ECOLOGICAL IMPLICATIONS OF GRASS BUD BANK AND TILLER DYNAMICS IN
MIXED-GRASS PRAIRIE


by


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B.S., Concordia University-Nebraska, 2006
M.S., Kansas State University, 2009


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# Abstract

Perennial grass populations propagate vegetatively via the belowground bud bank. Climate, photosynthetic pathway, and growth form impact bud production, longevity, and dormancy; leading to alterations in bud bank and tiller dynamics. Previous research in mesic $C_4$-dominated tallgrass prairie revealed that a $C_4$ grass had greater bud longevity and differing bud bank dynamics than a $C_3$ species. This study examined the bud bank dynamics of rhizomatous and caespitose grasses in a more arid $C_3$ dominated prairie to gain insights into how bud banks differ among grass species, growth forms, and environments, and the relationship between bud bank characteristics and grass architecture and growth patterns. The bud bank and tiller dynamics of four perennial grasses in the $C_3$-dominated northern mixed grass prairie were examined over 15 months.

The $C_3$ caespitose and rhizomatous grasses produced similar numbers of buds per tiller and their bud longevity was $\geq 2$ years. Tiller longevity drove the turnover within the bud bank of the dominant $C_3$ caespitose grasses *Hesperostipa comata* and *Nassella viridula*. Their polycyclic tillers (tillers that lived for more than one year) created multi-aged bud banks. The rhizomatous $C_3$ grass *Pascopyrum smithii* also had a multi-aged bud bank because buds were able to live longer than its annual tillers. Differences between caespitose and rhizomatous $C_3$ grass bud banks were driven by differences in tiller and rhizome production and spatial distribution. Responses to water availability fluctuations are likely buffered by the maintenance of polycyclic tillers in the caespitose grasses and flexible timing of annual tiller recruitment in the rhizomatous grass.

The $C_4$ rhizomatous grass *Andropogon gerardii* had similar phenology to populations in its tallgrass prairie range center. Despite declines in bud production per tiller and lowered flowering probability in mixed-grass prairie, *A. gerardii* maintained a multi-aged bud bank and a positive population growth rate via vegetative reproduction at both the center and edge of its range.

Bud bank dynamics of different growth forms and photosynthetic pathways, as they offer insight into the control of grass population dynamics and production, will enhance understanding of the mechanisms by which management practices and environmental change can alter perennial grasslands.

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# Dedication

**Soli Deo Gloria**

I dedicate this work to the glory of God who has given me eternal salvation through Jesus Christ His Son and to the wonderful people, my family and friends, He has given me on this earth.

To my family and friends, who have been and continue to be a constant source of encouragement.  My life is so much richer having you in it.  I would especially like to recognize my parents and brother, who constantly remind me what life is all about.  Dad, thanks for your scientific inspiration.  Mom, thanks for being my good listener.  Paul, thanks for helping me put everything into perspective.  A special thanks to Hope Lutheran Church, SOS and WWA and the many writing venues of this dissertation (IL, ND, SD, KS, and TX).

I also dedicate this work to those curious botanists who look belowground.  There is so much to discover.

# Chapter 1 - Introduction

Grasslands, which are estimated to cover 40.5% (52,544,000 km$^2$) of global land area, provide valuable ecosystem goods and services, such as food, carbon storage, and recreation (White et al. 2000; Gibson 2009). The amount of ecosystem goods and services a grassland provides can be strongly affected by its aboveground net primary production (ANPP). Both the number of ramets (aboveground stems) that are recruited each growing season and the size of those ramets determine ANPP (Hartnett and Fay 1998). In perennial grasslands, most ramet recruitment occurs from belowground buds rather than from seeds. For example, >99% of all established stems in tallgrass prairie in both burned and unburned communities were recruited from the bud bank (Benson and Hartnett 2006). Vegetative recruitment was also more common than seed recruitment in the shortgrass steppe of northern Colorado as the seed bank primarily consisted of annuals rather than the dominant perennials (Coffin and Lauenroth 1989).

Seedling recruitment of the dominant grasses across the Great Plains is rare but is more common in grasslands with low mean annual precipitation. In short grass prairie and the Chihuahuan Desert, between zero and 74.6 seedlings/m$^2$ of *Bouteloua gracilis* can be recruited depending on environmental conditions (Peters 2000). In southern mixed grass prairie, 2.4 seedlings/m$^2$ were recruited of the dominant grass *B. gracilis* (Fair et al. 1999). In tallgrass prairie, recruitment was limited to 0.5 – 1.5 seedlings/m$^2$ of each grass species (Benson and Hartnett 2006). These low amounts of seedling recruitment underscore the importance of tiller recruitment from the bud bank in perennial grasslands.

As the primary source of new tillers, bud banks are a major underlying mechanism determining grassland ANPP spatially and temporally. In North American grasslands, ANPP and herbaceous belowground bud densities increase across an increasing precipitation gradient (Sala et al. 1988; Dalgleish and Hartnett 2006). When compared to desert and forest biomes, grassland ANPP had the largest inter-annual variability as well as the largest pulses in response to above average annual precipitation (Knapp and Smith 2001). Knapp and Smith (2001) hypothesized that grasslands maintained adequate meristem (i.e. bud) densities enabling them to respond to moderate inter-annual variability in precipitation.

Bud bank demography, especially annual bud production of grasses, can introduce lag effects on ANPP in grasslands. Current year precipitation fails to fully explain current year productivity but an additional 13 to 30% of current year ANPP can be explained by previous year tiller production or ANPP (Lauenroth and Sala 1992; Oesterheld et al. 2001; Reichmann et al. 2013). The effect of previous year ANPP and tiller production on current year ANPP is mediated by the bud bank (Dalgleish and Hartnett 2009). Grass bud production is closely tied to tiller growth. Grass tillers are modular units comprised of multiple phytomers and each phytomer consists of an internode, leaf sheath, leaf blade, and potentially an axillary bud (Etter 1951; Briske 1991; Evert 2006). As a result, a bud is likely produced whenever a new leaf is produced. However, a phytomer may fail to produce a bud or its axillary bud may produce additional buds (i.e. higher order buds; Ott and Hartnett 2012b). Axillary buds accumulate belowground because grasses condense their nodes at the base of the tiller only exposing their leaves aboveground during vegetative growth (Hyder 1972; Jewiss 1972). Individuals of several grass species appear to maintain consistent bud production per tiller regardless of their previous grazing history (Hendrickson and Briske 1997; N'Guessan and Hartnett 2011). However, bud production per tiller could be reduced or bud dormancy increased if the tiller was injured or resource limited (i.e. reduced in size) during its time period of maximum growth and bud formation (Vanderweide 2013). Therefore, alterations in tiller density and size can alter annual bud production, which is the primary source of the next year's tiller recruits and thus ANPP. Annual bud production might also explain why demographic responses, such as survival, of perennial grassland species can lag climatic patterns by at least one year (Dalgleish et al. 2011).

Bud banks play a critical role in other aspects of perennial grassland function and structure. The stability of belowground bud banks on a grassland experiencing a two-year severe drought enabled aboveground resilience following drought (Vanderweide 2013). Bud bank density remained stable throughout the drought while aboveground biomass production and flowering declined during the drought but quickly recovered following the drought (Vanderweide 2013). Abundance of various clonal traits varied across a range of communities with different soil conditions (Rusch et al. 2011). Therefore, clonal traits, such as bud banks, should be included when considering factors involved in determining plant community assembly and composition (Klimesova and Klimes 2008). Belowground bud banks contributed to the maintenance of a diverse plant community in grasslands experiencing and recovering from

grazing (Dalgleish and Hartnett 2009; Vanderweide 2013). The temporal and spatial distribution of bud dormancy and outgrowth also drives the variation in growth form among grasses, their architecture, clonal growth patterns, and spatial distribution within a community.

Detailed understanding of bud bank characteristics and life histories of common grasses offers insight into larger ecological questions. For example, additional lag effects impacting ANPP can occur when the bud longevity of dominant grasses exceeds one year and older buds participate in seasonal tiller recruitment (Ott and Hartnett 2012a). Greater bud longevity in dominant grasses may buffer their populations and enable them to persist in fluctuating environments. Both spatial and temporal bud availability can influence the dominance, competitive ability, and clonal expansion of a species. Bud availability is dependent on bud natality, longevity, and dormancy as well as the spatial placement of those buds (Watson et al. 1997). These bud bank characteristics would be expected to vary among species but species with similar growth forms, photosynthetic pathway guilds, or phylogeny may share some similar bud bank characteristics. Intra-specific plasticity in bud bank characteristics and vegetative reproduction may impact the local and regional distributions of a species.

