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Inter-specific variation in bud banks and flowering effort among semi-arid African savanna grasses

H.J. Dalgleish [a,*], J.P. Ott [a], M.P. Setshogo [b], D.C. Hartnett [a]

[a] Division of Biology, Kansas State University, United States
[b] Department of Biological Sciences, University of Botswana, Botswana

Abstract

Population viability and productivity of grasses in southern African savannas are dependent upon both successful seed production and tiller recruitment from the belowground bud bank. Relative recruitment rates from buds versus seeds influence population dynamics, genetic diversity, and patterns of vegetation productivity. We assessed patterns in bud bank size and flowering effort in fourteen semi-arid savanna grass species in the Kalahari region of Botswana. There was high inter-specific variability and between-year variability in flowering effort (percentage of tillers flowering). Bud production (number of buds per tiller) exhibited high inter-specific variability, but was more consistent between-years than flowering effort. Relative allocation to flowering versus bud production varied with life history, with longer-lived perennial grasses showing higher bud production and lower flowering effort relative to shorter-lived grasses. Several species showed higher bud production and lower flowering effort in a wet year compared to a dry year, and grass species that are regularly grazed maintained significantly larger bud banks than non-grazed species. These differential demographic responses among co-occurring species suggest that environmental change in semi-arid savannas may alter the composition, relative abundances and diversity of grasses, and that the maintenance of a belowground bud bank is an important factor influencing their resiliency, their capacity to recover from grazing and/or drought, and their persistence and sustainability under changing environmental conditions. Meristem-limitation in species that maintain few viable buds may constrain their population viability under changing conditions in semi-arid savannas.
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1. Introduction

In the semi-arid savannas of southern Africa, perennial grasses are the co-dominant plant growth form with trees and shrubs and are ecologically and economically important as the key food resource for a diverse guild of grazers including wildlife and livestock. However, complex interactions among changing land use, land management, and climate are driving degradation processes and reducing perennial grass cover and productivity in the region. During the past several decades, increased grazing pressure and drought have caused declines in the cover of perennial grass species, along with increases in cover of annual grasses and other species of low economic and ecological value (Moleele and Mainah, 2003; Rutherford et al., 2012; Skarpe, 1986; Van Vegten, 1981).

The sustainability and productivity of perennial grasses relies not only on successful recruitment from seed, but also on vegetative reproduction or tillering from a population of meristems (the bud bank sensu Harper, 1977). Production of seed is important for new genet recruitment, both short- and long-distance dispersal, and for conserving genetic variability, thus maintaining the capacity of grass populations to adapt to environmental change (Fenner, 1985). By contrast, the production of vegetative buds associated with rhizomes or other perennating organs is important in local plant population persistence and integrated responses to

* Corresponding author at: Department of Biology, The College of William and Mary, United States.
E-mail address: hjdalgleish@wm.edu (H.J. Dalgleish).

environmental alterations such as herbivory (Briske and Derner, 1998; Fenner, 1985). Together, the longevity of and recruitment from seed and bud determine spatial and temporal patterns of vegetation productivity (e.g. Guardia et al., 2000). In many mesic grasslands, aboveground recruitment is driven principally by patterns of vegetative reproduction and the demography of the bud bank (Benson and Hartnett, 2006; Benson et al., 2004) and successful establishment of new plants (genets) from seed is rare and episodic (Benson and Hartnett, 2006; Hartnett and Fay, 1998; Pyke 1990; Thompson and Grime 1979). However, in semi-arid or arid grasslands and savannas, or those subject to intense soil disturbance, recruitment from seed plays a more important role (Rogers and Hartnett, 2001; Veenendaal et al., 1996a). Therefore, the patterns and relative allocation to the production of seeds and vegetative propagules are likely key determinants of the dynamics, genetic structure, and metapopulation processes in semi-arid savanna grass populations, and their resilience to factors such as drought, defoliation, and fire.

In general, population dynamics of African semi-arid perennial savanna grasses are primarily affected by rainfall variability (O'Connor, 1993, 1994). Depending on the onset of the rainy season, seedling recruitment may occur in waves or as a solitary event but will only occur following a sizable rainfall event (Veenendaal et al., 1996a). Seed production, as well as its phenology, is influenced by rainfall pattern and decreases with intra-seasonal drought (O'Connor and Pickett, 1992; Veenendaal et al., 1996b). Although fire can directly increase the mortality rate of perennial grasses, fire can indirectly reduce mortality caused by self-shading and neighbor abundance (Zimmermann et al., 2010).

