.5).

Discussion

Nitrogen addition significantly altered bud bank demography in both *S. heterolepis* and *K. macrantha*. In 2005, emergence from the bud bank and λ were significantly higher in *S. heterolepis* genets that received N. While N addition also affected the bud demography of *K. macrantha*, N decreased, rather than increased, λ. Both prospective and retrospective analyses of tiller population models indicated that, in both species, bud bank dynamics were the most important demographic process driving genet responses to increased nutrient availability. Bud production and emergence from the bud bank were consistently important for driving changes in the population growth rate of plant parts for both species and for *S. heterolepis* in both years. The results support my hypothesis that plants respond to increased resource availability through a demographic response principally by changing the number of plant parts within a genet rather than through changing tiller growth and size. Additionally, my results demonstrate that the bud bank is crucial for these plant responses.

Neither species responded to N addition by increasing bud natality (the number of buds produced per tiller). In addition, bud natality was relatively constant within a species and between years for *S. heterolepis*. Therefore, bud banks within a genet increased solely as a function of the number of existing buds activated and the number of tillers produced. Fertilized genets with higher recruitment from the bud bank ended the season with a larger bud bank because they recruited more tillers than control genets. The pattern of increased tiller recruitment with increased nutrient availability has been demonstrated for other graminoids (Noble et al. 1979, Briske and Butler 1989, Derner and Briske 1999). For example, the rhizomatous sand sedge, *Carex arenaria*, increased tiller densities and increased tiller turnover rates with added N (Noble et al. 1979). My study demonstrates how the demography of belowground bud banks drives aboveground population responses. Understanding bud bank dynamics is important because increased tiller recruitment may not always lead to increases in the bud bank. For example, grazing has been shown to increase tiller recruitment in tallgrass prairie likely as a compensatory growth mechanism (Vinton and Hartnett 1992). However, long-term grazing leads to a depauperate bud bank compared to prairie that is not grazed (Chapter 4). Tillers may be unable to replenish the bud bank due to lack of resources in times of nutrient stress or drought or because carbon is allocated to re-growth of photosynthetic tissue such as with compensatory growth after grazing.

The belowground bud bank is a key population of plant parts influencing patterns of vegetative reproduction and genet growth. A trade-off between reproduction and growth is a foundation of plant life-history theory, but there is little empirical evidence for such a trade-off (Reekie and Avila-Sakar 2005). Some evidence for a trade-off between sexual and vegetative reproduction or growth was observed in both *S. heterolepis* and *K. macrantha* in 2005 with flowering tillers tending to produce fewer belowground buds per tiller. This same trend was observed in 2004 for tillers that did not receive additional N. The trend was opposite, however, for tillers that received N: flowering tillers tended to have greater vegetative bud production. While the current study provides some support for a trade-off between sexual fecundity and vegetative reproduction or genet growth, sample sizes were not sufficient in either year to demonstrate statistically significant reduction in vegetative tiller reproduction with flowering and bears further study. Since N addition also increased the probability of flowering, a shift in N availability, or indeed a shift in any resource that increases allocation to flowering, could lead to long-term decreases in the bud bank if flowering comes at a cost to belowground bud production.

Coexisting perennial grass species can vary greatly in life history characters such as longevity, sexual and vegetative reproductive effort, dispersal, and patterns of growth (O'Connor 1991). Understanding the relative contribution and importance of sexual and vegetative reproduction in clonal species is important for understanding the genetic diversity as well as spatial and temporal dynamics, of populations (Benson et al. 2004). Eriksson (1997) proposed a continuum of seedling recruitment strategies in clonal plants from initial seed recruitment within a population with continued maintenance through vegetative reproduction to repeated (though perhaps low) seedling recruitment. In 40% of the 68 clonal species examined by Eriksson (1989) seedling recruitment contributed to population growth rates. *Sporobolus heterolepis* and *K. macrantha* are both sub-dominant tallgrass prairie bunch grasses. In addition to differing phenologies and photosynthetic pathways, this study provides evidence that they may have different reproductive strategies as well. Regardless of treatment or year, *S. heterolepis* produced an average of three times as many buds per tiller than *K. macrantha*. On the other hand, *K. macrantha* tillers had a much higher probability of flowering and the proportion of tillers that flowered within a genet was much greater (~5% for *S. heterolepis*, > 50% for *K. macrantha*). Caespitose grasses are generally thought to rely more heavily on seed reproduction for recruitment than rhizomatous species (Sackeville Hamilton et al. 1987, Briske and Derner 1998, Liston et al. 2003). My data indicate that *S. heterolepis* allocates less to sexual reproduction than *K. macrantha.* Although I did not follow the fate of seeds produced for this study, differences in seed production, seedling establishment, and vegetative reproduction were shown to explain abundance and dominance patterns of two other perennial bunchgrass species in the semi-arid western U. S. (Peters 2002). Further study of species-specific reproductive allocation and establishment patterns of tallgrass prairie species may help to explain species coexistence and perhaps give insight to species' projected responses to environmental change.

Emergence from the bud bank and the probability of flowering were significantly lower in 2005 for *S. heterolepis*. Similarly, tiller population λ was much lower in 2005 and differences in emergence from the bud bank contributed most to the difference in λ between the years. The observed differences between 2004 and 2005 for *S. heterolepis* could be a response to another important limiting resource in tallgrass prairie, water. Though the total rainfall in both years was average or slightly above, the timing of precipitation events in 2005 was such that the plants were likely water stressed during critical growth times. Because the experiment was conducted on plants in the same location and at the same time of the year, it is reasonable to assume that the difference in water availability was the driving force behind the differences between the years. If the different response between years was due to differences in water availability, then my data indicate that the response of *S. heterolepis* to water availability was mediated through the bud bank. However, further research is required to test this hypothesis before general conclusions about plant responses to water can be made.

Understanding the grassland's ability to mobilize the bud bank in response to a resource pulse, such as N or an unseasonable rain event, is potentially important for predicting regarding plant responses to other environmental changes such as exotic species invasion. Davis et al. (2000) developed a general theory arguing that fluctuations in resource availability are the key factor controlling invasibility, and that successful invasion events occur intermittently when specific conditions of resource enrichment or release coincide with adequate propagule supply of the invasive species. Thus, invasions will occur during windows of opportunity when propagules of the invader can capitalize on newly available limiting resources. If resident species have the capacity to rapidly pre-empt and monopolize new resources, such as through rapid recruitment from the bud bank, it will result in invasion-resistant communities (Davis et al. 2000). My results support the hypothesis that tallgrass prairie plants do respond to resource pulses through increasing recruitment from their bud banks. An important consequence of this is that grasslands that maintain large bud banks may be more resistant to invasion, a hypothesis currently under investigation (Hartnett and Dalgleish unpublished).

My analyses support the hypothesis that the production potential of a genet, and hence the grass community, is driven by the demographic dynamics of its belowground bud bank (Murphy and Briske 1992). Because neither *S. heterolepis* nor *K. macrantha* increased tiller size in response to N addition, an increase in biomass production by genets was achieved solely through increases in tiller number. Identifying these underlying mechanisms and the sources of variation in ANPP will be critical to the development of accurate predictive models of ecosystem responses to environmental change. Most current models for predicting ANPP in grasslands (e.g. CENTURY, SOILWAT) and other terrestrial systems (Parton et al. 1987) are based on underlying physiological responses to resources at the canopy level (e.g. photosynthesis, C_3 vs. C_4 physiology and phenology, and growth of plant parts) rather than potentially important demographic mechanisms (e.g. bud natality, survivorship, densities and tillering dynamics). My data show that the demography of bud bank populations plays an important role in increases in ANPP in response to resource availability. A better understanding of bud bank dynamics in grasslands may lead to better predictive models of productivity and potential grassland responses to environmental change.

My study strongly supports that demographic mechanisms of the bud bank are important for driving grass responses to resource availability. Understanding bud bank dynamics has important implications far beyond the individual plant. The maintenance of a bud bank influences the dynamics of the entire population, plays a role in plant species coexistence, contributes to the invasibility of a community, and influences ecosystem productivity. Enhanced knowledge of the bud bank, as the current study provides, will lead to a better mechanistic and predictive understanding of grassland dynamics.

Acknowledgements

I thank two anonymous reviewers for their helpful comments to improve this manuscript; In addition, I thank Janel Sinn, Jennifer Hill, Zoe Gill, Melinda Williamson, Jim Birmingham, and Jayne Jonas for field assistance. This work was supported by the Konza Prairie LTER, the Kansas State University Division of Biology, NSF grant DEB-0234159 and one REU supplement grant to DEB-0234159.

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Figure and tables

Table 3.1 Parameterization of elements in projection matrices. VT = vegetative tiller; FT = flowering tiller.

Element	Definition	Equation
P_1	probability of buds remaining in the bud bank	$1 - G_1$
P_2	probability of a VT remaining a VT	1 Š ((VT$_{\mathrm{peak}}$ Š VT$_{\mathrm{end}}$ Š FT$_{\mathrm{max}}$) / VT$_{\mathrm{peak}}$)
P_3	probability of a FT remaining a FT	1 - ((FT$_{\mathrm{max}}$ Š FT$_{\mathrm{end}}$) / FT$_{\mathrm{max}}$)
G_1	probability of a bud becoming a VT	(VT$_{\mathrm{peak}}$ Š VT$_1$) / ((VT$_1$ $*$ (# buds per tiller)$_1$ + VT$_1$))
G_2	probability of a VT becoming a FT	$\mathrm{FT}_{\mathrm{max}} / \mathrm{VT}_{\mathrm{peak}}$
V_v	Vegetative bud production of VT	Average number of buds produced per VT
V_f	Vegetative bud production of FT	Average number of buds produced per FT

Table 3.2 Summary of matrix elements and λ for two species of bunch grass in tallgrass prairie.

Values are means ± 1 SE. Boldface represents significant differences between treatments within a species at $P < 0.05$.

	Sporobolus heterolepis				*Koeleria macrantha*	
	2004		2005		2005	
	Control	+ N	Control	+ N	Control	+ N
P_1	0.44 ± 0.01	0.45 ± 0.01	0.77 ± 0.002	0.75 ± 0.01	0.18 ± 0.03	0.18 ± 0.04
P_2	0.69 ± 0.02	0.72 ± 0.03	0.87 ± 0.03	0.86 ± 0.02	0.84 ± 0.03	0.79 ± 0.04
P_3	0.81 ± 0.04	0.87 ± 0.03	1.00 ± 0.00	0.90 ± 0.06	0.32 ± 0.11	0.45 ± 0.12
G_1	0.55 ± 0.01	0.54 ± 0.01	**0.23 ± 0.002**	**0.25 ± 0.01**	0.82 ± 0.03	0.82 ± 0.04
G_2	**0.03 ± 0.01**	**0.07 ± 0.01**	**0.001 ± 0.001**	**0.03 ± 0.01**	**0.05 ± 0.02**	**0.08 ± 0.02**
V_v	3.38 ± 0.15	3.29 ± 0.16	3.37 ± 0.25	4.00 ± 0.27	1.70 ± 0.26	1.20 ± 0.32
V_f	4.26 ± 0.36	4.35 ± 0.35	4.17 ± 0.51	5.39 ± 0.62	1.29 ± 0.34	1.15 ± 0.54
λ	1.96 ± 0.02	1.99 ± 0.02	**1.70 ± 0.02**	**1.82 ± 0.02**	**1.75 ± 0.02**	**1.56 ± 0.04**

Table 3.3 Summary of elasticity values for *S. heterolepis* and *K. macrantha.*

Values are means ± 1 SE. Values ≥ 0.25 in boldface.