My previous studies in tallgrass prairie examined the bud bank characteristics and life history of a dominant $C_4$ rhizomatous grass (*Andropogon gerardii*) and a sub-dominant $C_3$ caespitose grass (*Dichanthelium oligosanthes;* Ott and Hartnett 2011, 2012a, 2012b). *Andropogon gerardii* had bud longevity $\geq 2.5$ years, synchronous bud development, and overwintered in the bud stage. *Dichanthelium oligosanthes* had bud longevity $\leq 1$year, asynchronous bud development, produced higher-order buds, and overwintered both in the bud stage and as juvenile (mostly pre-emergent) tillers (Ott and Hartnett 2012a, 2012b). Buds were used by *A. gerardii* to overwinter and produce spring tillers whereas buds were primarily used by *D. oligosanthes* to survive and produce tillers following summer dormancy (Ott and Hartnett 2012a). Many of the bud bank characteristics of these two species could be due to their growth form or photosynthetic pathway guild. Bud development and dormancy timing were closely tied to the aboveground phenology of their respective $C_3$ and $C_4$ photosynthetic pathway guild. Overall bud production per tiller and asynchrony in bud development could also differ between caespitose and rhizomatous growth forms. In a rhizomatous grass, rhizomes and tillers could potentially create asynchrony in bud development by producing buds and recruiting them to tiller at different times. *Andropogon gerardii* rarely produced buds along its short rhizomes and never

recruited them to tiller (Ott and Hartnett 2012a).  Therefore, its rhizomes did not alter the bud

bank dynamics or contribute to tiller recruitment as much as they might in a strongly

rhizomatous grass.  The caespitose *D. oligosanthes* was able to increase its bud production per

tiller via higher-order bud production (branching of axillary buds to produce secondary or

tertiary buds), unlike the rhizomatous *A. gerardii* (Ott and Hartnett 2012b).  Differences in bud

longevity could be a major contributing factor determining local dominance among grass

species.  Long-lived buds of dominant species, such as *A. gerardii*, would buffer population

dynamics similar to the role of seed banks.

Further studies of co-occurring grasses, especially in $C_3$ dominated grasslands, are

needed to ascertain how bud and tiller dynamics vary among species, growth forms, and

grassland ecosystems.  In the North American Great Plains, the dominant photosynthetic

pathway guild of grasses shifts from $C_4$ to $C_3$ as mean annual precipitation (MAP) decreases to

the northwest and mean annual temperature (MAT) declines to the north (Epstein et al. 1997).

Therefore, $C_3$ grasses are more productive and common in the northern Great Plains compared to

the southern Great Plains and eastern tallgrass prairie (Terri and Stowe 1976; Epstein et al 1997).

Determining the bud and tiller dynamics of perennial grasses in a $C_3$-dominated system would

complement previous research conducted in $C_4$-dominated tallgrass prairie and enable further

examination of bud bank characteristics that contribute to dominance and that are affected by

growth form or photosynthetic pathway guild.

Understanding the demography and dynamics of bud production, tiller recruitment, and

tiller establishment of common grasses in multiple grasslands is necessary to understanding the

mechanism by which climatic variability and land management determines grassland

productivity across regions such as the Great Plains.  The dissertation research presented in the

following chapters studied bud and tiller dynamics of three dominant $C_3$ grasses and one sub-

dominant $C_4$ grass in northern mixed-grass prairie in western South Dakota.  Two of the $C_3$

grasses (*Hesperostipa comata* and *Nassella viridula*) had a caespitose (bunchgrass) growth form

while the remaining $C_3$ species (*Pascopyrum smithii*) had a rhizomatous growth form.  The sub-

dominant $C_4$ grass examined was *A. gerardii*, the same species that is the dominant $C_4$ grass in

tallgrass prairie examined in my previous studies.  The over-arching objectives of this research

were to 1) compare the bud bank structure and dynamics of dominant grasses of different

grassland ecosystems, 2) determine how bud bank traits of the dominant grass *A. gerardii*

differed between the center and periphery of its range, and 3) assess whether bud bank characteristics varied between different grass guilds ($C_3$ vs. $C_4$ species) and grasses of different growth form (caespitose and rhizomatous species).

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# Chapter 2 - Tiller population dynamics drive genet bud bank formation and composition in two $C_3$ caespitose grasses: The role of polycyclic tillers

## Abstract

The bud bank of a caespitose grass is an important feature mediating its tillering response to the environment. Tiller population dynamics in turn can strongly influence its belowground bud bank size and dynamics. Because co-occurring species can greatly differ in their reproductive life histories and grasses primarily reproduce vegetatively, bud production and maintenance on tillers (i.e. ramets) of varying flowering status, photosynthesizing status, and age will likely differ among co-occurring species. The tiller dynamics of these tiller types along with their bud production differences determine genet bud bank size and dynamics. Comparison of the bud bank and tiller populations of two co-occurring caespitose grasses would enable deeper understanding of 1) how overall genet bud bank differences contribute to species life history differences, 2) how tiller types contribute to the bud bank, and 3) how tiller cycling impacts cycling within the bud bank. The bud bank and tiller dynamics of two dominant $C_3$ caespitose grasses, *Hesperostipa comata* and *Nassella viridula*, were assessed throughout an entire annual cycle in the northern mixed grass prairie of the North American Great Plains. Both species maintained polycyclic tillers, tillers that lived for more than one year, creating genet bud banks comprised of multiple annual bud cohorts. Neither species' tiller population growth was meristem limited. In both species, older tiller generations had more buds per tiller than younger tiller generations. Buds lived for two or more years but bud longevity rarely exceeded tiller longevity. Therefore, tiller longevity drove the turnover within the bud bank. *Hesperostipa comata* and *N. viridula* also transitioned similar numbers of vegetative tillers to flowering tillers. *Nassella viridula* had a larger bud bank size and supply of juvenile tillers, due to its larger genet basal area and greater number of buds produced per tiller. *Hesperostipa comata* displayed greater fluctuations in tillering responses to inter-annual precipitation variability than *N. viridula*. The consistent tiller recruitment and larger bud and juvenile tiller supply of *N. viridula* likely contributed to its greater capacity for vegetative reproduction and potentially greater genet

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longevity than *H. comata*. The sensitivity of the demography of *H. comata* to inter-annual precipitation variability may be indicative of a capacity to capitalize on periods of high resource availability. In comparison with a subdominant $C_3$ grass in tallgrass prairie, all species maintained a supply of potential tiller recruits in multiple stages of development but the mixed grass species maintained more tiller generations than the tallgrass prairie species. Although bud production differed between tiller types, tiller population dynamics played a larger role than bud production per tiller in determining the differential contribution of the various tiller types to the bud bank. Therefore, polycyclic tillers and their effect on bud bank dynamics could act as a stabilizing force within perennial grass populations. Maintenance of a dense belowground bud bank is a key trait driving the success of the ecologically successful caespitose grass growth form.

Key words: bud bank, caespitose, genet longevity, grasses, polycyclicity, tiller dynamics

## Introduction

Caespitose grass species (bunchgrasses) are found throughout the grassland biome, which covers 24 million square kilometers of the earth and encompasses tropical and temperate grasslands, savannas, and shrub steppe (Leith 1978). The ecological success of the caespitose growth form can be attributed to its effective monopolization of local environmental resources by sharing resources through physiological integration within ramet hierarchies, regulating ramet natality and mortality via density-dependent growth, and consolidating pools of soil resources (e.g. soil organic carbon and total N) beneath the genet (Derner et al. 1997; Briske and Derner 1998; Derner and Briske 1998). Individual genets of caespitose grasses can be very long-lived, surviving from several decades to a century (Briske and Derner 1998). Their longevity is dependent on the consistent recruitment of tillers from their reserve of belowground buds (the bud bank *sensu* Harper 1977). Although overall tiller population sizes within a genet may follow a relatively stable annual cycle following genet establishment, tiller natality and mortality can exhibit dramatic fluctuations within the annual cycle resulting in highly dynamic tiller populations (Langer 1956; Langer et al. 1964; Garwood 1969; Robson 1968; Jonsdottir 1991).

Tiller population dynamics of a genet can greatly influence the size and dynamics of its belowground bud bank. Tiller natality and growth is inherently tied with bud production

(Sharman 1942; Langer 1972; Briske 1991). Tiller developmental stages can also impact bud production. For example, flowering tillers produced more buds per tiller than vegetative tillers in *Andropogon gerardii* (Ott and Hartnett 2011) but not in *Sporobolus heterolepis* or *Koeleria macrantha* (Dalgleish et al. 2008). Buds are assumed to live at least as long as their actively assimilating parent tiller and interconnected sister tillers. Grass buds can obtain resources from their parent tillers for several years as some species produce polycyclic tillers (i.e. living for two or more years) with some parent tillers living six years (Langer 1956; Robson 1968; Cable 1971; McKendrick et al. 1975; Jonsdottir 1991; Herben et al. 1993; Tamm et al. 2002; Janisova 2006). Grass buds, with their low maintenance costs, usually live longer than their aboveground parent tiller and persist belowground following aboveground tiller senescence (McKendrick et al. 1975; Hendrickson and Briske 1997; Vesk and Westoby 2004; Ott and Hartnett 2012a). Therefore, aboveground tiller mortality may or may not be closely linked to bud mortality. However, bud longevity is limited by the longevity of the belowground crown of the plant (Noble et al. 1979; Klimesova and Klimes 2007).

Climate and disturbances such as grazing and fire can greatly impact perennial grassland aboveground net primary production, community composition, and population processes (Knapp et al. 1998; Oesterheld et al. 2001). For long-lived perennial species, such as caespitose grasses, population dynamics and population basal area growth are more impacted by climate's effect on genet survival and growth rather than its effect on genet recruitment (Franco and Silvertown 2004; Dalgleish et al. 2011). In order to gain a better understanding of how climate and disturbances such as herbivory affect caespitose grass growth and survival, we need to understand the size, development, and turnover of the belowground bud bank at both the ramet (i.e. tiller) and genet levels. At the genet level, the bud bank determines genet growth and survival as it is the source for all new tiller recruitment. Genet tiller populations can be comprised of tillers belonging to different cohorts and at various developmental stages. Because the genet bud bank is comprised of all buds produced on each of the genet's tillers, the genet bud bank characteristics are determined by a genet's tiller composition and the bud production of each tiller group. Examination of bud production, development, and mortality of different tiller groups will provide insight into how belowground bud bank dynamics and aboveground tiller dynamics relate to one another.