Differences in population dynamics among species are influenced by their life histories and their interaction with grazing and rainfall regimes. For example, under heavy grazing and variable rainfall, high seed producers that are palatable may be more likely to decline locally than unpalatable species due to reduced flowering and seed bank inputs (O'Connor, 1994; O'Connor and Pickett, 1992). However, interspecific differences in the bud bank and how it relates to seed production have not been extensively examined in African semi-arid savanna grasses. Such knowledge would enhance our understanding of the demographic drivers of savanna vegetation dynamics, which is essential to developing a mechanistic and predictive understanding of savanna responses to environmental change, including regional climate change and changes in key drivers under human control (e.g. grazing and fire regimes).

Based on an initial study of three species, African semi-arid perennial grasses showed similar but low bud production and high flowering effort compared to North American tall-grass prairie species (Hartnett et al., 2006). The objective of this study was to examine bud bank size and the relative importance of flowering versus vegetative buds in fourteen grass species in semi-arid savanna in the Kalahari region in Botswana. We addressed three questions:

1. How does bud bank size (estimated as mean number of buds per established tiller) vary among co-occurring grass species and between years in semi-arid savanna?

2. Are the number of buds per tiller and proportion of tillers flowering negatively related within species or among species, indicating trade-offs between investment in buds vs. flowering and seed production?
3. Are there emergent patterns among different groups of grass species (e.g. short-lived versus long-lived perennials, palatable vs. non-palatable species, drought-tolerant versus non-tolerant species) in their bud bank size or their allocation to vegetative bud versus flowering effort?

2. Material and methods

2.1. Field site descriptions

In 2007, grass populations were sampled at two sites within the Kalahari sandveld region of Botswana: the Khama Rhino Sanctuary (KRS) and the Khutse Game Reserve (KGR). The KRS is a 4300 ha reserve in the Central District of Botswana approximately 25 km N of Serowe (22°13′15″ S, 26°41′44″ E). Prominent features of KRS include the wildlife-rich Serwe Pan (a large grass-covered depression with several natural water holes), resident populations of white and black rhinoceros and other herbivores, and diverse plant communities including tree and shrub savanna and open grasslands on the pans. The trees are predominantly *Terminalia sericea*, *Burkea africana*, *Peltophorum africanum*, *Croton gratissimus*, *Philoneptera nelsii*, *Combretum zeyheri*, *Combretum apiculatum*, *Ziziphus mucronata* and various *Acacia* species such as *Acacia erioloba*, *Acacia fleckii*, and *Acacia fleckii luederitzii*. The shrub savanna between the taller trees is mainly composed of *Dichrostachys cinerea*, *Grewia flava*, *Grewia flavescens*, *Acacia mellifera*, *Bauhania macrantha* and *Ximenia caffra*. The grass cover includes *Aristida meridionalis*, *Aristida congesta*, *Eragrostis pallens*, *Eragrostis superba*, *Pogonarthria squarrosa*, *Heteropogon contortus*, *Digitaria eriantha* and *Cymbopogon excavatus*.

The KGR is a 2500 km^2 reserve in the Kweneng District approximately 170 km NW of Molepolole (23°26′11″ S, 24°40′28″ E). The KGR adjoins the southern border of the larger Central Kalahari Game Reserve. The vegetation of KGR is predominantly shrub-savanna, dominated by *T. sericea*, *P. nelsii* and *A. erioloba* (Bekker and De Wit, 1991). In addition to a diverse fauna of large herbivores, the KGR supports populations of large predators including lion, cheetah, brown hyena and wild dog. The Kalahari sandveld region is characterized by deep, sandy soils, normally referred to as arenosols (Moganane et al., 2000). The topography is characterized by low dunes, wide plains, depressions and pans. There is both high local spatial variability and a strong seasonality to the distribution of rainfall in the region. The summer–wet season typically occurs from October to April, with January being the month of highest precipitation. The onset of the rains varies among years, occurring as early as September or as late as November. The dry season typically occurs from May through September, with the lowest rainfall in June and July. Over longer time scales, rainfall in Botswana shows a cyclical pattern, with clustering of wet and dry years (Tyson, 1978).