	Sporobolus heterolepis				*Koeleria macrantha*	
	2004		2005		2005	
	Control	+ N	Control	+ N	Control	+ N
P_1	0.10 ± 0.003	0.09 ± 0.003	0.21 ± 0.008	0.19 ± 0.005	0.03 ± 0.006	0.05 ± 0.012
P_2	0.19 ± 0.005	0.19 ± 0.007	**0.26** ± 0.010	0.24 ± 0.007	**0.30** ± 0.008	**0.31** ± 0.020
P_3	0.01 ± 0.001	0.02 ± 0.003	0.001 ± 0.01	0.01 ± 0.003	0.01 ± 0.003	0.01 ± 0.005
G_1	**0.35** ± 0.003	**0.33** ± 0.004	**0.26** ± 0.002	**0.27** ± 0.003	**0.32** ± 0.005	**0.30** ± 0.004
G_2	0.01 ± 0.002	0.02 ± 0.003	0.001 ± 0.01	0.01 ± 0.003	0.01 ± 0.003	0.02 ± 0.004
V_v	**0.33** ± 0.005	**0.31** ± 0.007	**0.26** ± 0.002	**0.27** ± 0.006	**0.31** ± 0.009	**0.28** ± 0.007
V_f	0.01 ± 0.002	0.02 ± 0.003	0.001 ± 0.001	0.01 ± 0.003	0.01 ± 0.004	0.02 ± 0.004

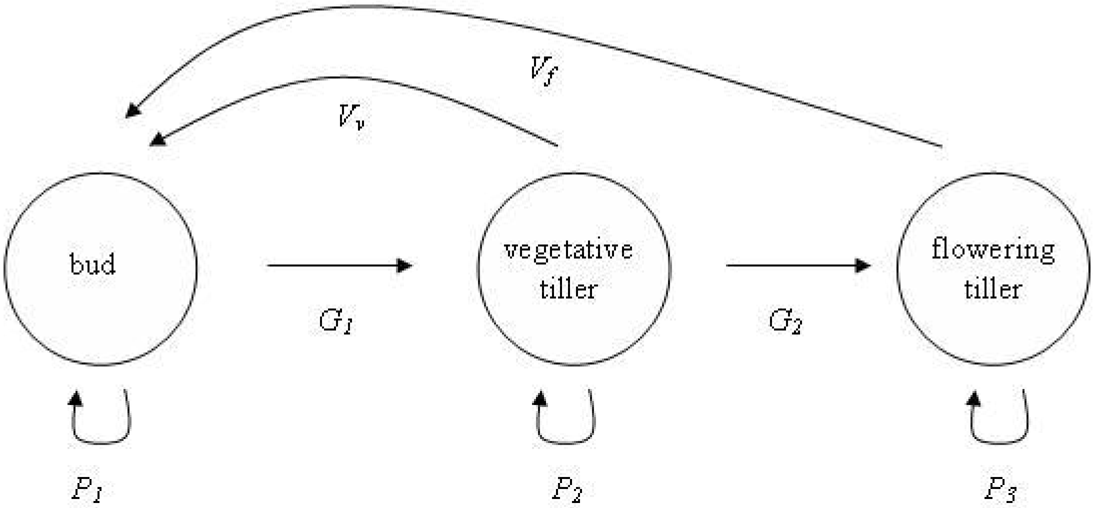

Figure 3.1 Life cycle diagram model of the tiller populations for *S. heterolepis* and *K. macrantha.*

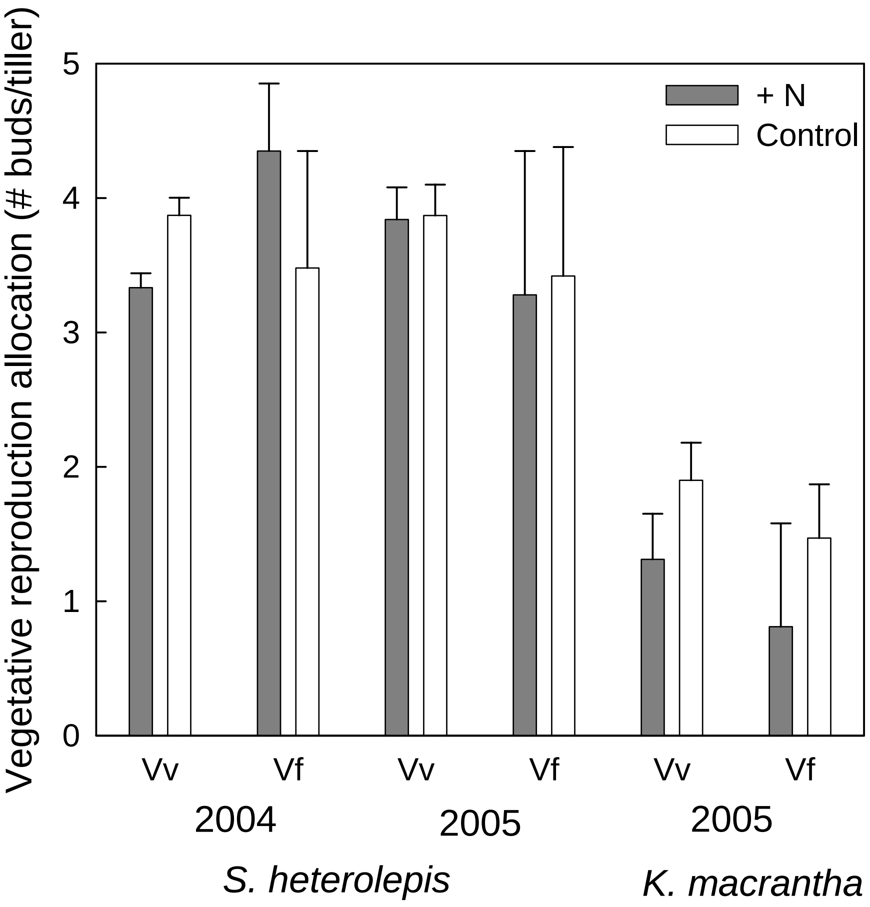

Figure 3.2 Allocation to vegetative reproduction (number of buds/tiller) by vegetative tillers (V_v) and flowering tillers (V_f) of *S. heterolepis* and *K. macrantha.*

Bars represent means ± 1 SE; *S. heterolepis* 2004 genet *n* = 37, flowering tillers *n* = 40, vegetative tillers *n* = 339; *S. heterolpeis* 2005 genet *n* = 107; flowering tillers *n* = 13, vegetative tillers *n* = 166; *K. macrantha* genet *n* = 6 flowering tillers *n* = 22, *Km* vegetative tillers *n* = 84. Tiller size was used as a covariate.

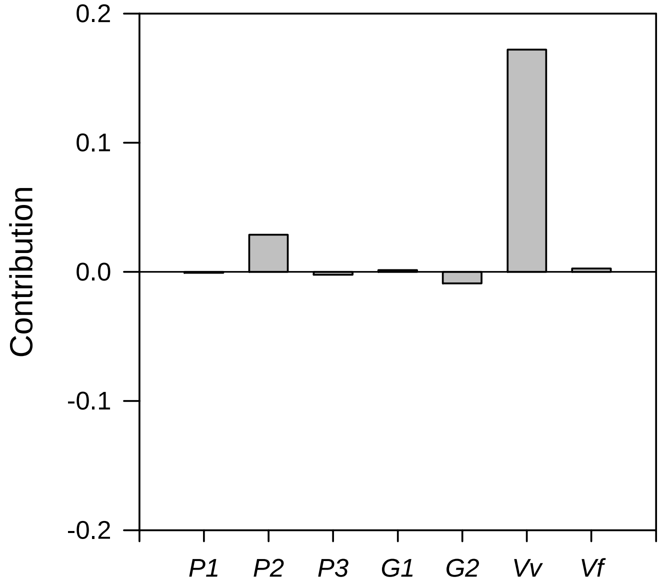

Figure 3.3 One-way LTRE (N addition) in *K. macrantha* illustrating the contributions of the different matrix elements to the difference in λ between the treatments.

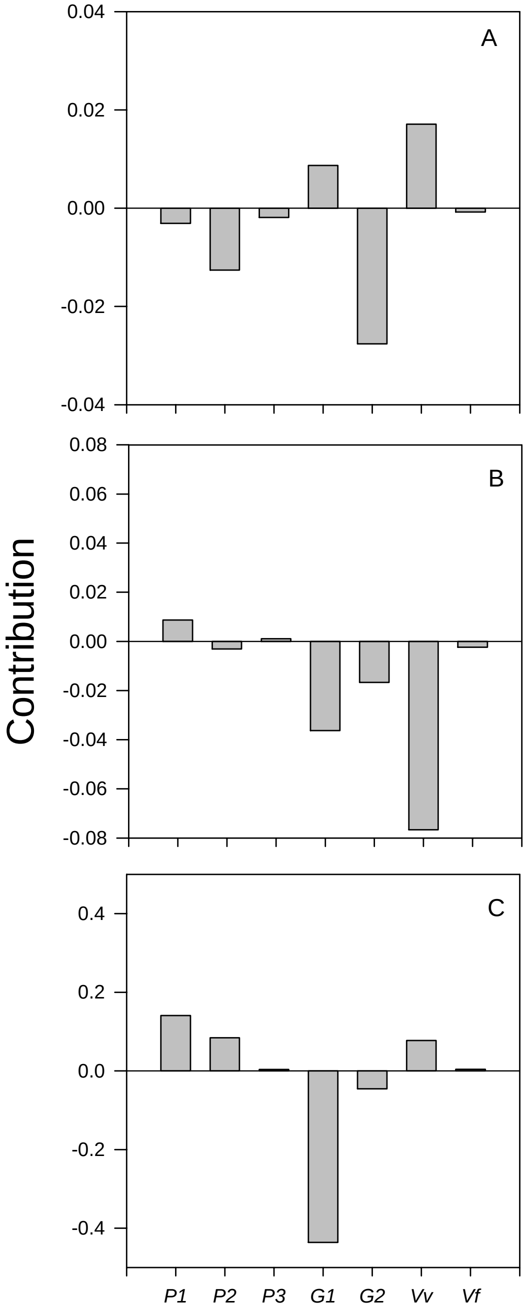

Figure 3.4 Contributions to the difference in λ between treatments for the one-way LTREs of *S. heterolepis*

Panel A: LTRE between treatments in 2004; Panel B: LTRE between treatments in 2005; Panel C LTRE between years 2004 and 2005.