Coexisting perennial grass species can vary greatly in life history characteristics, such as longevity, sexual reproductive effort, dispersal, and patterns of vegetative reproduction and growth (O'Connor 1991). Most studies focusing on the basic patterns of vegetative reproduction and growth of grass species examined seedlings established in controlled plantings (Lamp 1952; Langer 1956; Langer et al. 1964; Robson 1968; Colvill and Marshall 1984) and only a few studies examined established populations (Herben et al. 1993; Janisova 2006), the role of bud banks (Dalgleish et al. 2008; Ott and Hartnett 2012a), or natural populations of coexisting species (Langer et al. 1964; Jonsdottir 1991).

*Hesperostipa comata* and *Nassella viridula* are two dominant $C_3$ caespitose grasses in the northern mixed grass prairie of the Great Plains region. *Hesperostipa comata* populations are often composed of individuals with small basal areas and are located in drier sites within the community than *N. viridula* (Redmann 1975). *Nassella viridula* individuals are very productive (Rogler 1960) and tend to have large basal areas once established. Although each species is palatable to grazers, *N. viridula* declines with heavy grazing while *H. comata* resists grazers due to production and retention of sharp, needle-like florets (Larson and Johnson 1999). These co-occurring species provide an opportunity to compare the life history characteristics, especially patterns of vegetative reproduction and growth, of two dominant caespitose grasses of varying size in northern mixed grass prairie while controlling for photosynthetic pathway and location effects.

The objective of this study was to quantify bud bank and tiller dynamics throughout an annual cycle of the perennial grasses *H. comata* and *N. viridula* in order to 1) better understand the life history patterns of dominant perennial $C_3$ grasses in the northern Great Plains, 2) determine whether tillers of varying age, flowering status, and photosynthesizing status differentially contribute to the genet bud bank and thus genet persistence, 3) identify whether these two co-occurring species have different life history characteristics involving investment in sexual and vegetative reproduction, and 4) consider whether the larger size (basal area) of *N. viridula* as compared to *H. comata* is indicative of greater genet longevity or faster basal rate expansion.

# Methods

## *Site description*

The study was conducted at Wind Cave National Park (WCNP), a 13,699 hectare mixed-grass prairie interspersed with ponderosa pine forest located at the southeastern extent of the Black Hills in western South Dakota (43º33'N, 103º29'W).  The vegetation is dominated by cool-season grasses such as *Hesperostipa comata*, *Pascopyrum smithii*, and *Nassella viridula* with discrete patches of less abundant warm-season grasses including *Andropogon gerardii*, *Bouteloua curtipendula*, and *Bouteloua gracilis*.  Bison (*Bison bison*), elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) are the major large herbivores.  However, bison and elk are the primary consumers of grasses due to their grazing habits and population sizes.  The region's semi-arid climate has cool winters (average Jan temp: 27.8ºF) and warm summers (average July temp: 73.2 ºF) with moderate rainfall (499 mm) primarily occurring April through October, especially in May and June.  During this study, annual precipitation in 2010 and 2011 was 645.92mm and 574.80mm respectively.  April, May, and June of 2010 and May of 2011 had at least 58mm of rainfall above the long-term average for each month.  WCNP has a hilly topography (elevation ranging from 1113m to 1527m).

For this study, the prairie portion of the 42 hectare Elk Mountain enclosure within WCNP was used.  The enclosure excludes bison but not other herbivores.  Although a seasonal campground is located in the southern forested portion of the enclosure, the large northern portion of the enclosure is undisturbed native mixed grass prairie.  Prescribed fire occurs every 5 to 7 years and the Elk Mountain enclosure was last burned in the fall of 2008.  The enclosure is at an elevation of 1310m and the prairie primarily had loamy-skeletal soils (Typic Argiustolls) but included a small area with fine-loamy soil (Fluventic Haplustolls); USDA-NRCS-WSS).

## *Field Sampling*

*Hesperostipa comata* (Trin. & Rupr.) Barkworth (needle and thread) and *N. viridula* (Trin.) Barkworth (green needlegrass) are both caespitose perennial $C_3$ grasses. Although both species flower May through July, *N. viridula* usually has larger flowering and vegetative tiller heights than *H. comata*.  Due to the caespitose growth form, discrete genets (i.e. individuals) of *H. comata* and *N. viridula* are easy to identify. Voucher specimens of each species were

collected from adjacent Custer State Park and are housed at the Kansas State University Herbarium (KSC).

In June and July 2010, ten sites separated by at least 50m were established within the grassland portion of the Elk Mountain enclosure. At each site, populations of *H. comata* and *N. viridula* were located and fourteen individuals of each species were randomly selected and marked using a metal tag and a wire ring. Basal areas of *H. comata* and *N. viridula* were determined by taking two perpendicular caliper measurements at the base of each individual and calculating the area of the ellipse. The 2010 flowering tillers of each individual were marked using small wire rings and counted.

Beginning on August 20, 2010, one individual of each species from each site was harvested to a 7cm depth approximately every 3 weeks during the growing season (i.e. while soil temperatures remained consistently above freezing) and washed to remove soil. At each sampling time, soil temperature was measured at a 5cm depth in three consistent locations at each site (Appendix Fig. 2-1). Soil temperatures were taken within the first 2 hours of dawn using a thermocouple (TH-65 Thermocouple Thermometer, Wescor, Inc or T-85154 Microprocessor thermometer Type J-K-T thermocouple Model HH23, Omega Engineering, Inc). Sampling occurred on 14 sampling dates over 15 months with the final harvest occurring on November 4, 2011. Although *N. viridula* was harvested every sampling date, samples from only nine sampling dates were analyzed in the lab due to time constraints. Therefore, a total of 140 *H. comata* and 90 *N. viridula* individuals were analyzed.

### *Lab analysis*

Buds and tillers from each individual plant were examined using a dissecting scope with magnifications between 7 and 40x. Tillers and basal/belowground buds were counted, assessed to be living or dead, and classified by size class and generation (Welker et al. 1987). Tillers were also classified according to flowering status. Although all tillers were counted and classified for the entire individual, buds were counted and classified on five randomly selected tillers of each generation and flowering status classification combination (exception: ten tillers were used to assess buds on residual tillers).

Tillers were distinguished from buds by their elongation in relation to the prophyll. Buds were contained within the prophyll and tillers had elongated past the prophyll. Live buds were

divided into two size classes: small and large (Table 2-1). Dead buds were identified by their soft, spongy or mealy brown interiors and easily distinguished from live buds. Seven tiller stages were identified (Table 2-1). Four stages were different size classes of vegetative tillers (Table 2-1). Small vegetative tillers ($VT_3$) are between 9 and 33% of the recorded vegetative tiller height for each species (Great Plains Flora Association, 1986). Heights of juvenile tillers ($VT_1$, $VT_2$) are smaller and large vegetative tillers ($VT_4$) are larger than heights of $VT_3$. For the first sample date (August 20, 2010), small juvenile tillers ($VT_1$) were counted as large juvenile tillers ($VT_2$). Juvenile tillers ($VT_{1,2}$) typically had not visibly emerged aboveground. Therefore, buds and juvenile tillers were considered collectively as "potential tiller recruits."

Tillers ($VT_{3,4}$, FT, ST) were further classified according to generation (primary/1, secondary/2, tertiary/3, quaternary/4, quinary/5). In a sequence of tillers ($VT_{3,4}$, FT, ST) directly growing from one another, generation was assigned oldest to youngest. For example, the oldest tiller is considered the primary tiller and the youngest is the tertiary tiller in a series of three attached tillers. Primary tillers are attached to RT. Hereafter, tillers may be referred to by their generation, if appropriate, and symbol (e.g. primary small vegetative tillers ($1VT_3$), secondary vegetative tillers ($2VT_{3,4}$), juvenile tillers ($V_{1,2}$), tertiary flowering tiller (3FT)). In previous work (Ott and Hartnett 2012a), $VT_1$ were classified as activated buds in both the $C_3$ grass *D. oligosanthes* and the $C_4$ grass *A.gerardii*. Classifying bud and tiller stages in relation to prophyll development will provide an objective standardized bud and tiller classification system that can be widely applied to many grass species to aid in future comparative studies.

### *Statistical analyses*

Mean individual basal area was evaluated using species (2-levels) as the treatment factor in a randomized complete block design (RCBD) blocking on site (PROC MIXED, SAS 9.2). Heterogeneous variances were used in place of a transform of the data as this allowed for direct analysis of the data in its original units. Satterthwaite's method was used to approximate the denominator degrees of freedom. Each individual genet was assigned to one of sixteen classes based on basal area. Size classes increased by $50cm^2$ increments (e.g. size class 1: $0$-$50cm^2$, size class 2: $50$-$100cm^2$, etc.). To compare the distributions of the basal areas of the two species, a two-sided large-sample approximate Kolmogorov-Smirnov test was conducted on the 2010 basal areas controlling for the median size of each species (PROC NPAR1WAY, SAS 9.2).