We chose the two sites because they had similar soil characteristics and grazing pressure, but differing mean annual

precipitation (KGR~340 mm; KRS~425 mm). The prominent land use of semi-arid savanna areas in Botswana is communal livestock grazing, and although both sites are currently managed as wildlife reserves, they have a previous history of several decades of intensive cattle grazing (Veenendaal and Molefi, 1987). Further detailed description of the climate, soil, and vegetation of the study region can be found in Veenendaal (1991) and Vossen (1988). We found no statistical differences between sites in either bud or flower production within or among species. Thus, all sites were pooled for the analyses presented here.

2.2. Sampling procedure and analysis

We sampled 14 species between 2007 and 2008 from lightly grazed areas (Table 1). Six of the species were sampled in both years and the other 8 in only 2007 or 2008. All 14 grasses exhibit a caespitose growth form (i.e., tufted or bunch growth form) which produce buds that, when released from dormancy, grow upward within the protective subtending leaf sheath to produce a dense clump of tillers (Briske, 1991). One of the species is classified as annual, three as short-lived perennials (lifespan=2–5 years), two can be either annuals or short-lived perennials, and the remaining eight are long-lived perennials, surviving 5 or more years (Van Oudtshoorn, 1999). We classified five species as 'palatable' because they are considered of either high or average grazing value (Van Oudtshoorn, 1999).

Grass sampling in each year occurred in March or May during the dormant (dry) season when all of the grasses had reached their peak biomass and had completed flowering and seed production. Thus, census during this period gives a good estimate of the "reserve" bud bank available for tiller regeneration in the next growing season. At each sample time, we located a population of grasses that was not intensely grazed and had many mature, reproducing genets (tufts). We haphazardly selected between 10 and 20 mature, flowering plants (entire genets) growing within an area of approximately 2–5 ha. We avoided sampling genets that were close enough together that they could have resulted from fragmentation of a single clone. Sampling 10–20 individuals provided an estimate of within species variation for several species without resulting in unmanageable numbers for the labor-intensive process of counting buds (described below). Each genet was carefully excavated to a depth of 15 cm and placed in plastic bags. Samples were transported to the University of Botswana herbarium where species identifications were confirmed and the numbers of vegetative and flowering tillers within each genet were counted. Tillers were clipped to a height of approximately 10 cm and the tillers and associated roots were thoroughly air-dried and transported to the laboratories at Kansas State University. After re-rehydration, we dissected the base of the cut tillers under a dissecting scope with magnifications between 7 and 25× to count the number of vegetative buds. Vegetative buds included both mature buds, which are contained within a prophyll, and activated buds, which extend past the prophyll but are shorter than 5 cm. For each grass species, the mean and standard error of proportion of tillers flowering, genet size (number of tillers per

Table 1
Life history characteristics, total sample size over all years sampled (N), and years and sites sampled for semi-arid savanna grasses in Botswana.

Species (N)	Life history [a]	Drought tolerance [b]	Grazing value [c]	Years and sites sampled [d]
Aristida congesta (40)	SP	DT	↓	2007a, 2008a,
Aristida diffusa (19)	LP	na	↓	2007a
Aristida junciformis (10)	LP	NT	↓	2007b
Aristida meridionalis (19)	LP	DT	↓	2008a
Aristida stipitata (10)	A/SP	DT	↓	2007a
Brachiaria nigropedata (19)	LP	DT	↑	2007a
Cymbopogon pospischilli (30)	LP	NT	↓	2007a, 2008a,
Digitaria eriantha (39)	LP	NT	↑	2007a, 2008a,
Eragrostis cylindriflora (10)	A	na	↓	2007a
Eragrostis rigidior (20)	SP	DT	↑	2007a
Hyperthelia dissoluta (40)	LP	NT	↑	2007a, 2008a,
Pennisetum macrourum (20)	LP	NT	↑	2007a
Perotis patens (40)	A/SP	DT	↓	2007ab, 2008a
Pogonarthria squarrosa (40)	SP	na	↓	2007ab, 2008a

[a] A = annual, SP = short-lived perennial (2–5 year lifespan), LP = long-lived perennial (>5 year lifespan).
[b] DT = drought tolerant, NT = non-tolerant (after Van Oudtshoorn 1999), na = not available.
[c] ↑ = high grazing value (palatable), ↓ = low grazing value (unpalatable) (after Van Oudtshoorn 1999).
[d] a = Khama Rhino Sanctuary, b = Khutse Game Reserve.

genet), and number of buds per tiller were calculated. The mean of each response variable was calculated using genets as replicates. The data for each trait were then analyzed with a one-way ANOVA using Tukey's test for comparison of means when appropriate. Correlations were investigated using the nonparametric Kendall's Tau. All data analysis was conducted using R (R Development Core Team, 2008).