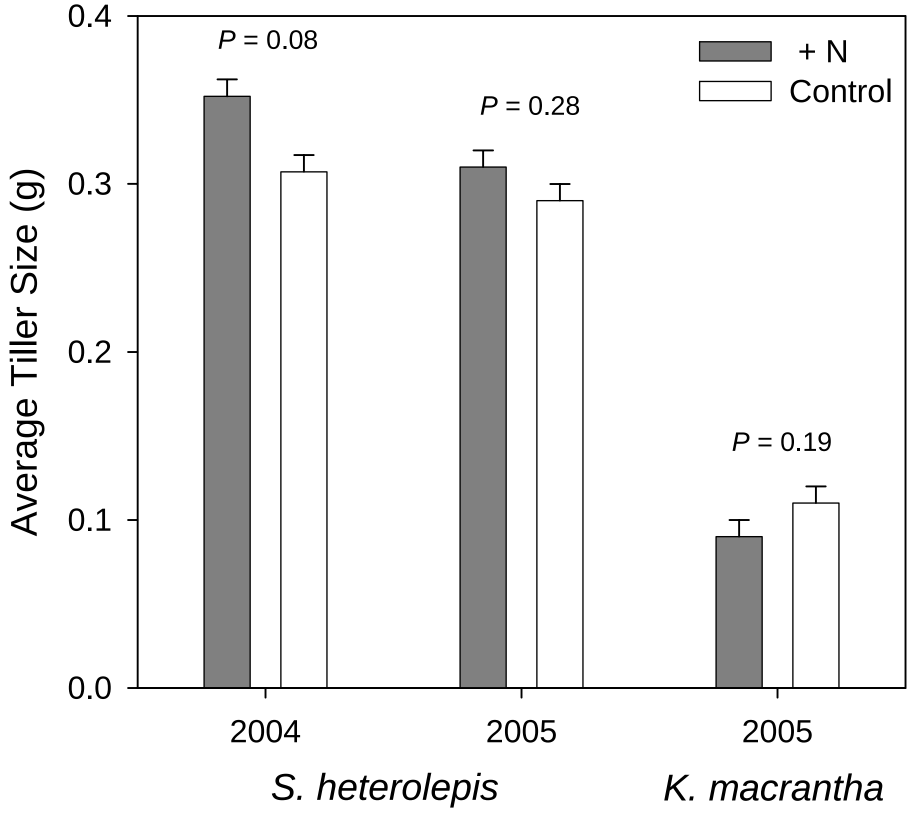

Figure 3.5 Mean tiller size (g biomass) for *S. heterolepis* and *K. macrantha* in 2004 and 2005. Nitrogen addition did not significantly increase average tiller size (g biomass) for either species.

Bars represent means ± 1 SE; *n* = 157 genets, 1548 tillers for *S. heterolepis* 2004; *n* = 57 genets, 1119 tillers for *S. heterolepis* 2005; *n* = 43 genets, 704 tillers for *K. macrantha* 2005.

Chapter 4 — The effects of fire frequency and grazing on tallgrass prairie plant composition and productivity are mediated through bud bank demography

Abstract

Periodic fire, grazing, and variable climate are considered the most important drivers of tallgrass prairie ecosystems, having large impacts on the component species and on ecosystem structure and function. Though the patterns of change in community composition and productivity in response to fire and grazing have been well described for tallgrass prairie, the underlying demographic mechanisms responsible are largely unexplored. My data indicate that in tallgrass prairie plants are responding to key ecological drivers such as fire and grazing with altered rates of belowground bud natality, bud emergence from the bud bank (belowground population of meristems associated with rhizomes), and both short-term (fire cycle) and long-term (>15 year) changes in bud bank density. Both fire frequency and grazing influenced belowground bud and aboveground stem populations of grasses and forbs in tallgrass prairie. My prediction that grass bud banks will increase with increasing fire frequency while forb bud banks will decrease was supported in the absence of grazers. Grazing increased the rate of emergence from the grass bud bank resulting in increased grass stems while decreasing grass bud banks compared to ungrazed prairie. By contrast, grazing increased both bud and stem density of forbs in annually burned prairie but grazing had no effect on forb bud or stem density in the four-year burn frequency

treatment. Overall, my results indicate that fire and grazing strongly interact in their regulation of belowground bud bank dynamics in these grasslands. Lastly, the size of the reserve grass bud bank is an excellent predictor of long-term ANPP in tallgrass prairie ($P = 0.006$, $r^2 = 0.99$), supporting my hypothesis that ANPP is strongly regulated by belowground demographic processes. Meristem limitation due to management practices such as different fire frequencies or grazing regimes may constrain tallgrass prairie responses to inter-annual changes in resource availability. An important consequence is that prairie with a large bud bank may be the most responsive to future climatic change or other global change phenomena such as nutrient enrichment, and may be most resistant to phenomena such as exotic species invasions.

Introduction

Both fire and ungulate grazing have shaped the evolution of the tallgrass prairie of central North America (Axelrod 1985). Along with a variable continental climate, fire and grazing are considered the most important drivers of tallgrass prairie ecosystems and both have large impacts on net primary productivity (NPP), plant population dynamics, and plant community composition (Briggs and Knapp 1995, Hartnett et al. 1996, Collins and Steinauer 1998). Annually burned tallgrass prairie generally has higher NPP, reduced plant species richness and evenness, and lower woody plant cover compared to infrequently burned tallgrass prairie (Collins and Steinauer 1998, Knapp et al. 1998). Grazing by bison, *Bos bison*, or cattle, *B. taurus*, increases plant species diversity by increasing richness and evenness (Hartnett et al. 1996, Towne et al. 2005).

Although the patterns of change in community composition and productivity in response to fire and grazing in grasslands have been well described, the underlying demographic mechanisms responsible are largely unexplored (Benson et al. 2004). The few studies that have examined soil seed banks in tallgrass prairie have shown that the seed bank is a poor predictor of aboveground community composition (Rabinowitz and Rapp 1980, Abrams 1988). By contrast, in perennial grasslands and many other herbaceous communities, the belowground population of meristems associated with rhizomes or other perennating organs (the “bud bank” *sensu* Harper, 1977) may play a fundamental role in local plant population persistence, structure and dynamics. In fact, in North American tallgrass prairie, recent studies indicate that regeneration and maintenance of plant populations is regulated principally by vegetative reproduction and belowground bud bank dynamics, with seed reproduction and seed banks playing a minor role (Benson et al. 2004, Benson and Hartnett 2006).

In grasslands dominated by clonal plant growth forms, such as the tallgrass prairie, the size of the bud bank available for tiller (ramet) recruitment, the patterns of bud dormancy and activity, and the rate of tiller emergence from the bud bank may determine both the population dynamics of individual species as well as species composition changes in response to fire frequency, grazing, and climate variability (Olson and Richards 1988). In addition, population processes such as the demography of buds and tillers may strongly regulate temporal and spatial variability in aboveground net primary productivity seen in response to fire and grazing. Previous studies have examined aboveground tiller population dynamics in response to density, nutrient availability, and/or grazing intensity (Kays and Harper 1974, Noble et al. 1979, Coughenour et al. 1985, Olson and Richards 1988, Briske and Butler 1989, Vinton and Hartnett 1992, Hartnett 1993, Wikberg and Svensson 2003), but few studies have examined the consequences of these factors, and of tillering rates, on the ultimate recruitment source for tillers: the belowground bud bank (Benson et al. 2004).

Previous research by Benson et al. (2004) compared the effects of two extremes of fire frequency in tallgrass prairie (annually burned and burned at 20-year intervals) on belowground bud densities. Benson et al. (2004) found that annually burned prairie had larger grass bud banks and smaller forb bud banks compared to infrequently (20-year) burned prairie and that, unlike seed banks, the composition of the belowground bud population closely resembled the aboveground plant community. My objectives were to extend the research of Benson et al. (2004) to examine effects of fire frequency to include an ‘intermediate’ (four-year) frequency and to examine the effects of large ungulate grazers (bison) and their interaction with fire frequency on belowground bud and aboveground stem demography. An additional objective was to examine the relationship between bud and stem demography and aboveground net primary productivity (ANPP) under different fire frequencies to assess the contribution of bud banks to variation in ANPP.

Plants can be studied at the level of populations of genets or populations of ramets (Harper and White 1974, Harper 1977). My approach was to study the grassland as a population of parts, namely ramets and their propagules (buds) and stems. I hypothesized that the effects of fire frequency and grazing on plant species composition and on ANPP are mediated principally through demographic effects on the bud bank (Figure 4.1). If the established changes in community composition response to fire frequency and grazing are mediated by altered demography of plant parts, namely buds and stems, then I predict a decrease in grass stems and buds and an increase in forb stems and buds with decreasing fire frequency. Similarly, grazing should decrease grass stems and buds and increase forb stems and buds. If long-term plant productivity in tallgrass prairie is also mediated by altered demography of plant parts, then tallgrass prairie with lower bud bank densities will have lower long-term productivity because the lower availability of meristems constrains aboveground stem population size and, thus, biomass production. I predict that fire, grazing, or climate regimes that reduce belowground bud bank densities will result in meristem limitation, constraining potential ANPP responses to available plant resources.

Materials and Methods

Site Descriptions

Konza Prairie Biological Station and Long-Term Ecological Research (LTER) Site. The Konza Prairie Biological Station (KPBS) is 3,487 hectare tallgrass prairie located in the Flint Hills of northeastern Kansas (39^o 05’ N, 96^o 35’ W). Vegetation is dominated by perennial, warm-season grasses such as *Andropogon gerardii*, *Sorghastrum nutans*, and *Schizachyrium scoparium*. Spring (April) burning treatments (burned at 1, 2, 4, 10, and 20 year intervals) have been maintained on replicate watershed units since 1971. Transects for this study were established in watershed units representing a factorial combination of grazer presence (bison present or absent) and fire frequency (1-year and 4-year average fire return intervals). Each treatment combination was replicated twice for a total of eight watersheds included in the study (1D, SpB, N1A, N1B, 4A, 4B, N4A, N4D). The bison population contained 217 animal units (AU) at the start of 2004, 210 AU at the start of 2005, and 208 AU at the beginning of 2006. Transects for the study were positioned on established grazing lawns (sites regularly utilized by bison and repeatedly grazed). Mean annual precipitation at KPBS is 834 mm/yr and mean January temperature is –3^{o}C with a mean July temperature of 27^{o}C. See www.konza.ksu.edu/konza for further description of the site and its biota.

Above and Belowground Sampling

In each watershed, two 50 m transects were placed near the established LTER plant species composition and ANPP study transects in the upland prairie vegetation growing on shallow, cherty, silty clay loam soil overlying limestone and shale layers (Udic Argiustolls, Florence series). Six random points along each transect were chosen for above ground stem and belowground bud sampling. At each random point, all live stems (defined as greater than 50% green, potentially photosynthetic tissue) within a 25 cm x 25 cm sampling frame were counted, clipped at ground level and sorted as grass or forb. Because sedges are indistinguishable from grasses belowground and constitute a small fraction of graminoid biomass, all graminoids were combined as ‘grass’ both above and belowground. In the grazed watersheds, the grazing intensity was estimated at each sub-sample along a transect before stem harvesting began, with 0 indicating none of the stems had been grazed, 1 indicating up to one-third of stems had been grazed, 2 indicating between one- and two-thirds, and 3 indicating a grazing lawn with almost all stems grazed. The soil within the frame was excavated to a 10 cm depth and all belowground perennating organs (rhizomes, etc.) were collected in a plastic bag and stored in a cooler for transport.