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Flowering tillers per basal area of the same individuals of *H. comata* and *N. viridula* were evaluated using a two-way factorial treatment of the 2-level factors of year and species in a RCBD with a split-plot-in-time with homogeneous variances (PROC MIXED, SAS 9.2). The factor of species was applied to the wholeplot experimental unit (WPEU) of individual genet and the factor of year was applied to the subplot experimental unit (SPEU) of individual genet occurring within year (i.e. repeated measure). Kenward-Roger's method was used to approximate the denominator degrees of freedom. Pairwise differences were assessed using the Bonferroni adjustment for alpha-level.

Seven response variables including total live and dead tillers ($VT_{3,4}$, FT, ST, RT) per basal area, $VT_{3,4}$ per basal area, ST per basal area, $B_{1,2}$ per basal area, $VT_{1,2}$ per basal area, total buds and juvenile tillers ($B_{1,2}$, $VT_{1,2}$) per vegetative tiller ($VT_{3,4}$) and total buds and juvenile tillers per ST were evaluated using a two-way factorial treatment structure with the factors of date and species in a RCBD blocking on site (PROC MIXED, SAS 9.2). First, a MANOVA including all seven response variables was conducted to test for overall treatment effects before proceeding with univariate analysis of each response variable (PROC GLM, SAS 9.2). Although there was a departure from multivariate normality, assumptions were deemed satisfactory enough to run a MANOVA. Significant differences among dates and species exist for some of the seven response variables (MANOVA, Wilk's $\lambda = 0.016$, $F_{147, 958.7} = 5.59$, $p < 0.0001$). Total buds and juvenile tillers per 2011 flowering tiller was analyzed similarly but separately from these seven variables. Because *N. viridula* did not undergo lab analysis for every sampling date, each univariate analysis was analyzed with missing treatment combinations and alternate main effects and interaction contrasts according to Milliken and Johnson (2009). In order to evaluate the sensitivity of this analysis to the missing treatment combinations, each univariate analysis was also evaluated using a reduced dataset with a balanced treatment design. The results were insensitive to the method used to analyze the data. Only one main effect F-test (noted in the results) was significantly different between the two methods.

To investigate generation effects within each species, $VT_{3,4}$ density and ST density were evaluated using a two-way factorial treatment structure with the factors of date and generation in a RCBD blocking on site with a split-plot (PROC MIXED, SAS9.2). The factor of date was applied to the WPEU of individual genet and the factor of generation was applied to the SPEU of tiller. Kenward-Roger's method was used to approximate the denominator degrees of freedom.

Contrasts compared the density of $1VT_{3,4}$ versus $2VT_{3,4}$ for each species in both Fall 2010 and 2011. Total buds and juvenile tillers per $VT_{3,4}$ were evaluated using a three-way factorial treatment structure with the factors of species, date, and generation in RCBD blocking on site with a split-plot (PROC MIXED, SAS9.2). The factors of species and date were applied to the WPEU of individual genet and the factor of generation was applied to the SPEU of tiller. Kenward-Roger's method was used to approximate the denominator degrees of freedom. Because *N. viridula* did not undergo lab analysis for every sampling date and tertiary tillers did not occur on every sampling date, the data was analyzed with missing treatment combinations and alternate main effects and interaction contrasts according to Milliken and Johnson (2009). In order to evaluate the sensitivity of this analysis to the missing treatment combinations, the data was also evaluated using a reduced dataset with a balanced treatment design. The significance of the main effects and interactions were insensitive to the method used to analyze the data. The full dataset was used to produce contrasts. Three contrasts compared the bud and juvenile tiller production of each species for each generation averaged over dates on which both species were sampled. Four contrasts compared bud and juvenile tiller production per $VT_{3,4}$ of primary to secondary $VT_{3,4}$ and of secondary to tertiary $VT_{3,4}$ within each species. Applying Bonferroni multiple comparison adjustments, these contrasts were only considered significant if $p < 0.007$.

## Results

### *Genet characteristics*

Average basal area of *N. viridula* genets ($206.6 \pm 9.8$ cm$^2$) was 3.6x larger than *H. comata* genets ($56.7 \pm 4.2$ cm$^2$, ANOVA, $F_{1,237} = 213.29$, $p < 0.0001$). Controlling for the difference in median basal area, the species also significantly differed in their genet basal area distributions (Kolmogorov-Smirnov, D=0.3423, $p < 0.0001$). Most individuals of *H. comata* were in the smallest two size classes and no individuals were in larger size classes (7-16) while *N. viridula* had similar numbers of individuals in the first six size classes and a few individuals in most of the larger size classes (Fig. 2-1). No genets of either species initially marked in June 2010 died before their harvest date during the 17 month study period.

Total tiller ($VT_{3,4}$, FT, ST, RT) density was significantly higher and juvenile tiller density was significantly lower in *H. comata* than in *N. viridula* throughout the study (Fig. 2-2, Table 2-2). Bud density was significantly higher in *H. comata* than in *N. viridula* in the 2010 growing

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season but not in the 2011 growing season (Fig. 2-2AB).  Due to its larger basal area, *N. viridula* always had a greater number of potential tiller recruits ($B_{1,2}$, $VT_{1,2}$) per genet than *H. comata* (Appendix Fig. 2-2).  *Hesperostipa comata* had more flowering tillers per basal area ($cm^2$) than *N. viridula* and both species had more flowering tillers per basal area ($cm^2$) in 2010 than in 2011 (Table 2-3; Species: $F_{1,73} = 11.3$, $p = 0.0012$; Year: $F_{1,82} = 37.3$, $p < 0.0001$; Spp*Year: $F_{1,82} = 0.68$, $p = 0.41$).  Because each species transitioned a similar percentage of $VT_{3,4}$ into FT (see below), the greater flowering tiller density of *H. comata* resulted from its overall greater tiller density as compared to *N. viridula*.

### *Hesperostipa comata*

$VT_{3,4}$ density decreased significantly during the summer of 2011 as a turnover between tiller generations occurred (Fig. 2-2C).  $1VT_{34}$ densities declined in 2011 and $2VT_{3,4}$ densities remained stable while $3VT_{3,4}$ and $4VT_{3,4}$ continually had very low densities (Fig. 2-3C).  $1VT_{3,4}$ had a significantly greater density in fall 2010 than $2VT_{3,4}$ (contrast, $F_{1, 245} = 22.59$, $p<0.0001$) but $2VT_{3,4}$ had a significantly greater density in fall 2011 than $1VT_{3,4}$ (contrast, $F_{1, 245} = 7.27$, $p = 0.008$; Fig. 2-3A). Tiller senescence and transition to flowering were greater among $1VT_{3,4}$ than $2VT_{3,4}$ (senescence: contrast, $t_{219} = 4.31$, $p<0.0001$, Fig. 2-3C).  Only $13.9 \pm 1.5$ % of vegetative tillers ($VT_{3,4}$) flowered and $96.2 \pm 1.7\%$ of flowering tillers were primary generation tillers (Fig. 2-4A).  $2VT_{3,4}$ comprised an increasing proportion of live tillers as $1VT_{3,4}$ amounts declined (Fig. 2-4A).  A large majority of $1VT_{3,4}$ were in the large size class ($VT_4$) throughout the year but $2VT_{3,4}$ were primarily in the small size class ($VT_3$) until genets flowered in the spring.  At that point, $2VT_3$ transitioned to $2VT_4$ (Fig. 2-4A).  Genets were not meristem limited as total bud and juvenile tiller density was always greater than live tiller density.  Because bud production is closely tied to tiller production, bud density had a similar declining trend as $VT_{3,4}$ density (Fig. 2-2AC).

The identity of a tiller, especially its generation and size, impacted its bud and juvenile tiller production.  Throughout the study, a $VT_{3,4}$ maintained between 0.5 and 3.4 buds and juvenile tillers (average: $1.95 \pm 0.05$ buds and juvenile tillers per $VT_{3,4}$) while $VT_2$ had between zero and two buds and juvenile tillers (average: $0.69 \pm 0.09$ buds and juvenile tillers per $VT_2$).  After winter, buds and juvenile tillers per $VT_{3,4}$ decreased because $VT_2$ transitioned to $VT_3$ (Fig. 2-5A) and the average $VT_{3,4}$ size was smaller as several $1VT_4$ transitioned to flowering tillers.

The strong increase in bud production per $VT_{3,4}$ in July was because $2VT_3$ transitioned to $2VT_4$ (Appendix Fig. 2-3B) and $1VT_{3,4}$ continued growth after $1FT$ had been recruited from them (Appendix Fig. 2-3A). Therefore, $VT_{3,4}$ had the greatest number of buds and juvenile tillers when the majority of $VT_{3,4}$ were large in the summer and fall (Figs. 2-4A, 5A). Overall, $1VT_{34}$ maintained significantly more buds and juvenile tillers than $2VT_{3,4}$ (contrast, $F_{1, 313} = 20.24$, $p<0.0001$) and $2VT_{3,4}$ maintained significantly more buds and juvenile tillers than $3VT_{3,4}$ (contrast, $F_{1,360} = 18.68$, $p<0.0001$). These differences were mainly evident when generations differed in their tiller size.