3. Results

Patterns of flowering effort and bud production varied greatly among these co-occurring grass species. Average bud bank size varied 4-fold among species, ranging from a low of 0.8 ± 0.3 buds/tiller in *Eragrostis cylindriflora* to 3.3 ± 0.4 buds/tiller in *Eragrostis rigidior* (mean ± 1 se; Fig. 1A). Flowering effort varied 10-fold among species, ranging from a low of $8 \pm 1\%$ of tillers flowering in *Cymbopogon pospischilli* to a high of $94 \pm 11\%$ of tillers flowering in *E. cylindriflora* (mean ± 1 se; Fig. 1B). There was no significant difference in flowering effort or bud bank size between the two sites for the two species sampled from both locations in 2007 (*Perotis patens* and *P. squarrosa*).

Patterns of both flowering effort and bud production varied significantly and inversely with grass life history. Mean bud
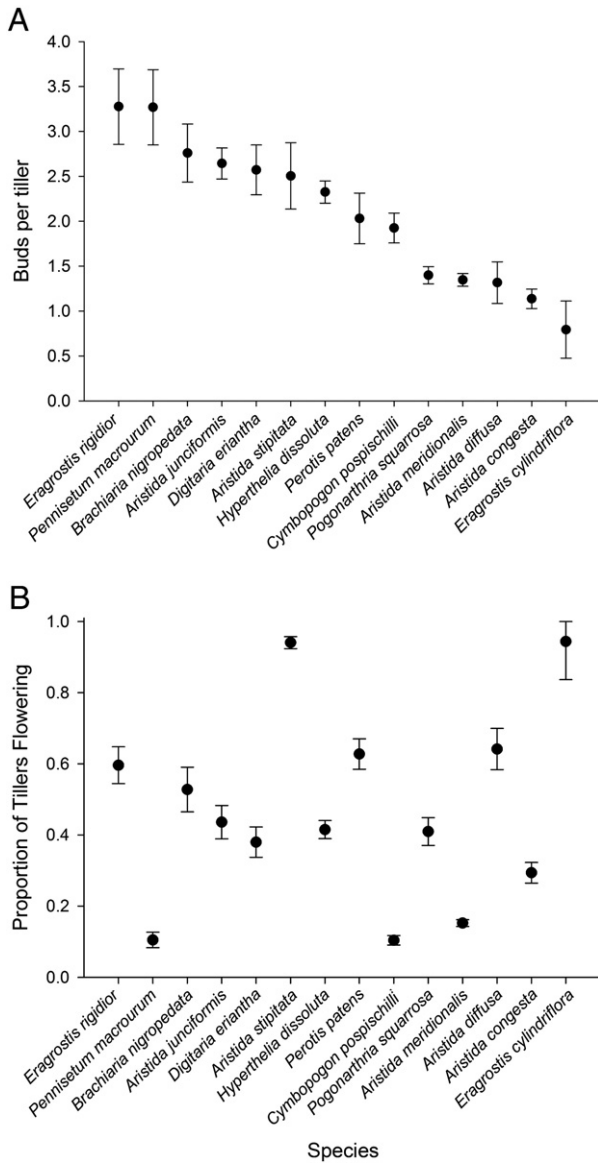
A

B

Fig. 1. Average (A) bud bank size and (B) flowering effort of 14 African savanna grasses. Data were averaged across years for species sampled in more than 1 year. Points are means ± 1 standard error.