Stem and bud density measurements were taken in March (late dormant season), June (peak growing season), and September (end of growing season) of 2004 and 2005, and March and June of 2006. All March meristem numbers were adjusted to include the buds that had already broken dormancy from the bud bank and initiated new stems before sampling occurred. Due to a laboratory processing error, most of the meristem data from March and June 2005 were not usable. To estimate March 2005 grass meristem density on a single transect, the grass meristem density in September was added to the aboveground grass stem density from June. This method provides reliable estimates because more than 99% of aboveground stems are recruited from the bud bank as opposed to originating from seed (Benson and Hartnett 2006), and because the seasonal pattern of bud development is known (Dalgleish and Hartnett 2006). Meristem data from three transects were available from March 2005 and were used to check the accuracy of the estimates, which were reasonable for grasses, but not for forbs. Therefore, grass meristem estimates are presented from all three years, whereas meristem data for forbs is only presented from 2004 and 2006. Probability of emergence from the bud bank was calculated by dividing number of above ground stems present in June by the number of belowground buds present in March. Because the June stem data were used to estimate the March bud data for 2005, the probability of emergence was only calculated for 2004 and 2006. Long-term ANPP data for the watersheds without grazers were obtained from the Konza Prairie LTER database (http://www.konza.ksu.edu/konza).

Sample Processing

Aboveground samples were dried at 60°C for at least 48 hours and weighed to the nearest 0.01 g. Belowground samples were washed free of soil and examined under a dissecting scope. Belowground buds (rhizome meristems) were counted and scored as either grass or forb based on bud morphology and the morphology of the attached root systems. Only developed meristems that formed a distinct stem tissue bud were counted. Different grass growth forms have different morphology and therefore require different counting techniques: rhizomatous grass buds can be found at the rhizome nodes, sometimes covered with a bud scale, but are quite visible without much dissection; caespitose (bunch or tufted growth form) grass buds can be found at the base of each stem and oftentimes partial dissection of the base of the tiller is required in order to count the buds. Many samples included both growth forms and the appropriate technique was used for each growth form within a sample.

Analysis

The mean of each response variable (stem and bud density of grasses and forbs) was calculated using the 12 sub-samples taken from each watershed at each sampling time. To test for differences in stem densities and March grass buds I used a two-way, repeated measures ANOVA with fire frequency and presence of grazers as fixed factors and year as the repeated measure using SAS 9.1 software (Proc Mixed, SAS 2003). I used an autoregressive covariance structure (ar(1) option in Proc Mixed) for the stem data and an unstructured model for the grass buds because these models had the lowest value of Akaike Information Criterion (AIC) of ten possible covariance structures fit to each data set. To test for differences in March forb meristem and June grass and forb meristem densities (only two years of data available), I used a three-way ANOVA design with fire frequency, presence of grazers, and year as fixed factors (Proc GLM, SAS, 2003). When there were no significant differences in the response variables between years, a reduced model was fit using only fire frequency and presence of grazers as fixed effects. All tests were two-tailed, based on Type III sums of squares and considered significant at α level = 0.05.

Linear regression was used to explore the relationship between grazing intensity and the response variables (Proc Reg, SAS, 2003). These analyses were conducted using transects as the experimental units because an average grazing intensity was measured using the average of six sub-samples at the transect scale, rather than simply the presence or absence of grazers which is applied to the entire watershed. Model fit was evaluated by examining studentized residuals and Cook's distances calculated for each data point. Outliers were identified as points having studentized residuals that did not fall between –2 and +2 and Cook's distances > 1. A single data point met these criteria in the June grass meristems data set and was removed for all of the analyses presented here. To examine the relationship between long-term average ANPP and the response variables, linear regression was again used with the watershed as the experimental unit.

Results

Aboveground stems

The effect of fire frequency and the presence or absence of grazers on average peak grass stem density differed among the three years of the study (Figure 4.2, fire*grazing*year: $F_{2,8} = 10.0$, $P = 0.007$). The three-way interaction indicated that there was no consistent, independent effect of either treatment on peak grass stem densities, and that the interaction between the presence of grazers and fire frequency was dependent upon the year. By contrast, forb stem densities responded to fire frequency and the presence of grazers similarly over the three years of the study. There was a significant interaction between fire frequency and the presence grazers (Figure 4.3, $F_{1,4}$ = 28.3, P = 0.006). Grazing significantly increased the average forb stem density in the annually burned treatments from 134.0 ± 22.7 to 401.3 ± 49.3 (Mean ± 1 SE, Figure 4.3); however, the presence of grazers did not affect forb stem densities in the four-year burn frequency (grazers absent: 227.33 ± 17.88, grazers present: 258.67 ± 28.68). In addition, the four year burn frequency had a forb stem density intermediate to the annually burned, grazers present treatment and the annually burned, grazers absent treatment (Figure 4.3).

Due to the patchy and variable nature of bison grazing, the presence or absence of grazers on an entire watershed may not accurately reflect the amount of grazing pressure that each sampled area actually experienced. A closer assessment of the relationship between grazing intensity and grass stem density revealed consistent patterns: peak grass stem density (June) increased linearly with grazing intensity in the annual burn frequency ($F_{1,10}$ = 5.80, P = 0.04, r^2 = 0.39; Figure 4.4). A similar trend was observed in the four-year burn frequency, though the relationship was only marginally significant ($F_{1,10}$ = 4.32, P = 0.06, r^2 = 0.30; Figure 4.4). While the slopes of both relationships were nearly identical (annual burn: 201.5, four year: 202.9), the values in the four-year frequency tended to be higher as did the intercept value, though the intercept values were not significantly different (mean ± SE: annual burn, 970 ± 160; four-year burn: 1298 ± 144). Forb stem density also increased with grazing intensity in the annually burned treatment ($F_{1,10}$ = 10.72, P = 0.008, r^2 = 0.52, Figure 4.4) but there was no relationship between grazing intensity and forb stem density in the four-year burn frequency ($F_{1, 10}$ = 0.03, P = 0.874).

Belowground buds

There was a significant interaction between fire frequency and grazer effects on peak belowground grass meristem density (fire*grazing: $F_{1,4}$ = 9.72, P = 0.04). Grass meristem density was lower in the presence of grazers than in their absence in the annually burned treatment, while no such trend was evident in the four-year burn frequency (Figure 4.5). A significant interaction between fire frequency and the presence of grazers was evident in the peak forb mersitem density as well (fire*grazing: $F_{1,4}$ = 39.51, P = 0.0002, Figure 4.6). The presence of grazers increased mean peak forb meristem density in the annual burn frequency from 114.7 ± 36.0 to 386.3 ± 47.3 in 2004 (mean ± 1SE). The presence of grazers did not change average peak forb meristem density in 2004, and means were similar to the annually burned and grazed treatment (388.00 ± 213.83 without grazers, 325.00 ± 195.71 with grazers; mean ± 1SE). There was also a significant interaction between grazing and year ($F_{1, 4}$ = 12.02, P = 0.0085); though the patterns of forb meristem density were similar among treatments, the densities decreased significantly from 2004 to 2006. There was no relationship between peak meristem density and grazing intensity (data not shown).

Grazing significantly reduced the reserve grass meristem density in June ($F_{1,8}$ = 11.97, P = 0.009), with no significant main effect of, or interaction with, fire frequency (Figure 4.7). Forb meristem density in June exhibited a similar response to fire frequency and grazing that is shown on Figure 4.3 (fire*grazing in June $F_{1,15}$ = 8.38, P = 0.02).

No significant linear relationship was detected between June meristem density (either grasses or forbs) and March grazing intensity (data not shown).

Effects of year since fire

In the four-year burn frequency, the probability of a grass tiller emerging from the bud bank peaked in the year after a spring fire (the second growing season after fire) in both the treatment with and without grazers (Figure 4.8a). In the treatment with grazers, the probability of emergence from the bud bank gradually declined with year since fire. Similarly, the number of buds produced per tiller was the lowest the year after fire (the second growing season). In the growing season immediately following the fire (year 0 on Figure 4.8), the probability of grass emergence and the number of buds per tiller are both similar to those measured on annually burned watersheds. However, four-year burned watersheds were more variable among years for both responses: the coefficient of variation (CV) for the probability of grass emergence was 0.30 and the CV for the number of buds per tiller was 0.36 compared to the annual burned watersheds which had values of 0.17 and 0.25 respectively. Grazing intensity showed a similar pattern, peaking the second growing season after the fire and declining subsequently (Figure 4.8c). The magnitude of the grazing intensity differed between the two watersheds that had both bison grazing and the four-year fire frequency, but the pattern of change over time was consistent.

Relation to long-term productivity

The average belowground reserve grass bud bank was a very strong predictor of long-term ANPP in prairie protected from grazing (Figure 4.9, $F_{1,2} = 12.81$, $P = 0.006$, $r^2 = 0.99$). Annually burned, ungrazed prairie had both higher meristem densities and higher average ANPP than ungrazed prairie burned every four years. Long-term average ANPP was not significantly, linearly related to peak stem density or to peak belowground meristem density ($P > 0.172$, data not shown).

Discussion

My data indicate that tallgrass prairie plants are responding to key ecological drivers such as fire and grazing with altered rates of belowground bud natality, bud emergence from the bud bank, and both short-term (fire cycle) and long-term changes in bud bank density. Both fire frequency and grazing influenced belowground bud and aboveground stem populations of grasses and forbs in tallgrass prairie. My prediction that grass bud banks would increase with increasing fire frequency while forb bud banks would decrease was supported, but only in the absence of grazers. Grazing had a consistent impact on both belowground bud and aboveground stem populations of tallgrass prairie grasses but, contrary to my hypothesis, grazing increased grass stem populations while decreasing grass bud banks compared to prairie that was protected from grazing. My data indicate that grazing increased the rate of transition from bud to tiller as the decrease in buds from March to June was well matched to the increase in stems over the same time period. By contrast, grazing increased both bud and stem density of forbs in annually burned prairie but grazing had no effect on forb bud or stem density in the four-year burn frequency treatment. Lastly, the size of the reserve grass bud bank available in June is an excellent predictor of long-term ANPP in tallgrass prairie in both the four-year and annually burned prairie supporting my hypothesis that ANPP is controlled by demographic processes, namely the density of bud and stem populations.

Complete exclusion of fire in tallgrass prairie has been shown to significantly decrease the grass bud bank and increase the forb bud bank (Benson et al. 2004). The results of the current study show the same trends in the bud bank after decreasing the fire frequency from one to four years. In addition, prairie that is burned at an intermediate fire frequency has a more temporally variable grass bud bank and temporally variable probability of emergence from the bud bank than annually burned prairie. In the growing season following a fire, the probability of bud emergence and the number of buds per tiller were similar to annually burned prairie. However, in the second year following the fire, bud emergence increased and the number of buds per tiller decreased. The increased temporal heterogeneity in grass bud and stem populations with the periodic stimulation of grass emergence from the bud bank may contribute to the increased heterogeneity observed on four-year, compared to annually, burned prairie (Collins and Steinauer 1998). Grasses may have increased abundance following fire due to their enhanced emergence rates from the bud bank, but then lose any competitive benefits of that fire event without continued burning. There may also be differences in tiller survival with the enhanced emergence rates due to density dependence. The size of the reserve bud bank also varied with the fire cycle in periodically burned prairie, reaching its lowest point the second growing season after fire. This indicates that bud bank size, and hence, degree of meristem limitation, varies both over the long-term and within the fire cycle.