The majority of a genet's potential tiller recruits ($B_{1,2}$ and $VT_{1,2}$) were produced by $VT_{3,4}$ (Fig. 2-6A). Buds and juvenile tillers on 2011 FT rapidly declined 6 weeks after flowering to an average of $0.21 \pm 0.06$ buds and juvenile tiller per FT (Fig. 2-5B). Once a $VT_{3,4}$ senesced, either its buds and juvenile tillers grew out into $VT_3$ or senesced (Fig. 2-5C, Appendix Fig. 2-4A). RT and 2010 FT contributed few to no buds and juvenile tillers to the genet (averages: $0.011 \pm 0.007$ buds and juvenile tillers per RT; $0.07 \pm 0.02$ buds and juvenile tillers per 2010 FT). The majority of buds and juvenile tillers were found on $1VT_{3,4}$ in the fall of 2010 and on $2VT_{3,4}$ in the fall of 2011 (Fig. 2-6A).

Because most buds and juvenile tillers were produced by $VT_{3,4}$, the developmental composition of a genet's supply of potential tiller recruits (i.e. buds and juvenile tillers) reflected the developmental composition and production of buds and juvenile tillers on $VT_{3,4}$. Small buds comprised at least $78 \pm 1\%$ of the bud and juvenile tiller supply throughout the year and their contribution increased to $92 \pm 1\%$ between May and August 2011 (Fig. 2-7A). Large buds and $VT_{1,2}$ were present in low amounts throughout the year (Fig. 2-7A) and were never found on 2011 FT and rarely observed on ST and $3VT_{3,4}$ (Fig. 2-5ABC). $VT_2$ rarely contributed to the supply of buds and juvenile tillers in June through August because they had either been recruited to $VT_3$ or died, and new $VT_2$ were not recruited from buds and small juvenile tillers until the fall.

The majority of $VT_2$ occurred on the most abundant generation of $VT_{3,4}$ at any given point throughout the year. $VT_{3,4}$ produced $94.8\pm2.8\%$ of $VT_2$. In fall 2010, $91.8 \pm 5.0\%$ of $VT_2$ originated on $1VT_{3,4}$. However, by fall 2011, $38.0 \pm 11.3\%$ and $59.1 \pm 12.0\%$ of $VT_2$ were from primary and secondary $VT_{3,4}$ respectively (Appendix Fig. 2-5).

### *Nassella viridula*

Due to generational $VT_{3,4}$ dynamics, overall $VT_{3,4}$ density fluctuated during the annual cycle. $VT_{3,4}$ density decreased significantly in fall 2010 due to $1VT_{3,4}$ senescence but increased in spring 2011 due to $2VT_{3,4}$ and $3VT_{3,4}$ production and initial $1V_{3,4}$ renewal (Figs. 2-2D, 3BD). The increase in $1VT_{3,4}$ density in early May was due to a brief renewal of 1ST to photosynthesizing status (i.e. $1VT_{3,4}$) as their growing points had not fully senesced along with their aboveground leaves over the winter (Fig. 2-3B). $1VT_{3,4}$ renewal was short-lived and $1VT_{3,4}$ increasingly transitioned to 1ST in early summer. However, by late summer, $3VT_{3,4}$ production increased and helped to minimize losses in overall $VT_{3,4}$ density due to $1VT_{3,4}$ senescence and $VT_{3,4}$ transition to FT (Figs. 2-2D, 3B). 1ST density was significantly greater than 2ST density throughout the study (contrast, $t_{149} = 9.17$, $p < 0.0001$; Fig. 2-3D). Of all live vegetative tillers, $11.8 \pm 1.3$ % flowered and $97.6 \pm 1.2$% of flowering tillers were from $1VT_{3,4}$. When FT were recruited, the majority of $2VT_3$ transitioned to $2VT_4$ (Fig. 2-4B). Therefore, as $1VT_{3,4}$ density decreased in the fall, an increasing proportion of $VT_{3,4}$ were $2VT_{3,4}$ (Fig. 2-4B). $1VT_{3,4}$ tillers had a significantly greater density in fall 2010 than $2VT_{3,4}$ (contrast, $F_{1, 160} = 14.53$, $p = 0.0002$) but $2VT_{3,4}$ had a significantly greater density in fall 2011 than $1VT_{3,4}$ (contrast, $F_{1, 160} = 16.30$, $p < 0.0001$; Fig. 2-3B). Genets were not meristem limited because bud and juvenile tiller density was always higher than live tiller ($VT_{3,4}$; FT) density (Fig. 2-2BD).

The per-tiller production of buds and juvenile tillers was impacted by differences in tiller generation and size. Throughout the study, a $VT_{3,4}$ maintained between 1 and 4.7 buds and juvenile tillers (average: $2.85 \pm 0.09$ buds and juvenile tillers per $VT_{3,4}$) while a $VT_2$ maintained between zero and two buds and juvenile tillers (average: $0.61 \pm 0.05$ buds and juvenile tillers per $VT_2$). A $VT_{3,4}$ had a greater number of buds and juvenile tillers in late summer and fall because the majority of $2VT_3$ and $3VT_3$ added buds as they transitioned to $VT_4$ and $1VT_4$ continued to add buds in the cooler late fall (Appendix Fig. 2-3DEF). In general, $1VT_{3,4}$ had significantly more buds and juvenile tillers than $2VT_{3,4}$ (contrast, $F_{1, 305} = 86.5$, $p<0.001$) and $2VT_{3,4}$ had significantly more buds and juvenile tillers than $3VT_{3,4}$ (contrast, $F_{1, 334} = 65.5$, $p<0.0001$; Appendix Fig. 2-3DEF).

Within a genet, $VT_2$ and $VT_{3,4}$ were the main sources of potential tiller recruits ($B_{1,2}$; $VT_{1,2}$; Fig. 2-6B). However, ST maintained a large portion of the overwintering genet supply of buds and juvenile tillers. ST density increased over the winter but buds and juvenile tillers on ST

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did not immediately senesce with their parent tiller (Fig. 2-6B). Instead, buds and juvenile tillers on ST were maintained over the winter because the apical meristem of the parent tiller had not fully senesced as evidenced by the 1ST renewal (see above). In the spring after the 1ST brief renewal was finished, buds and juvenile tillers on ST rapidly decreased due to senescence and $VT_{1,2}$ transitioning to $VT_{3,4}$ (Fig. 2-5F, Appendix Fig. 2-4B). Residual tillers had few to no buds and juvenile tillers throughout the study (average: $0.033 \pm 0.010$ buds and juvenile tillers per RT). Flowering tillers contributed low amounts to the bud and juvenile tiller supply. FT from 2010 maintained considerably fewer buds and juvenile tillers following spring 2011 flowering (before July: $1.24 \pm 0.15$ buds and juvenile tillers per 2010 FT; after August: $0.26 \pm 0.08$ buds and juvenile tillers per 2010 FT; Appendix Fig. 2-6). 2011 FT maintained their supply of buds and juvenile tillers following flowering, which stops bud production, indicating that few to none of these buds and juvenile tillers died or transitioned to $VT_{3,4}$ (Fig. 2-5E).

The developmental composition of a genet's supply of buds and juvenile tillers reflected the developmental composition and production of buds and juvenile tillers on $VT_{3,4}$ throughout the year and on ST over the winter. All bud and juvenile tiller developmental stages occurred throughout the annual cycle of *N. viridula* and occurred on FT, ST, and $VT_{3,4}$ of every generation ( Figs. 2-5EF, 7B, Appendix Fig. 2-3DEF). Approximately half of a genet's supply of buds and juvenile tillers was comprised of small buds throughout the year (study average: $57.7 \pm 1.3\%$; Fig. 7B). Large buds, $VT_1$, and especially $VT_2$ made up smaller but notable portions of the bud and juvenile tiller supply.

At any time during the annual cycle, the majority of $VT_2$ occurred on the most abundant ST or $VT_{3,4}$ generation at that time (Fig. 2-3BD, Appendix Figs. 2-7,8). $VT_2$ were maintained primarily on ST during the winter and $VT_4$ during the growing season (Appendix Fig. 2-7A). Increases in the numbers of $VT_2$ on secondary and tertiary vegetative tillers ($2VT_{3,4}$ and $3VT_{3,4}$) occurred when these tillers transitioned from $VT_3$ to $VT_4$ (Fig. 2-4B, Appendix Fig. 2-7B). $VT_2$ abundance on $VT_{3,4}$ only declined slightly when increased recruitment of $2VT_{3,4}$ and $3VT_{3,4}$ from $VT_2$ occurred in the spring (Figs. 2-3B,5D, Appendix Fig. 2-A3DEF).

## *Comparison of* H. comata *and* N. viridula

### *Characteristics of the bud and juvenile tiller supply*

$\quad$ *Nassella viridula* produced a greater number of buds per tiller than *H. comata* on most tillers, including $VT_{3,4}$, 2011 FT, and ST (Fig. 2-5). Bud production was significantly higher on $1VT_{3,4}$ and $2VT_{3,4}$ of *N. viridula* than comparable tillers of *H. comata* (Appendix Fig. 2-3; contrast, Primary: $F_{1,439} = 148.8$, p<0.0001, Secondary: $F_{1,441} = 43.1$, p<0.001). However, bud production on $3VT_{3,4}$ was not significantly different between species (contrast, Tertiary: $F_{1,484} = 5.10$, p= 0.024 n.s. according to bonferroni). For both species, $1VT_{3,4}$ and $2VT_{3,4}$ increased their number of buds and juvenile tillers at the end of the summer after the majority of $2VT_3$ had transitioned to the larger size class ($VT_4$, Appendix Fig. 2-3). *Nassella viridula* maintained buds and juvenile tillers for longer periods of time after tillers had flowered or senesced and its $VT_2$ supplied more buds and juvenile tillers per genet than $VT_2$ of *H. comata* (Figs. 2-5BCEF, 6).