bank size was lowest among annual/biennial grasses, intermediate in short-lived perennials, and greatest among long-lived perennial grasses (Fig. 2). By contrast, flowering effort was significantly greater in annual/biennial grasses than in the perennial species (Fig. 2). Half of the long-lived species were classified as having high grazing value and half were classified as having low grazing value. If life span were more important than grazing value, then we would expect to see no difference based upon grazing value. However, grass species classified as having high grazing value produced significantly greater number of buds per tiller (2.70 ± 0.13) than species of low grazing value (1.42 ± 0.07, $P < 0.0001$), but they did not differ significantly in flowering effort ($39 \pm 4\%$ of tillers flowered in both groups, $P = 0.87$). Grass species classified as drought-tolerant produced significantly fewer buds per tiller (1.97 ± 0.13) than non-tolerant species (2.38 ± 0.10, $P = 0.014$).
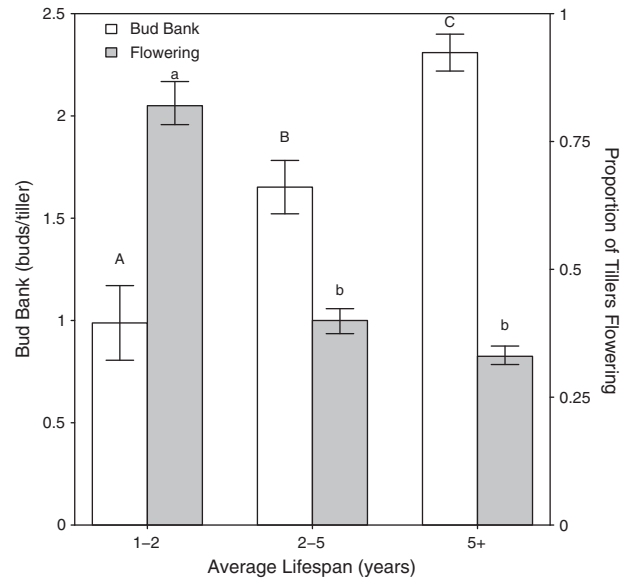

Fig. 2. Bud bank size and flowering effort related to life span in 14 African savanna grasses. Bars are means ± 1 standard error over all samples (2007 and/or 2008). Letters represent statistically significant differences at $P < 0.05$.

Within species, flowering effort showed greater variation between years than did bud bank size (Fig. 3). Precipitation at KRS during the 2006–07 growing season (7 months prior to 2007 sampling) was 386.7 mm which was 10% below the MAP of 425 mm, whereas total precipitation during the 2007–08 season was 473.3 mm, 28% higher than 2006–07 and 11% higher than MAP. Flowering effort was significantly lower in 2008 (a wet year) than in 2007 (a dry year) for three of the six species sampled in both years (*D. eriantha*, *Hyperthelia dissoluta*, and *P. squarrosa*). Bud bank size showed less variability between years: only one of the six species that we sampled in both years, *P. patens*, displayed statistically significant inter-annual variability in bud production as its number of buds per tiller in 2008 (a wet year) was almost an order of magnitude higher than in 2007 (Fig. 3). Overall, there was no significant correlation between flowering effort and bud production among species ($P = 0.79$) and no consistent patterns of relationships between flowering effort and bud production within species. Only two species showed significant correlations. Individuals of *P. squarrosa* showed a significant negative correlation between flowering effort and bud production (Tau = −0.31, $P = 0.005$) whereas *C. pospischilli* showed a significant positive relationship (Tau = 0.31, $P = 0.014$).