While annual burning increased bud banks, persistent grazing over the long-term (> 10 years of grazing pressure) resulted in depleted bud banks. Several studies have documented decreases in individual species' biomass of belowground storage or perennating organs in response to grazing, indicating that aboveground compensatory re-growth comes at a cost to belowground growth of roots, rhizomes, and buds (Biswell and Weaver 1933, Weaver and Hougen 1939, Albertson et al. 1953, Archer and Detling 1984, Hartnett 1989). Depletion of bud banks has several potential consequences such as decreased ability to respond to resource pulses, decreased rates of stem population recovery after disturbance or stress, decreased productivity of the grassland, and decreased potential for compensatory re-growth following herbivory.

While my study suggests that an increase in tiller density is an important mechanism of compensatory re-growth in tallgrass prairie, previous studies examining the effects of grazing on tiller density have found differing results. Hartnett (1989) documented increases in *A. gerardii* tillering in response to simulated grazing under greenhouse conditions at low initial tiller density; however, *Panicum virgatum* consistently exhibited decreased tillering in response to simulated herbivory at three initial densities (Hartnett 1989). Under heavy cattle grazing in the field, Olson and Richards (1988) found reduced tillering in *Agropyron desetorum*. In contrast to earlier greenhouse studies, Vinton and Hartnett (1992) documented an increase in tiller density under field conditions in response to grazing pressure experienced in the previous year for both *A. gerardii* and *P. virgatum*. The current study extends the previous species-specific results by demonstrating that the grass guild as a whole experiences an overall increase in tillering in response to increasing grazing intensity.

The current study effectively connects observed increases in aboveground tillering due to ungulate grazing to changes in belowground bud demography that are consistent with previously observed decreases in belowground allocation. One explanation for the long-term decline in bud banks in the presence of grazers may be an increased risk of tiller mortality. While grazing stimulated an increase in tillering for *A. gerardii* and *P. virgatum* in the year after grazing, the tillers that emerged had a higher probability of mortality by the end of the growing season than tillers that did not experience grazing (Vinton and Hartnett 1992). Similarly, Archer and Detling (1984) found increased mortality in *A. gerardii* and *Carex filifolia* tillers that experienced both biomass removal and competition, conditions that likely mirror field situations. Because tiller vegetative fecundity (number of new rhizome buds produced per tiller) does not peak until the following spring (Dalgleish and Hartnett 2006), tillers that die the previous fall are unable to contribute to replenishing the bud bank. Even if the grazed tillers survive the growing season through to the next spring, a reduction in biomass accumulation will reduce bud production (Chapter 3). Both the death of tillers before they produce buds as well as lowered bud production due to decreased growth rates and biomass accumulation would explain the observed decreases in the bud bank with grazing over time.

The resulting changes in bud bank demography in response to key ecological drivers may help explain previously documented community composition shifts in grazed and periodically burned prairie. Previous research on Konza Prairie has demonstrated that species richness increases as fire frequency decreases (Collins and Steinauer 1998). Tallgrass prairie that is burned every year and protected from grazing is strongly dominated by C_4 perennial grasses. In the four-year burn frequency, C_4 perennials decrease in abundance while C_3 grasses and forbs increase. Belowground bud banks of grasses and forbs respond to fire frequency as I predicted based upon established patterns of species composition, with grass bud banks increasing in annually burned prairie and forb bud banks increasing in infrequently burned prairie. Species-specific studies have demonstrated that decreased fire frequency stimulated bud production and increased ramet densities in perennial forbs such as *Solidago canadensis* and *Ratibida columnifera* (Hartnett 1991, Elder 2001). Grazing increases plant species richness in tallgrass prairie, largely driven by an increase in forb species (Hartnett et al. 1996). The pattern of increased forbs in grazed prairie is clearly observed in the belowground bud demography.

Hartnett et al. (1996) state that the increase in species richness and spatial heterogeneity observed in bison-grazed prairie is likely due primarily to the increase in establishment sites created by bison through wallowing and other non-grazing activities. By contrast, increased evenness and diversity in grazed prairie is due to competitive release experienced by the sub-dominant forbs in response to the heavy preferential grazing of C_4 grasses (Hartnett et al. 1996, Damhoureyeh and Hartnett 1997). Increased recruitment from the forb bud bank likely explains much of the observed increase in forb cover. For example, grazing increased recruitment from belowground bud banks in some forb species examined by Damhoureyeh and Hartnett (1997), even though these species were not directly consumed by bison. In a ten-year study comparing the effects of bison and cattle grazing on the tallgrass prairie, Towne et al. (2005) found that increases in just two perennial forb species, *Symphyotrichum ericoides* and *Solidago missourienses*, were the primary cause for the observed increase in total forb cover. Both of these perennial forbs reproduce vegetatively though belowground buds and much of their spread is likely due to recruitment from the bud bank. In addition, Towne et al. (2005) documented an increase in annual forb species richness and cover in bison-grazed prairie (though the total cover remained below 10%), and some of the increase in the forb stem population in bison grazed prairie observed in this study was due to increases in annual forb stem density. The concomitant increases in the belowground bud population documented in this current study suggest, however, that the annual forbs had a small contribution to the aboveground stem population.

It has been hypothesized that maintaining a dormant bud bank may be an adaptive response to herbivory (Tuomi et al. 1994, Nilsson et al. 1996). Tuomi et al.’s (1994) mathematical model predicted that the maintenance of a bud bank may serve as a primary mechanism for compensatory growth after tissue loss due to herbivory. Recruitment from a bud bank in response to grazing constitutes a demographic response to tissue loss, as herbivory stimulates an increase in the number of plant parts (ramets), rather than simply re-growth of existing parts. Though Tuomi et al. (1994) modeled an annual plant, my results support their conclusions being extended to perennial grasslands, as increased tiller densities were observed in response to grazing pressure. Support for a strong demographic response to ecological drivers such as grazing, fire or climatic variability, has important implications for my understanding of ANPP variability in tallgrass prairie. For example, variability (either within or between years) in ANPP can be due to either variability in stem size (primarily an individual ramet growth response) or variability in stem number (primarily a demographic response) (Hartnett and Fay 1998). My results support the hypothesis that variability in ANPP is principally driven by modular demography. In addition, my results link the demographic response to grazing directly to the bud bank. It is the bud bank that serves as the source for recruitment for increased growth and, therefore, it is likely that the community and ecosystem consequences of grazing in grassland are mediated through the effects on the bud bank.

Population processes such as the demography of buds and tillers have the capacity to explain temporal and spatial variability in ANPP. For example, long-term studies at KPBS have shown higher temporal variability in ANPP in the four-year burn frequency treatments with maximum productivity after a fire that follows several years without fire (Knapp et al. 1998). Such pulses of productivity in response to fire after several years of fire exclusion can be explained by bud bank demography. My data show a gradual increase in bud bank densities over a two to three year period that allow a larger response in the season immediately following fire. Annually burned sites do not experience a two to three year period of reserve bud accumulation, and, therefore, I do not observe similar temporal variability in ANPP with high pulses in productivity. However, long-term averages of ANPP on annual and four-year burned sites show that four-year burned sites have lower productivity overall, creating spatial variability in ANPP at KPBS in response to fire frequency. I hypothesized that altered bud demography should explain the decreases in productivity observed between the annual and the four-year burn frequency. My results show that reserve bud density, or the size of the bud bank, is an exceptionally good predictor of long-term ANPP, accounting for 99% of the variation in productivity among sites. A similar relationship between bud bank size and productivity has been observed at large scales incorporating grasslands across the Great Plains of the central United States (Dalgleish and Hartnett 2006).

My research, both at local and regional scales, strongly supports the conclusion that ANPP may be constrained by the size of the bud bank and that the demography of plant parts is important for understanding long term patterns of productivity in grasslands as well as predicting grassland responses to global environmental change. Consequently, management activities that deplete bud banks, such as decreased fire frequencies and persistent grazing in tallgrass prairie can potentially result in decreased ability of the grassland to capitalize on new resource pulses. Decreased ability to capitalize on available resources may result in increased invasibility if the propagule pressure of non-natives is sufficient to capitalize on new resource pulses. Preliminary results from my current study at KPBS indicate that a minimum threshold bud density may be an important factor that allows residents to rapidly pre-empt resources and resist invasion by exotic species (Hartnett and Dalgleish, in prep.) Lastly, decreased bud populations could lead to decreased productivity under increasingly variable precipitation regimes. Both annual burning and grazing are common management practices in the Flint Hills tallgrass prairie region where the study was conducted. While annual burning increases bud bank densities, grazing decreases bud banks. In addition, my results are consistent with previous research that bison preferentially graze recently burned areas (Vinton et al. 1993), as grazing intensities were higher the year after fire. Fire frequency and grazing may interact to create both spatial and temporal heterogeneity in bud bank densities. The effects of management activities will, of course, depend upon site history, frequency of fire, and grazing intensity.

The effects of fire frequency and grazing on the patterns of plant community composition and productivity in tallgrass prairie have been previously described. The current study provides a mechanistic explanation for previously described patterns, demonstrating a strong link between ecosystem processes (*e .g.*, productivity patterns) and the demography of plants and plant parts and between belowground and aboveground dynamics. Population processes, namely the demography of buds and tillers, have the capacity to explain plant community composition shifts and temporal and spatial variability in ANPP in response to ecological drivers such as fire and grazing, and represent a crucial link between organismal, community, and ecosystem level processes. In addition, meristem limitation due to management practices such as reduced fire frequency or increased grazing intensity may constrain tallgrass prairie responses to inter-annual changes in resource availability. An important consequence is that prairie with a large bud bank may be the most responsive to future climatic change or other global change phenomena such as nutrient enrichment and may be most resistant to phenomena such as exotic species invasions.

Acknowledgements

I thank Jon Dalgleish, Abby Kula, Janel Sinn, Jayne Jonas, Jennifer Hill, Zoe Gill, Melinda Williamson, Rider Frye, Crystal Sinn, Julie King, and Jim Birmingham for field and sample processing assistance. This work was supported by the Konza Prairie LTER, the Kansas State University Division of Biology, and NSF grant DEB-0234159.