$\quad$ Within a genet, the majority of buds and juvenile tillers of *H. comata* and *N. viridula* were located on $VT_{3,4}$ throughout the year and were small buds (Figs. 2-6, 7). However, almost half of the overwintering buds and juvenile tillers of *N. viridula* were located on either ST or $VT_2$. *Nassella viridula* also maintained more of its potential tiller supply as $VT_2$ than *H. comata* throughout the year. The bud and juvenile tiller supply of both species is dependent on live or recently senesced tillers as only low amounts of buds and juvenile tillers were located for an extended period of time on ST, FT, and RT (Fig. 2-6).

### *Tiller population characteristics*

$\quad$ The entire life cycle of both species beginning with a small bud and ending with a flowering or senesced tiller spans three years (Fig. 2-8). Recruitment of a new cohort of juvenile tillers begins in July and increases in late fall. Juvenile tillers are especially recruited from buds on the tiller generation that has just transitioned the majority of its tillers from the small ($VT_3$) to large ($VT_4$) size class. Overwintered juvenile tillers transition into $VT_3$ as part of a new vegetative tiller generation beginning in March and mostly finishing by the onset of winter. Therefore, the majority of a generation's vegetative tillers spend one year in the small ($VT_3$) size class. In June, these $VT_3$ transition into $VT_4$. One year later, approximately 10% of these tillers will flower. Those that do not flower either senesce or live for another year. In summary, tillers ($VT_{3,4}$) of both *H. comata* and *N. viridula* can live at least 26 months because an average $VT_3$

would be recruited from a $VT_2$ in March, transition to a $VT_4$ sixteen months later in July, and flower or senesce the following spring (Fig. 2-8, cohort A).

Although the transition of $2VT_3$ to $2VT_4$ in both species was mostly synchronous at the time of flowering (Fig. 2-4), low but consistent amounts of $VT_3$ recruitment to $VT_4$ occurred before May 2011 for secondary tillers and after May 2011 for tertiary tillers. This early transition to large vegetative tiller of $2VT_3$ and $3VT_3$ may be a result of the high precipitation in 2010 and 2011. The presence of juvenile tillers on all tiller generations indicates that tiller ($VT_{3,4}$) recruitment can happen into any generation at any time. However, tiller longevity greater than 22 months offers an alternative explanation for the low perpetual amounts of $2VT_4$ (Fig. 2-8, cohort A arrow extending into growing season 5). At the end of the study, all $1VT_{3,4}$ of either species had not entirely senesced (Fig. 2-3AB). In spring 2011, a two-year-old $1VT_4$ could maintain a one-year old $2VT_4$.

Due to the lack of complete synchrony in tiller transitions, it can only be generally stated in this study that $1VT_{3,4}$ originated in 2009, $2VT_{3,4}$ originated in 2010 and $3VT_{3,4}$ originated in 2011. Correspondingly, buds can be aged according to the tiller generation that produced them. Therefore, the bud and juvenile tiller supply of each species was composed of multiple annual cohorts (Fig. 2-6).

## Discussion

### *Tiller population comparison of* H. comata *and* N. viridula

*Hesperostipa comata* and *N. viridula* had similar tiller population dynamics and phenology (Fig. 2-8). Both overwintered juvenile and vegetative tillers ($VT_{1-4}$) and maintained multiple generations of annual tillers throughout an annual cycle (i.e. polycyclic tillers). The live tiller populations of the genets experienced consistent patterns of turnover as the primary (oldest) tiller density decreased, the secondary tiller density remained stable, and the tertiary (youngest) tiller density increased in both species over the course of the study. Both species also invested a similar proportion of their tillers to sexual reproduction. Although the hollow crowns found in a large portion of *N. viridula* genets enabled *H. comata* to maintain a greater tiller density than *N. viridula*, *N. viridula* genets had more tillers than *H. comata* due to their larger basal areas.

***Bud and new tiller recruit comparison of* H. comata *and* N. viridula**

*Nassella viridula* consistently produced more buds per tiller than *H. comata* at each stage of tiller development (vegetative, flowering, and senescence) and on primary and secondary tiller generations.  In particular, *N. viridula* maintained a greater number of buds than *H. comata* on senesced tillers over the winter and on both current and older flowering tillers.  Bud development in both species could begin on juvenile tillers and occurred when tillers increased in size, especially when juvenile tillers transitioned to $VT_1$ and when $VT_3$ transitioned to $VT_4$.  Within each species, older tiller generations showed greater bud production.

The buds of all types of *N. viridula* tillers (i.e. defined by flowering status, photosynthesizing status, and generation) had a greater rate of transition beyond the small bud stage than comparable *H. comata* tillers.   Most tiller types of *N. viridula*, except for tertiary vegetative tillers and senesced tillers during the growing season, had similar proportions of potential tiller recruits developed beyond the small bud stage.  However, older generations of *H. comata* vegetative tillers tended to have greater numbers of potential tiller recruits transitioned to more developed stages than younger generations.

Bud longevity was dependent on the aboveground longevity of its parent tiller.  Bud mortality was rarely seen on live tillers.  Therefore, buds of these two species can live for 2 or more years.  As tillers senesced or flowered, buds usually senesced with them.  However, *N. viridula* overwintered buds on senesced tillers and maintained buds for an additional year after its parent tiller flowered.  As a result, some buds of *N. viridula* may have greater longevity than *H. comata* buds.

Neither *H. comata* nor *N. viridula* genets were meristem limited (as defined in Dalgleish and Hartnett 2006).  Both species maintained stable supplies of potential tiller recruits throughout the year in the form of mixed-aged bud and juvenile tiller banks originating from multiple annual bud cohorts.  The consistent production of at least one bud by most tillers prevented genet meristem limitation.  *Hesperostipa comata* did have higher bud densities than *N. viridula* in 2010 and similar bud densities to *N. viridula* in 2011.  However, due to its larger basal area and higher juvenile tiller density throughout the study, *N. viridula* genets always had higher numbers of potential tiller recruits ($B_{1,2;}$ $VT_{1,2}$) than *H. comata*.  Due to their greater number of buds and higher proportion of buds transitioned to the juvenile tiller stage, genets of *N. viridula* would be more apt than genets of *H. comata* to quickly recover from localized small-

scale disturbances and natural fragmentation that occurs in larger genets as they age (Briske and Derner 1998; Dalgleish et al. 2011). However, selective foraging on the palatable *N. viridula* could explain its decline under intense grazing despite its large bud bank (Teague and Dowhower 2001).

### *Tiller contribution to the bud bank and new tiller recruits*

Different tiller types contributed unequally to the genet's supply of potential tiller recruits primarily because of differences in tiller population size fluctuations and bud longevity among tiller types rather than differences in the number of buds produced per tiller type. Tiller classes $VT_{2-4}$ were the main sources of potential tiller recruits. However, the pool of potential tiller recruits from $VT_{3,4}$ was undergoing dynamic changes. Potential tiller recruits were lost from the oldest tiller generation ($1VT_{3,4}$) as it declined but were added from the youngest tiller generation ($3VT_{3,4}$) as its population and tiller size increased. A constant refreshing of the potential tiller recruits benefits the tiller recruitment capacity of the genet as most tillers are recruited from the youngest buds belonging to the most recently produced annual bud cohort (Hendrikson and Briske 1997; Ott and Hartnett 2012a). Although flowering tillers contributed little to the overall supply of potential tiller recruits, the longevity of *N. viridula* buds following parent tiller senescence was 6 months greater in flowering tillers than their vegetative tiller counterparts. Buds on flowering tillers are usually larger and may be better provisioned than buds on vegetative tillers (Ott and Hartnett 2011). Any additional enhancement to bud longevity and therefore bud dormancy of a select subset of buds would be beneficial to genet persistence, especially following disturbance (e.g. Nilsson et al. 1996) or in ecosystems with large interannual climatic variability where bud banks can act to buffer population responses (Ott and Hartnett 2012a).

### *Sexual and vegetative reproduction life history characteristics*

*Hesperostipa comata* and *N. viridula* genets had similar flowering effort but *N. viridula* genets had more consistent annual tiller recruitment from a more developed and larger supply of potential tiller recruits than *H. comata* genets. At the end of the 2011 growing season, the consistent annual tiller recruitment of *N. viridula* was evident. Although $3VT_{3,4}$ densities of each species were similar, *N. viridula* had produced approximately 2x the number of $3VT_{3,4}$ per $2VT_{3,4}$ than *H. comata*. A previous comparison of two $C_3$ caespitose *Agropyron* grass species

with different grazing tolerances emphasized the importance of bud activation (i.e. B to $VT_1$ and thus the ability to break dormancy) over bud availability in order to have a successful tillering response following grazing events (Caldwell et al. 1981; Mueller and Richards 1986). Even in recently ungrazed situations (i.e. 1 year post-clipping), both *Agropyron* species displayed high bud activation tendencies as daughter tillers arose on live tillers, especially for the grazing-tolerant grass, in the spring six months before their typical fall recruitment period (Mueller and Richards 1986).