4. Discussion

Almost all perennial plant species maintain some dormant buds below- and/or above-ground, but the size of the bud bank and the proportion of dormant and active buds can vary both within and among species (Hartnett et al., 2006; Hendrikson and Briske, 1997; Lehtila, 2000; Mueller and Richards, 1986; Ott, 2009). The grass plant is composed of a population of phytomers (the basic modular unit including a node, internode, leaf, and axillary bud). Bud production in perennial grasses can vary
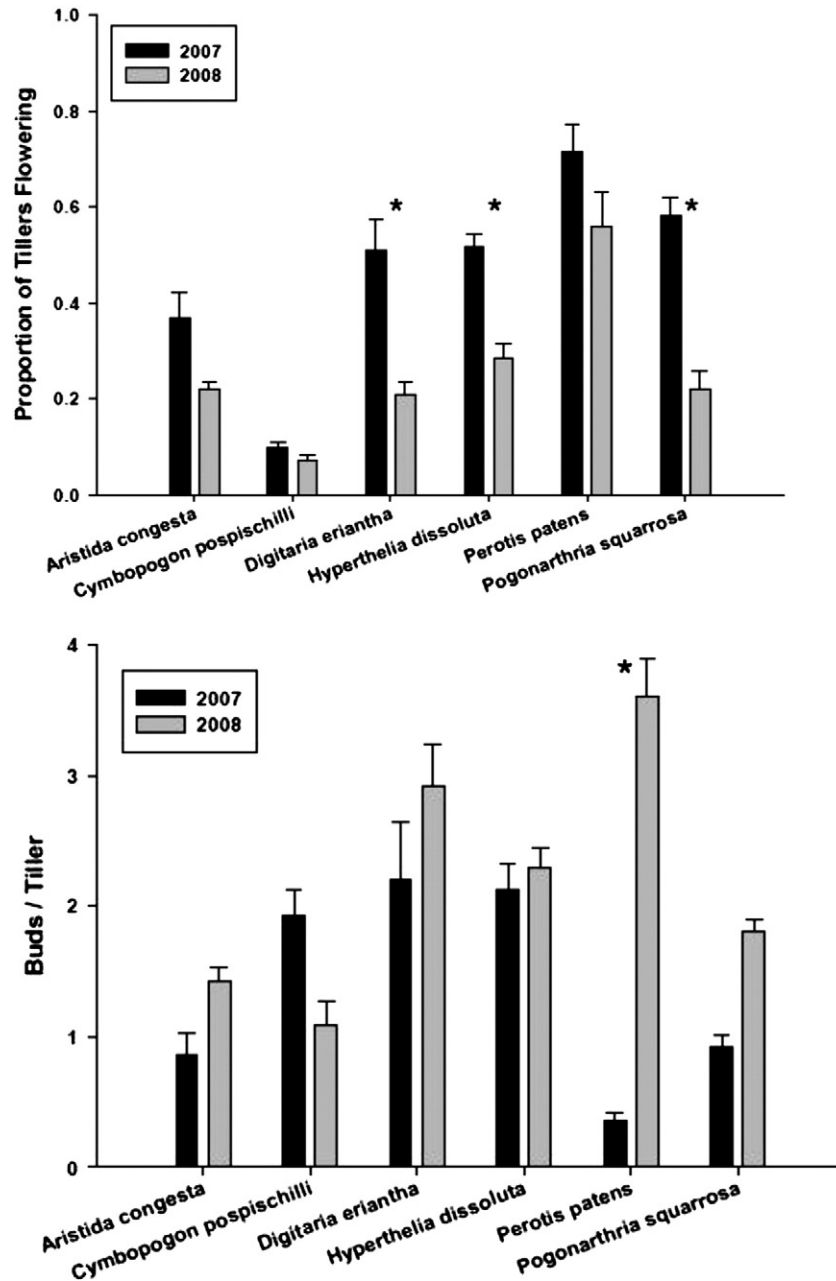
Fig. 3. Inter-annual variability in flowering effort (top) and bud bank size (bottom) in six African savanna grasses. Bars are means ± 1 standard error within a year, * = statistically significant differences between years at $P < 0.05$.

through variation in the number of successive phytomers comprising the basal crown, through the ability of axillary buds to branch and produce secondary or tertiary buds (Ott, 2009), and due to the flowering status of the tiller (Ott and Hartnett, 2011). The density of buds or the bud:tiller ratio provides an estimate of the degree of meristem limitation in perennial grasses (Benson et al., 2004).

The co-occurring semi-arid savanna grasses studied here showed high inter-specific variability in their numbers of buds. This variability in bud bank size has the potential to strongly influence spatial and temporal patterns of grass population growth and net primary production in grass-dominated ecosystems. Meristem limitation at the community level across a precipitation gradient of grasslands in North America is correlated with a

decrease in the temporal variability of aboveground net primary productivity (Dalgleish and Hartnett, 2006; Knapp and Smith, 2001). At the genet level, meristem limitation may constrain primary production and its inherent temporal variability in species with a small bud bank. The size of the bud bank may also be a critical determinant of the resiliency and recovery rates of perennial savanna grass populations, and their viability and sustainable production under changing environmental conditions. Although we expected that a large bud bank may be advantageous for withstanding drought conditions, we found that drought-tolerant species did not have larger bud banks. Drought-tolerant species may have differences in bud longevity or may strongly depend on seed banks for regeneration, but further research is

required to determine any differences in reproductive strategies of drought-tolerant vs. non-tolerant grass species.