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Figures and tables

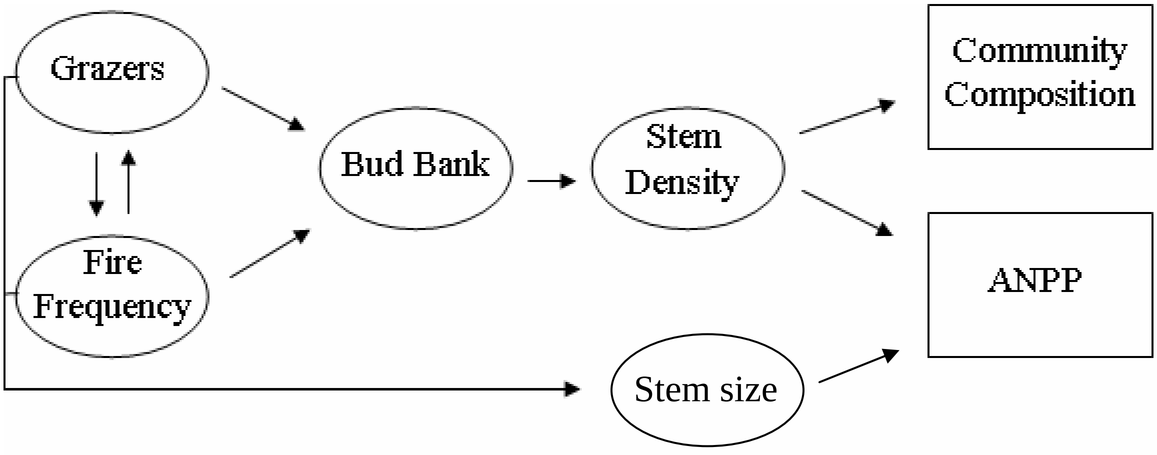

Figure 4.1 Conceptual model illustrating a mechanistic hypothesis of how grazing and fire frequency influence community composition and productivity.

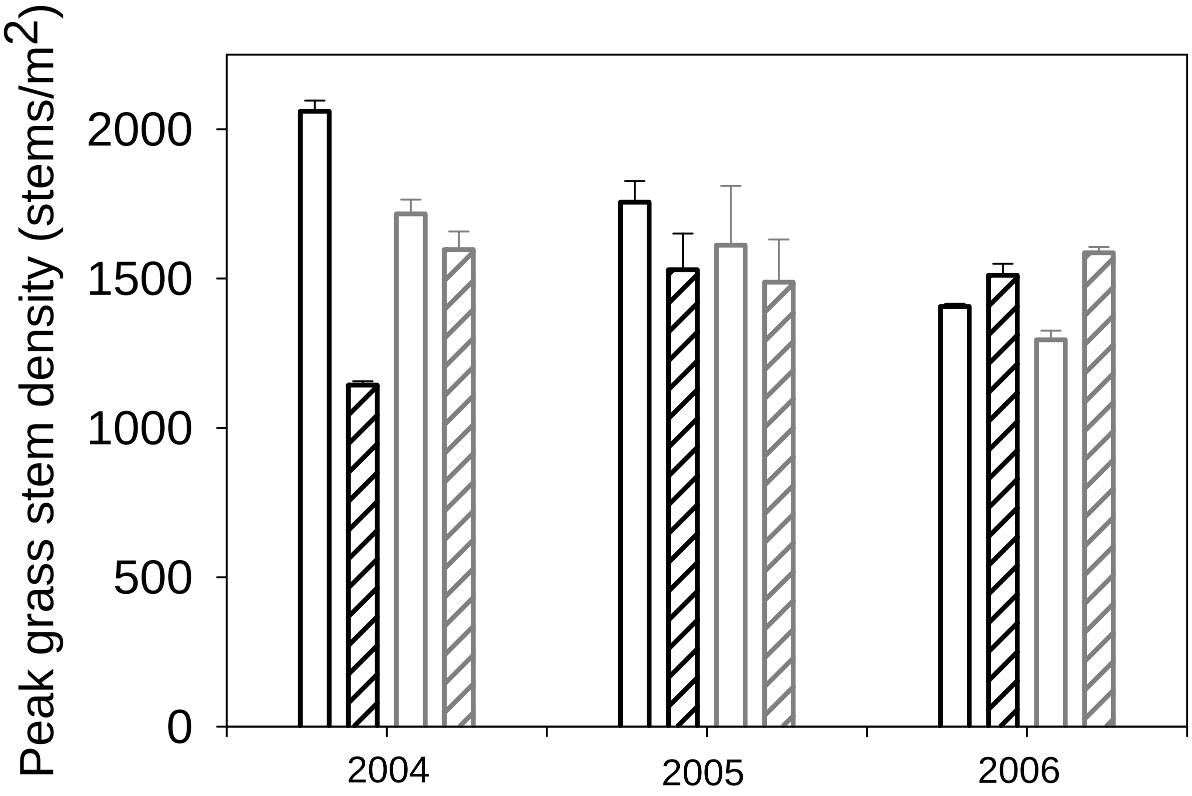

Figure 4.2 The effects of fire frequency and grazing on peak (June) grass stem density. The effect was not consistent over the three years of the study (fire*grazing*year *P* = 0.0007). Grazing tended to reduce peak grass stem density in both fire frequency treatments in 2004 and 2005; however,this trend was reversed in 2006. Bars represent means with 1 SE.

■ Annual burn ▒ 4-year burn □ Grazers absent ▨ Grazers present

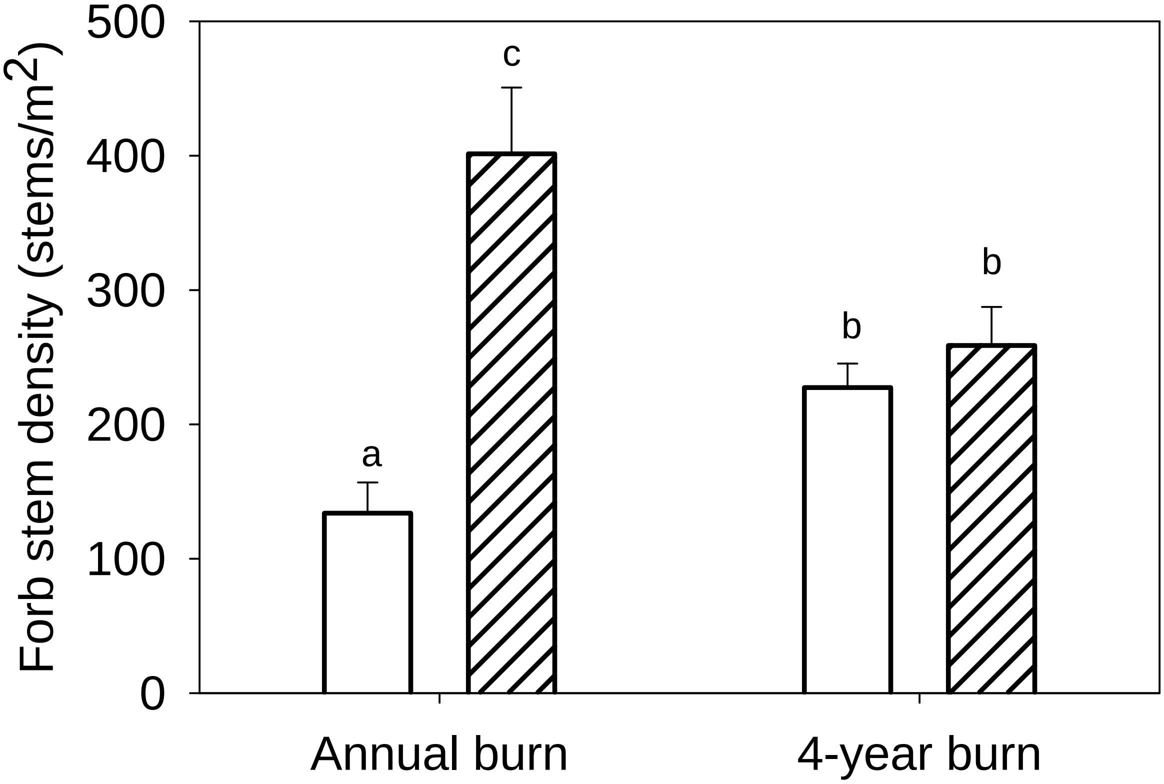

Figure 4.3 The effect of fire frequency and grazing on peak (June) forb stem density. The effect was consistent among years (fire*grazing P = 0.0005). Bars represent means with SE; letters represent significant differences at alpha = 0.05. Grazers absent ☐ Grazers present ▨

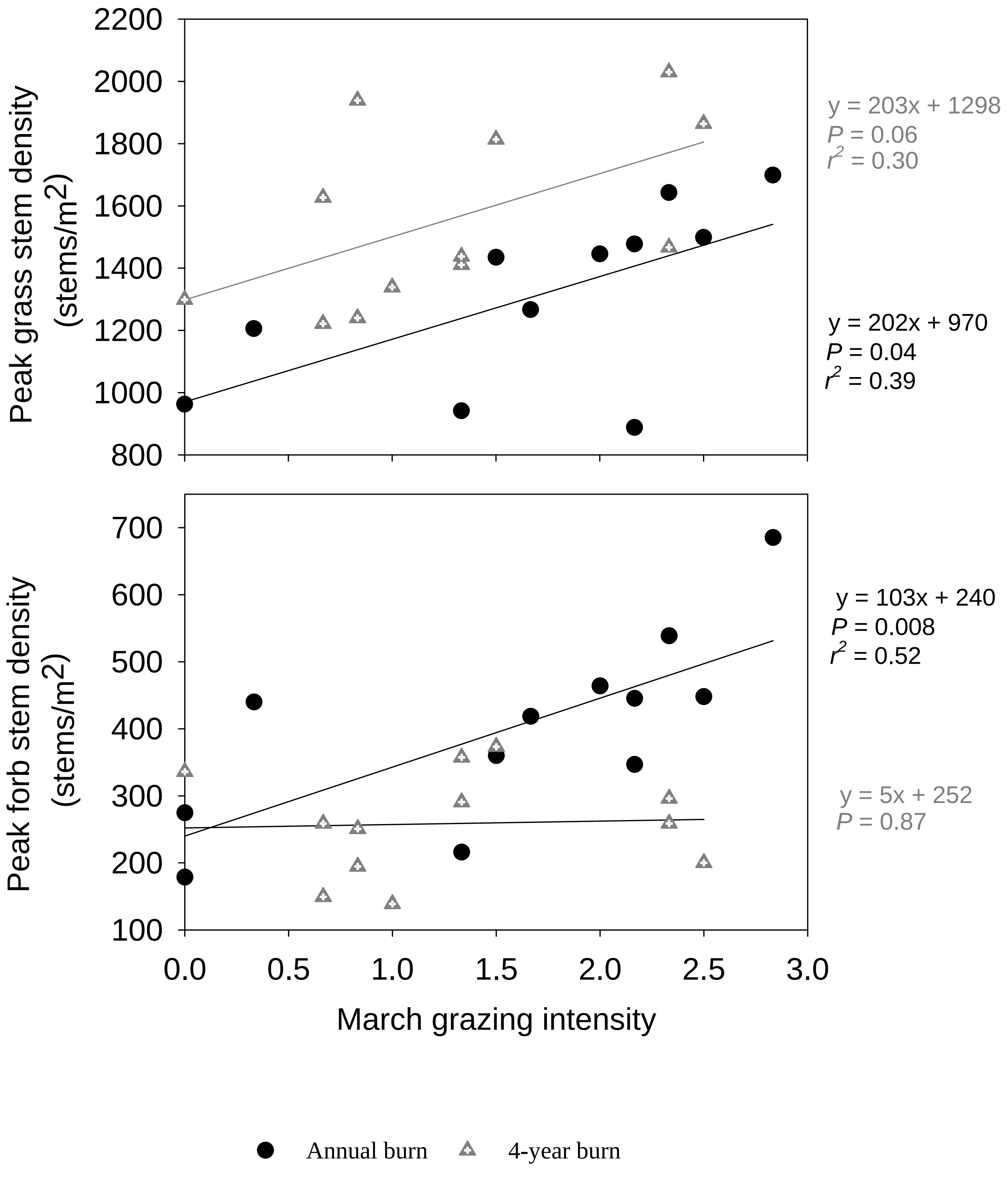

Figure 4.4 Relationship between grazing intensity and stem density.