Although the supply of potential tiller recruits and the tiller production of *N. viridula* indicated a greater capacity for vegetative reproduction, *H. comata* displayed greater fluctuations in tillering responses to interannual precipitation variability than *N. viridula*. *Hesperostipa comata* may be very sensitive to precipitation and may be well-suited to capitalize on periods of high resource availability. Precipitation conditions following fire determined the effect of fire on the biomass of *H. comata* (Vermeire et al. 2011). In the current study, *H. comata* recruited a large (i.e. above average) tiller generation in 2010 when annual precipitation was high. Although rainfall was plentiful in 2011, less rain fell in the spring months in 2011 than in 2010 preventing another large recruitment event of the next tiller generation.

Light availability may also play a role in tillering responses of *H. comata* and *N. viridula* to precipitation. The smaller basal area of *H. comata* individuals would allow for greater light availability and therefore reduced effects of self-shading within genets (Caldwell et al. 1983; Ryel et al. 1994). In addition, R:FR light ratios would be more favorable for tillering in smaller bunchgrasses (Deregibus et al. 1983; Tomlinson and O'Connor 2004). Lowered light availability could be regulating tillering responses to precipitation in established large *N. viridula* tussocks with their large and well-developed supply of potential tiller recruits. However, *H. comata* would have no such light limitations and would therefore be able to respond to periods of high resource availability, such as high precipitation years, with increased tillering.

### *Basal area differences between* H. comata *and* N. viridula

*Nassella viridula* genets, with their larger basal areas, are either longer-lived or have a faster rate of tiller population growth and basal area expansion than *H. comata* genets. *Nassella viridula* could have a greater genet longevity than *H. comata* because of its higher bud production per tiller, larger supply of potential tiller recruits, and greater bud longevity of buds

on senesced and flowering tillers.  Hollow crown development, as seen in *N. viridula*, often occurs in older genets (Gatsuk et al. 1980).  The tiller recruitment sensitivity of *H. comata* to annual environmental conditions could reduce the longevity of its genets under heavily fluctuating or poor environmental conditions.   Therefore, the consistent annual tiller recruitment of *N. viridula* would also favor a greater genet persistence and longevity than *H. comata.* Generational tiller cycling rates were not faster in *N. viridula* as would be expected if it had a faster rate of basal area expansion.   Therefore, based on the characteristics of tillers and potential tiller recruits observed in this study, *N. viridula* genets appear to have greater longevity than *H. comata* genets.

## Comparison with other C$_3$ grasses

*Hesperostipa comata* and *N. viridula* usually produced two to three buds per tiller.  Bud production per adult tiller of *H. comata* and *N. viridula* was similar to the lower range of bud production of other dominant and sub-dominant C$_3$ caespitose grasses (Mueller and Richards 1986; Dalgleish et al. 2008; Pelaez et al. 2009; Ott and Hartnett 2012a) and was very similar to the dominant C$_3$ caespitose *Nassella tenuis* in Argentina (Busso et al. 1993).

In comparison with the genet bud bank and tiller characteristics of another C$_3$ caespitose grass *Dichanthelium oligosanthes* in tallgrass prairie (Ott and Hartnett 2012a), *H. comata* and *N. viridula* maintained a similar aboveground cool-season growth phenology, oftentimes overwintering tillers in addition to buds.  All three species maintained a supply of potential tiller recruits in multiple stages of development throughout the annual cycle.  However, the supply of potential tiller recruits of *H. comata* and *N. viridula* was comprised of multiple annual generations while *D. oligosanthes* only maintained a single generation.  *Andropogon gerardii*, a C$_4$ tallgrass prairie perennial grass, maintains multiple generations of buds (Ott and Hartnett 2012a).  However, unlike *H. comata* and *N. viridula*, *A. gerardii* has annual tillers.

## Role of polycyclicity in bud bank formation and maintenance in caespitose grasses

In grassland systems where tillers survive for more than one year, polycyclic tillers could enhance the stability and persistence of perennial grasses.  Because multiple annual generations of tillers are alive during the same growing season, genet growth should be buffered against interannual variability in growing conditions as years of low tiller recruitment could be ameliorate by years of high tiller recruitment.  Resource storage in older tiller generations

provide an important source of reserves for younger tiller generations (Jonsdottir and Callaghan 1988). However, populations of polycyclic species would not retain any buffering capacity in successive years of unfavorable growing conditions characterized by low tiller recruitment. A species may demonstrate plasticity in its polycyclicity (e.g. Serebrakov 1952 in Soukupova 1988). Some populations in grasslands with annual fire, intense grazing, or a harsh dry season may have monocyclic tillers while other populations in grasslands with a lower frequency of disturbance may have polycyclic tillers.

Maintaining a population of polycyclic tillers does not mean tiller development (vegetative, flowering, senescence) will correspond with tiller age (i.e. all younger adult tillers are vegetative, all older adult tillers are flowering or senesced). If it did, the loss of older tiller generations to grazing, drought, fire, and other disturbances would destabilize plant populations. Shoot size, not shoot age, is a better predictor of shoot fate in grasses once shoots are >1 year old (Hara and Herben 1997). Similar to a field study in Montana, vegetative tillers of both species were at least two years old before flowering (White 1977). Even though the oldest tiller cohorts of *H. comata* and *N. viridula* produced almost all of the flowering tillers in this study, flowering is usually more dependent on tillers reaching a minimum size threshold rather than age threshold (Langer 1972; Ott and Hartnett 2011). Instead, polycyclic tillers are take more time than monocyclic tillers to reach an appropriate size to flower, and thus, might actually increase flowering capabilities of slow growing perennial grasses.

Polycyclic tillers can create mixed-age bud banks composed of multiple annual bud cohorts, each formed under different conditions, which could uniquely impact a bud cohort's survival and/or degree of dormancy. Diversifying the buds in the bud bank and having younger bud cohorts already produced as older bud cohorts die could also buffer tiller population dynamics. However, polycyclic tillers could destabilize the long-term persistence of perennial grass populations through lag effects. Impacts of precipitation or resource inputs on the current year's bud formation or tiller recruitment might not be evident until one or two years later when that cohort would become adult tillers. For example, tiller polycyclicity could explain why demographic responses of *H. comata* lagged climate by at least one year (Dalgleish et al. 2011).

### *Summary of species' differences and further studies*

Because of its larger genet size (basal area and number of tillers), *N. viridula* maintained a larger supply of potential tiller recruits than *H. comata*. In general, *N. viridula* also had longer-lived buds and a larger proportion of potential tiller recruits in juvenile tiller stages than *H. comata*. Together, these characteristics indicate that *N. viridula* has a greater capacity for vegetative reproduction (i.e. tiller population growth) and greater genet longevity than *H. comata*. As knowledge of bud banks and juvenile tiller supplies is accumulated for more species, general models of tiller population growth and dynamics could be developed for different photosynthetic guilds ($C_3$ vs $C_4$) and growth forms (caespitose vs rhizomatous). Also, classification of bud banks similar to seed banks could be developed to further compare these two modes of tiller reproduction (Ott and Hartnett 2012a).

The demography of *H. comata* appears to be more sensitive than that of *N. viridula* to inter-annual precipitation variability. *Nassella viridula* showed a more constant annual tiller recruitment than *H. comata*. Studies manipulating intra- and inter-annual precipitation variability or resource availability timing during the year would further evaluate the degree and source of the tiller demography sensitivity of *H. comata*. In a changing climate, the sensitivity of forage grasses to climate alterations needs to be understood to effectively manage rangeland.

### *Conclusion*

Maintenance of a dense belowground bud bank is a major demographic mechanism conferring ecological success to the caespitose growth form enabling it to use the local resources it effectively monopolizes. Caespitose grasses sometimes invest in higher-order bud production to achieve a dense belowground bud bank (Ott and Hartnett 2012b). Although the size of a genet's bud bank may remain relatively stable, the bud bank is dynamic, undergoing continuous inputs and outputs closely tied with the tiller dynamics of the genet. Genet longevity is dependent on the consistent recruitment of tillers, production of buds, and maintenance of a bud bank.

Polycyclic tillers likely assist in stabilizing populations of perennial grasses. Shoot cyclicity has been recently included as a trait in a clonal growth database (Klimesova and Klimes 2008). Polycyclicity is mentioned in both European and North American grasses but receives little attention (White 1977, Jonsdottir 1991, Zhang and Romo 1995, Janisova 2006). More

research on polycyclic tillers is needed to enhance our understanding of how this trait contributes to clonal growth and impacts population dynamics.