Among the African savanna grasses studied here, species such *E. rigidior*, *Brachiaria nigropedata*, *Aristida junciformis* and *Pennisetum macrourum* maintained a relatively large number of buds (>2.5 buds per adult tiller). The productivity of these species is not likely to be meristem-limited, and their large bud banks may be an important population stabilizing feature. Their maintenance of a large number of buds in the dormant state may limit rapid population increase during favorable conditions, but buffer local populations against extinction risks in the face of unfavorable or unpredictable conditions. If their large bud banks are maintained in an active (non-dormant) state, outgrowth of these buds would enable populations to opportunistically capitalize on periods of high resource availability and increase productivity through the rapid production of a large population of new tillers, when other species may be unable to respond due to meristems limitation. By contrast, species that produce few buds, such as *E. cylindriflora* and *A. congesta* are more likely meristem-limited. They may show stronger temporal dynamics and may be limited in their capacity to respond to resource pulses or to recover from stresses imposed by drought, grazing, or other factors. Contrary to many other grasslands, African semi-arid grass seed bank composition partially reflects the aboveground species composition (O'Connor and Pickett, 1992). Thus, having a bud bank and a seed bank may both substantially contribute to population persistence and greatly affect the overall dynamics of semi-arid African savanna grasses.

Savanna grass species that are regularly grazed such as *B. nigropedata*, *D. eriantha*, *E. rigidior* and *P. macrourum* (classified as high grazing value by Van Oudtshoorn, 1999) maintained significantly larger bud banks than unpalatable species. This pattern is consistent with a recent study of a palatable bunchgrass in a North American mesic grassland that maintained average bud production on newly recruited tillers following a release from grazing across a wide range of grazing intensities (N'Guessan and Hartnett, 2011). These similar patterns in southern African and North American grasses suggest that the maintenance of a large bud bank may be generally important to the resiliency of palatable perennial grasses in response to grazing, as it enables demographic compensation and rapid replacement of tiller populations following herbivory.

Some of the patterns in bud production and flowering effort among the species studied here are indicative of a life history allocation trade-off between seed reproduction and vegetative reproduction or tillering in savanna grasses. Bud bank size increased and flowering effort decreased with life span, with longer-lived perennial grasses maintaining a larger number of buds per tiller but fewer flowering tillers than shorter-lived species. Seed production of annual and short-lived perennial semi-arid African savannas is higher than longer-lived perennials (Veenendaal et al., 1996b). These patterns are consistent with life history theory, which states that short-lived ruderal species should invest more in seed reproduction while longer-lived species should invest more in vegetative reproduction and survival (Grime, 2001).

Flexibility in relative allocation to seed versus buds may be an important strategy of savanna grasses in a dynamic environment subject to high inter-annual variability in precipitation, grazing, or other disturbances. However, we only observed inter-annual differences in bud production in one species, *P. patens*. Variation in its bud production may be related to its flexible life history as it can be either be an annual or a short-lived perennial. In contrast, half of the species we sampled in both years altered their flowering effort between years indicating that allocation to flowering effort may be more closely related to resource availability, such as the rainfall, than bud production. Although tradeoffs between sexual and vegetative reproduction have been readily observed in many forbs (e.g. Abrahamson, 1975; Hartnett 1990), direct negative effects of sexual reproduction on vegetative reproduction have not been observed in grasses (e.g. Ott and Hartnett, 2011; Reekie, 1991). A tradeoff between these two modes of reproduction may not be detected if the allocation tradeoff is dependent on low variation in the amount of resource acquired by the individuals and/or species (Van Noordwijk and De Jong, 1986), the position of the two allocation traits measured in the allocation tree (Worley et al., 2003), and the magnitude of the difference in the amount of resources translocated to the reproductive mode (De Jong, 1993). However, developmental constraints on bud production during tiller ontogeny may result in no correlation or a positive correlation between these reproductive modes (Ott and Hartnett, 2011).

Understanding grass reproductive strategies and the relative contributions of bud banks and seed production to population recruitment and dynamics is important to gaining a mechanistic and predictive understanding of savanna vegetation productivity, dynamics, and responses to environmental change. Veenendaal (1991) noted that traits associated with the seed reproduction process such as high seed production, drought-avoidance seed dormancy, and sequential germination phenology are all important in the adaptive strategy of semi-arid savanna grasses. Our results suggest that the life history and dynamics of belowground bud banks are also important components of the life history strategies of perennial savanna grasses. Given their contribution to population recruitment and maintenance, the dynamics of belowground bud banks are important to the conservation, management, and sustainable productivity of the savannas and grasslands of southern Africa. A better understanding of the ecology and dynamics of grass bud banks would assist in the formulation of management strategies to maintain sustainable perennial forage grass populations and conserve species diversity in savanna vegetation (Veenendaal, 1991).

Acknowledgments

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