Points represent averages on a single transect.

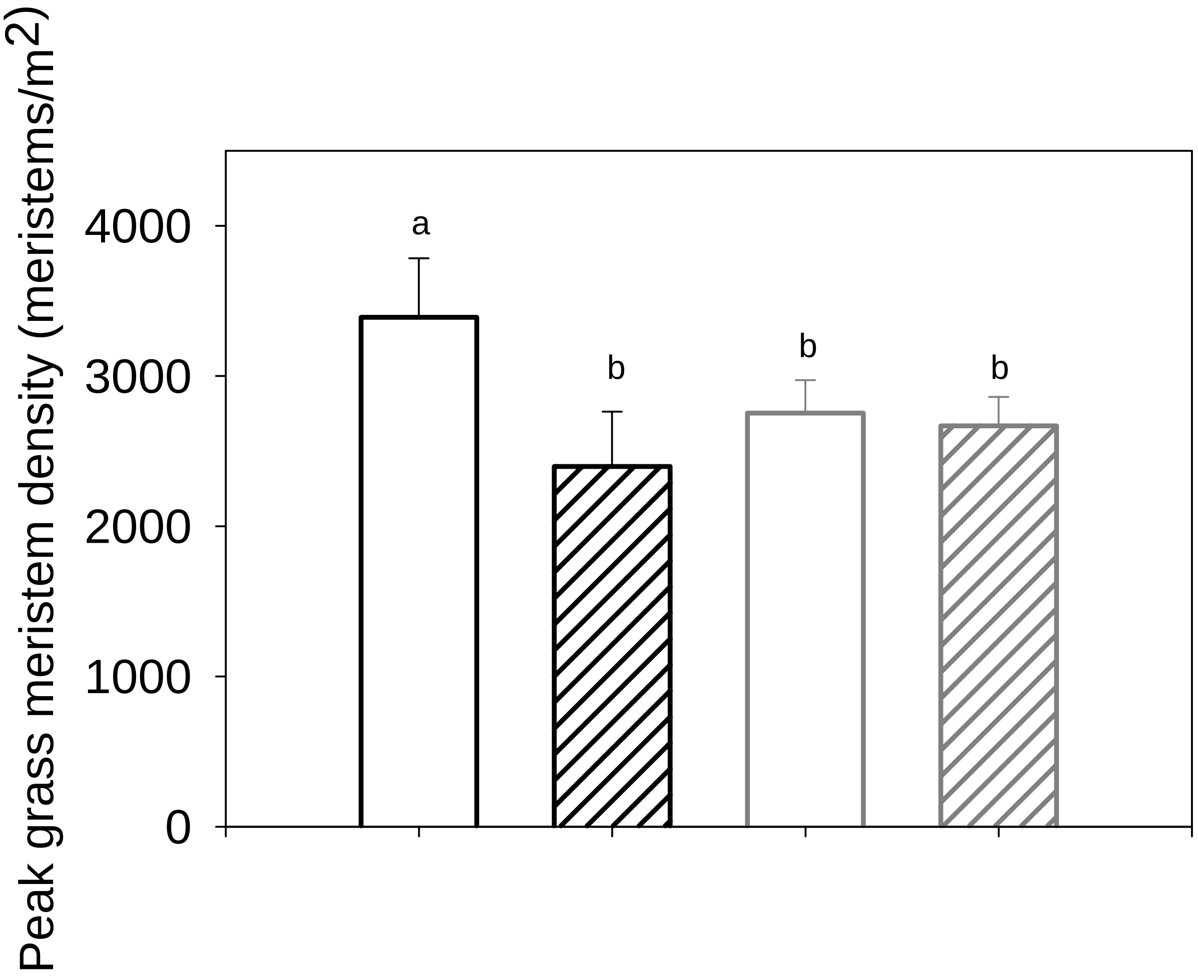

Figure 4.5. The effects of burning and grazing on peak meristem density.

Bars represent means with 1 SE; letters represent significant differences at alpha < 0.05.

■ Annual burn ▒ 4-year burn □ Grazers absent ▨ Grazers present

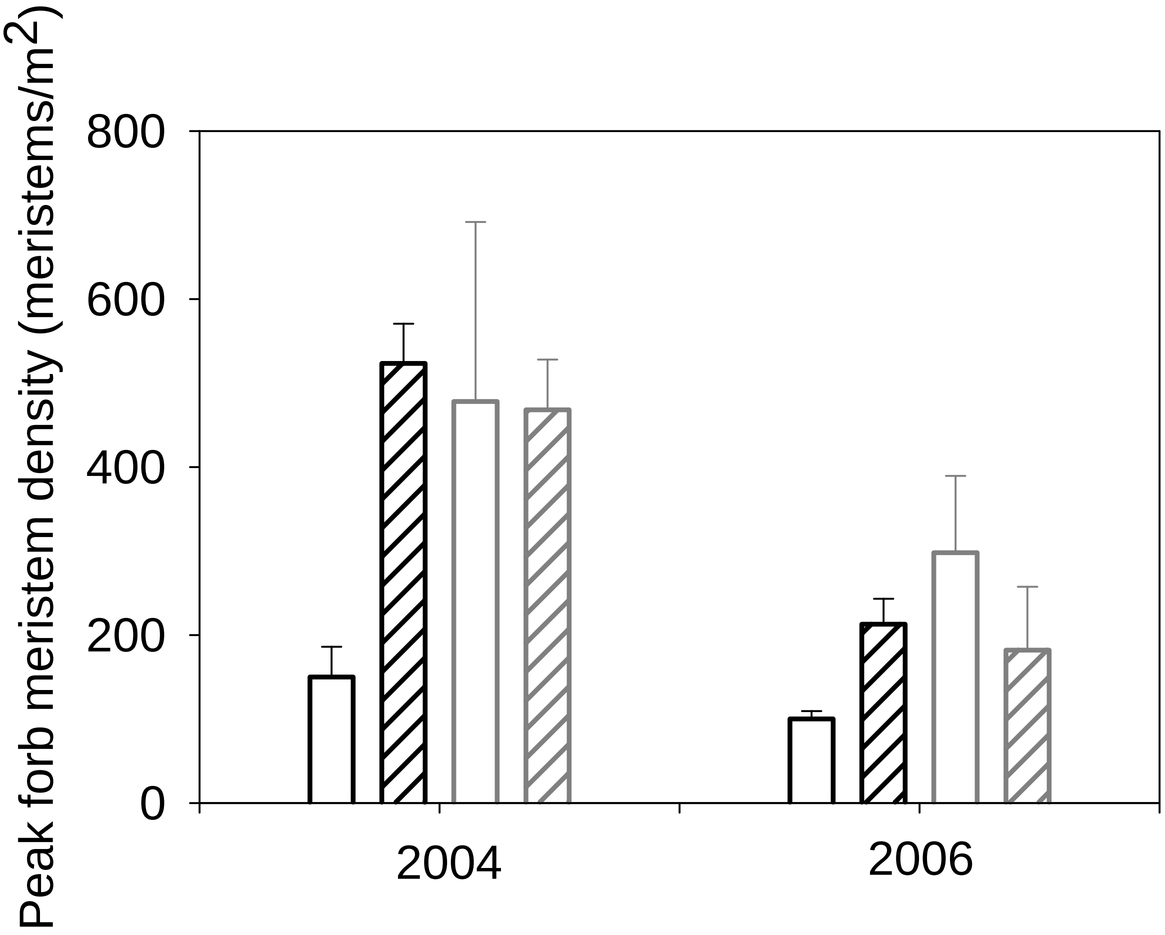

Figure 4.6. The effects of fire and grazing on forb meristem densities.

The patterns belowground were similar to the stem patterns aboveground (fire*grazing *P* = 0.0002). Bars represent means with 1 SE.

■ Annual burn ▒ 4-year burn □ Grazers absent ▨ Grazers present

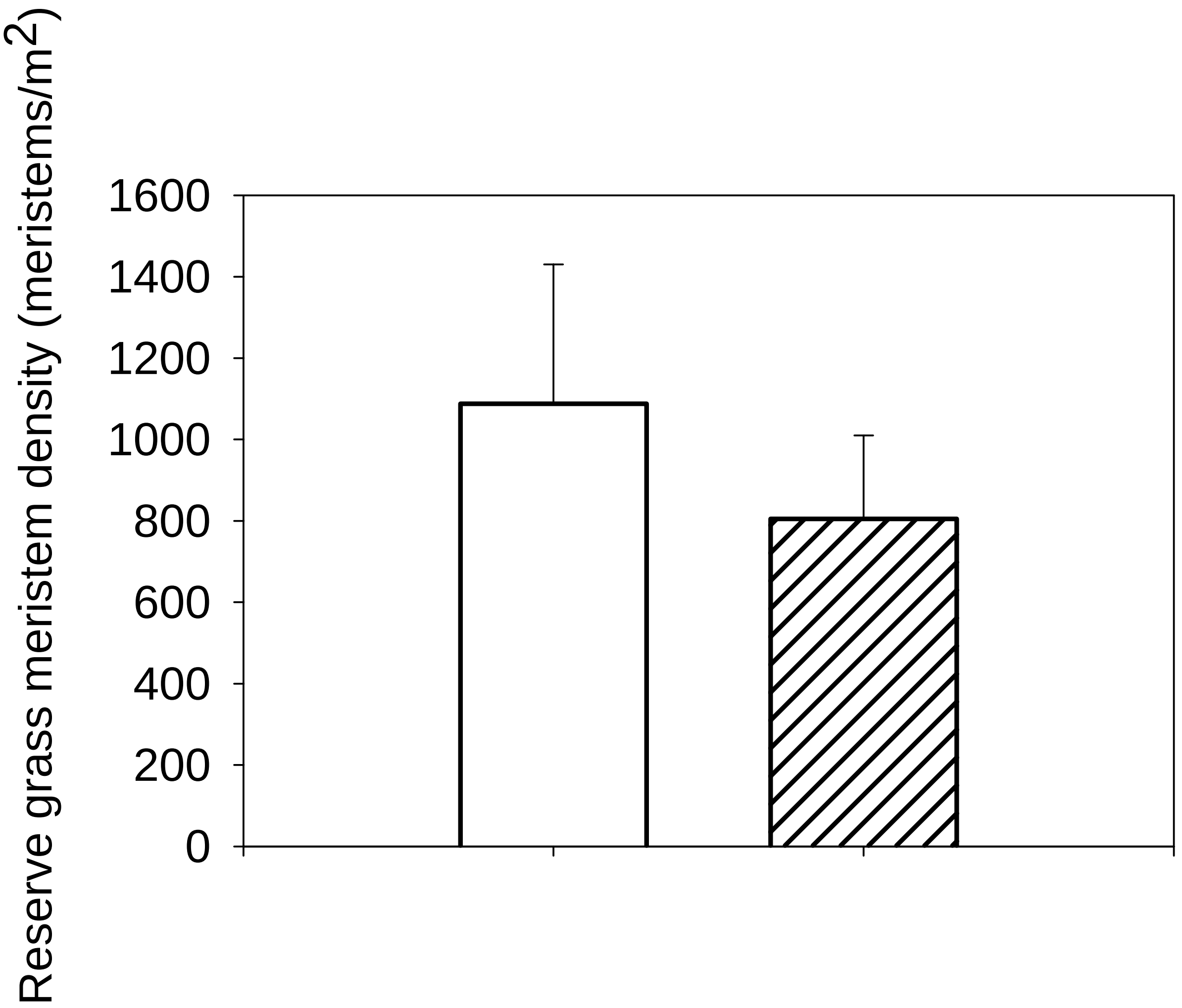

Figure 4.7 The effects of grazing on reserve meristem densities.

Grazing significantly reduced the reserve grass meristem densities in both fire treatments. (*P* = 0.009). Bars are means with 1 SE. ☐ Grazers absent ▨ Grazers present

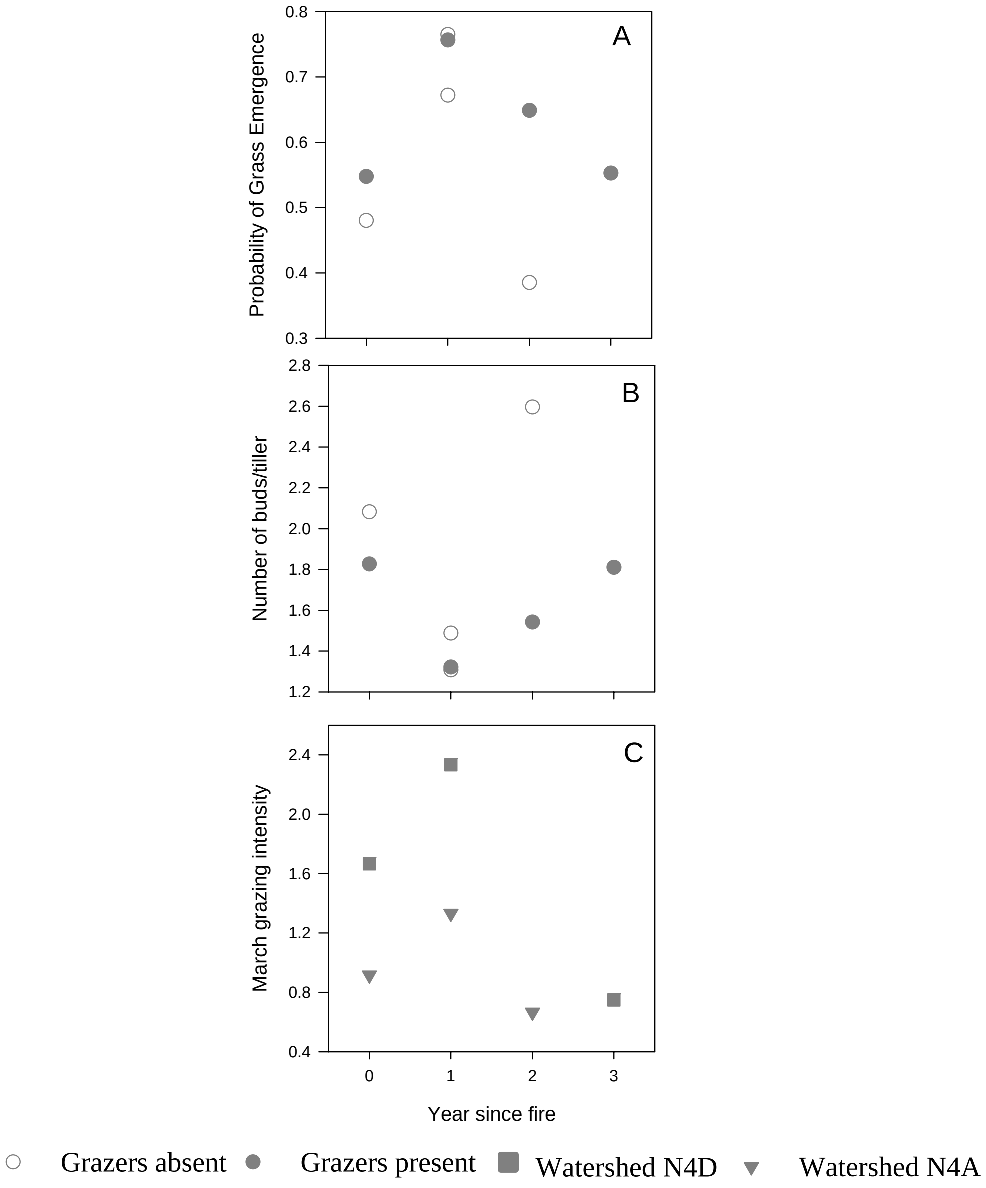

Figure 4.8 The effects of year since fire on the probability of grass emergence from the bud bank (A), number of buds/tiller (B) and on grazing intensity (C).

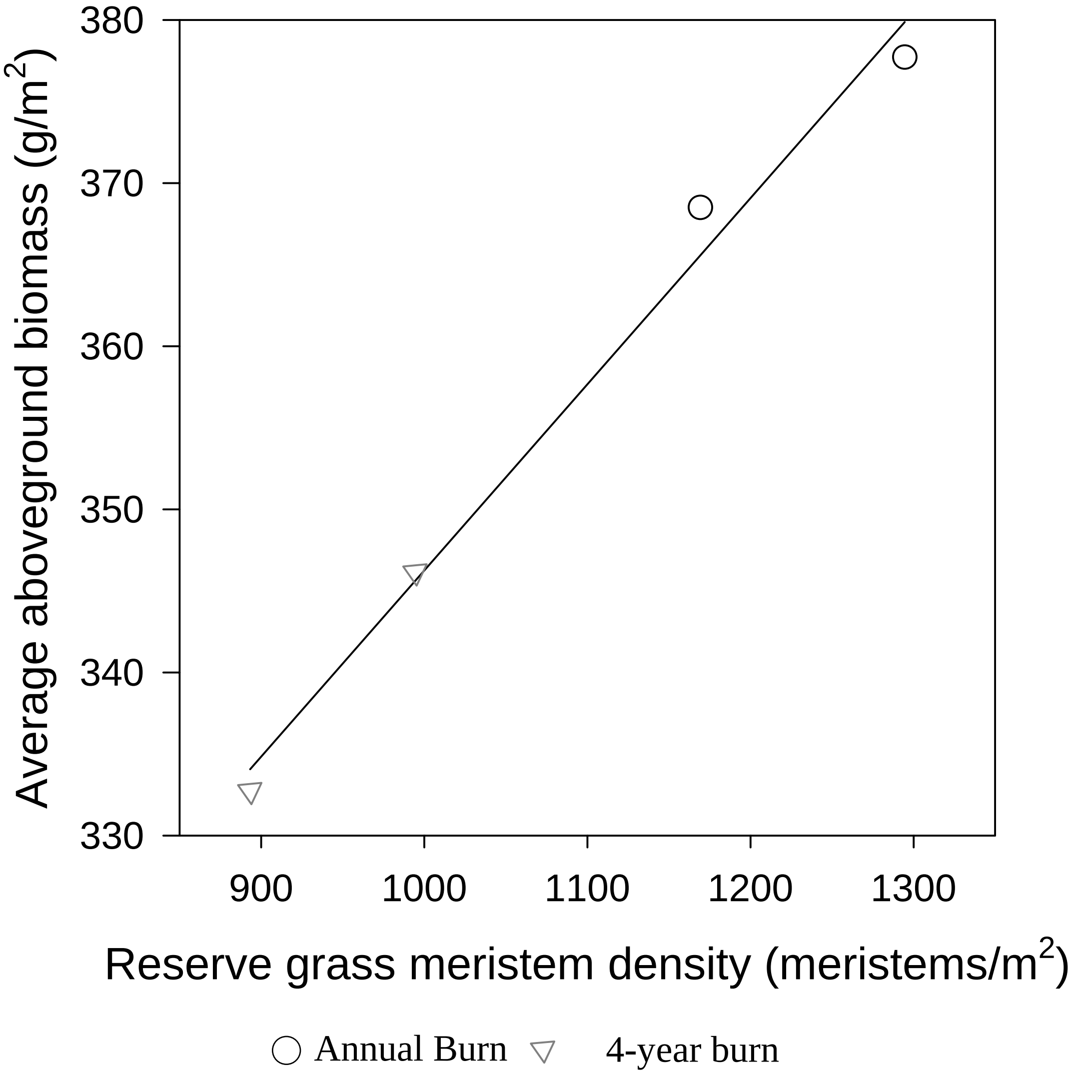

Figure 4.9 June bud banks are a very good predictor of long-term aboveground net primary productivity on annual burn and 4-year fire frequency watersheds without grazers.

Points represent averages in the uplands for an entire watershed.

Chapter 5 — Conclusions

The belowground bud bank is the primary source of recruitment for new grass and forb stems in tallgrass prairie. Population processes such as the demography of buds and tillers have the capacity to explain temporal and spatial variability in ANPP and represent a crucial link between organismal and ecosystem level processes. Meristem limitation along the regional gradient studied here may constrain responses to inter-annual changes in resource availability. An important consequence is that biomes with high bud bank densities may be the most responsive to future climatic change or other global change phenomena such as nutrient enrichment, and they may be most resistant to phenomena such as exotic species invasions. If meristem limitation is an important constraint on potential ANPP responses to environmental variability, then bud bank populations must be considered in the development of predictive models for grassland and savanna ecosystem dynamics, and their responses to environmental change. The clearer understanding of the regional patterns and dynamics of these belowground populations of plant parts presented in this study is a vital step to obtaining a better mechanistic and predictive understanding of the dynamics of grasslands and savannas and their projected responses to environmental change phenomena.

My study of plant responses to nitrogen addition strongly supports that demographic mechanisms of the bud bank are important for driving grass responses to resource availability. Understanding bud bank dynamics has important implications far beyond the individual plant. The maintenance of a bud bank influences the dynamics of the entire population, plays a role in plant species coexistence, contributes to the invasibility of a community, and influences ecosystem productivity. The enhanced knowledge of the bud bank that my study provides will lead to a better mechanistic and predictive understanding of grassland dynamics.

The effects of fire frequency and grazing on the patterns of plant community composition and productivity in tallgrass prairie have been previously described. My research provides a mechanistic explanation for previously described patterns, demonstrating a strong link between ecosystem processes (*e .g.*, productivity patterns) and the demography of plants and plant parts and between belowground and aboveground dynamics. Population processes, namely the demography of buds and tillers, have the capacity to explain plant community composition shifts and temporal and spatial variability in ANPP in response to ecological drivers such as fire and grazing, and represent a crucial link between organismal, community, and ecosystem level processes. In addition, meristem limitation due to management practices such as reduced fire frequency or increased grazing intensity may constrain tallgrass prairie responses to inter-annual changes in resource availability. An important consequence is that prairie with a large bud bank may be the most responsive to future climatic change or other global change phenomena such as nutrient enrichment and may be most resistant to phenomena such as exotic species invasions.