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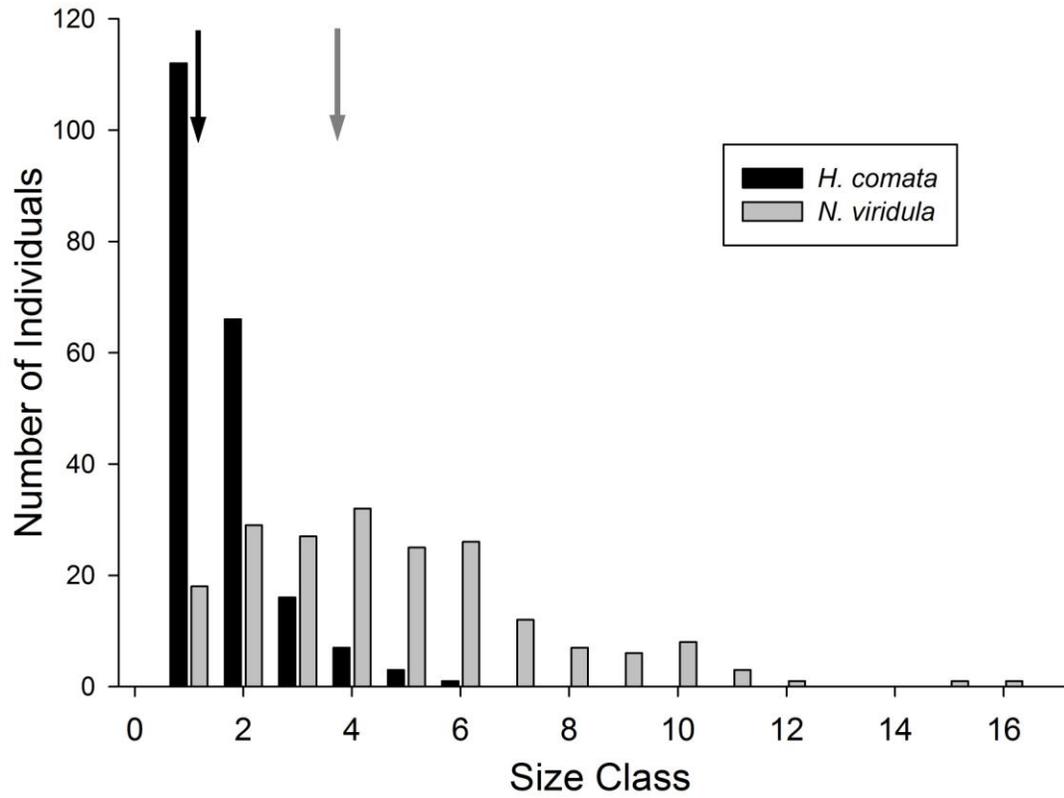
**Figure 2-1  Size structure of *H. comata* and *N. viridula* at Wind Cave NP in June 2010.** Size classes based on basal area increased by 50cm$^2$ increments.  Arrows indicate the median basal area of each species.
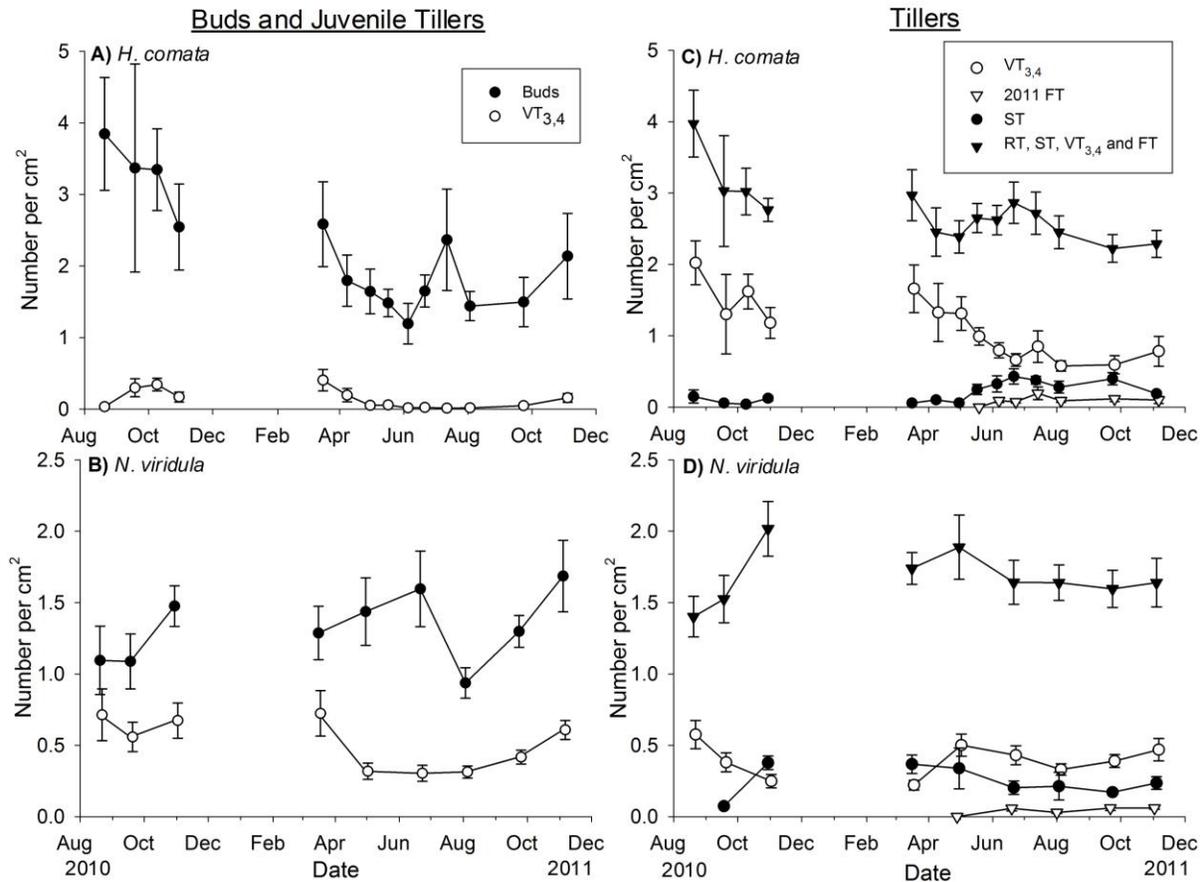
**Figure 2-2. A,B) Buds and juvenile tillers and C,D) adult tillers per cm² genet basal area of H. comata and N. viridula.** AB) Buds had a greater density than juvenile tillers for both species. CD) Live vegetative tillers (VT$_{3,4}$) usually had the greatest density of any type of adult tiller except in the case of *N. viridula* over the winter. Potential tiller recruits (i.e. buds and juvenile tillers) had a greater density than live tillers (VT$_{3,4}$ and 2011 FT) throughout the study. Main and interaction effects of date and species for many of these variables are available in Table 2-1. Note that the y-axis scale differs between species. Error bars are ± 1 s.e.
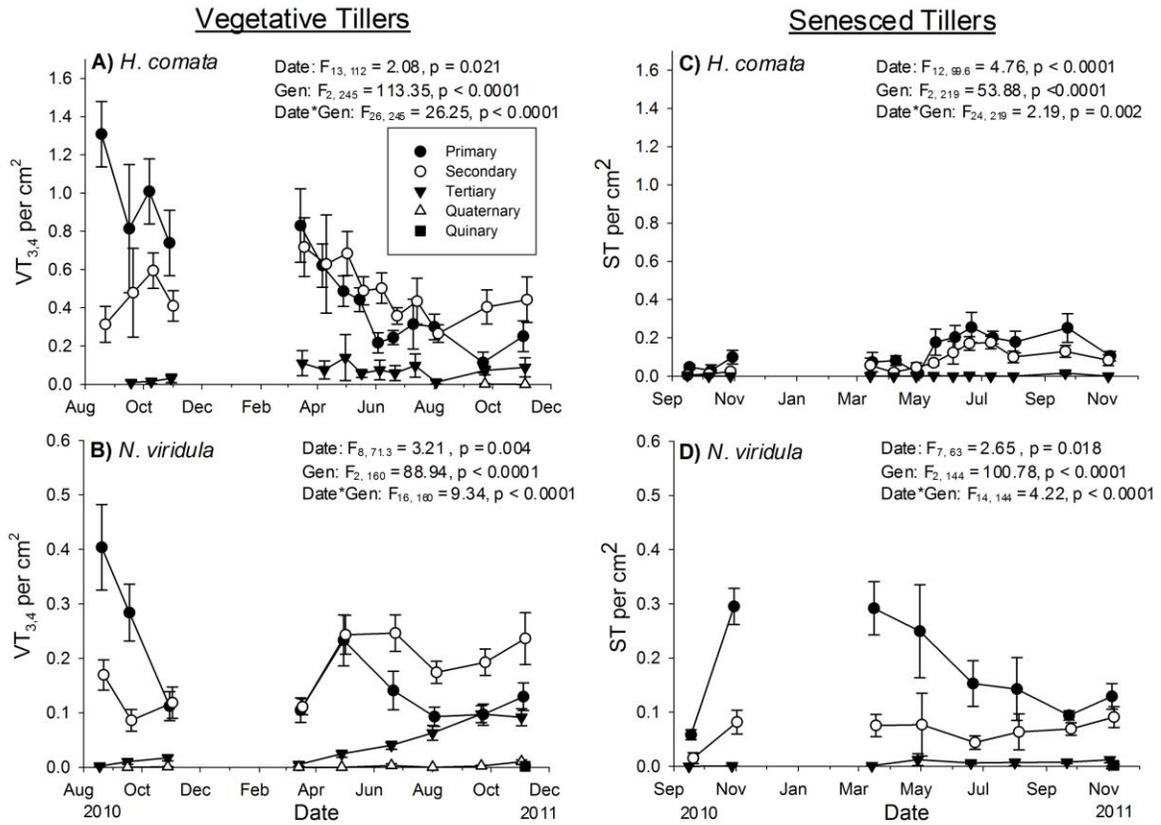
**Figure 2-3. A,B) Live (VT$_{3,4}$) and C,D) senesced (ST) tiller density according to tiller generation of *H. comata* and *N. viridula*.** In general, 1VT$_{3,4}$ declined throughout the study, 2VT$_{3,4}$ remained stable, and 3VT$_{3,4}$ increased. ST was greater in older generations. Note that quaternary and quinary tillers were not included in the statistical analyses. Y-axis scales are unique to each species. Error bars are $\pm$ 1 s.e.
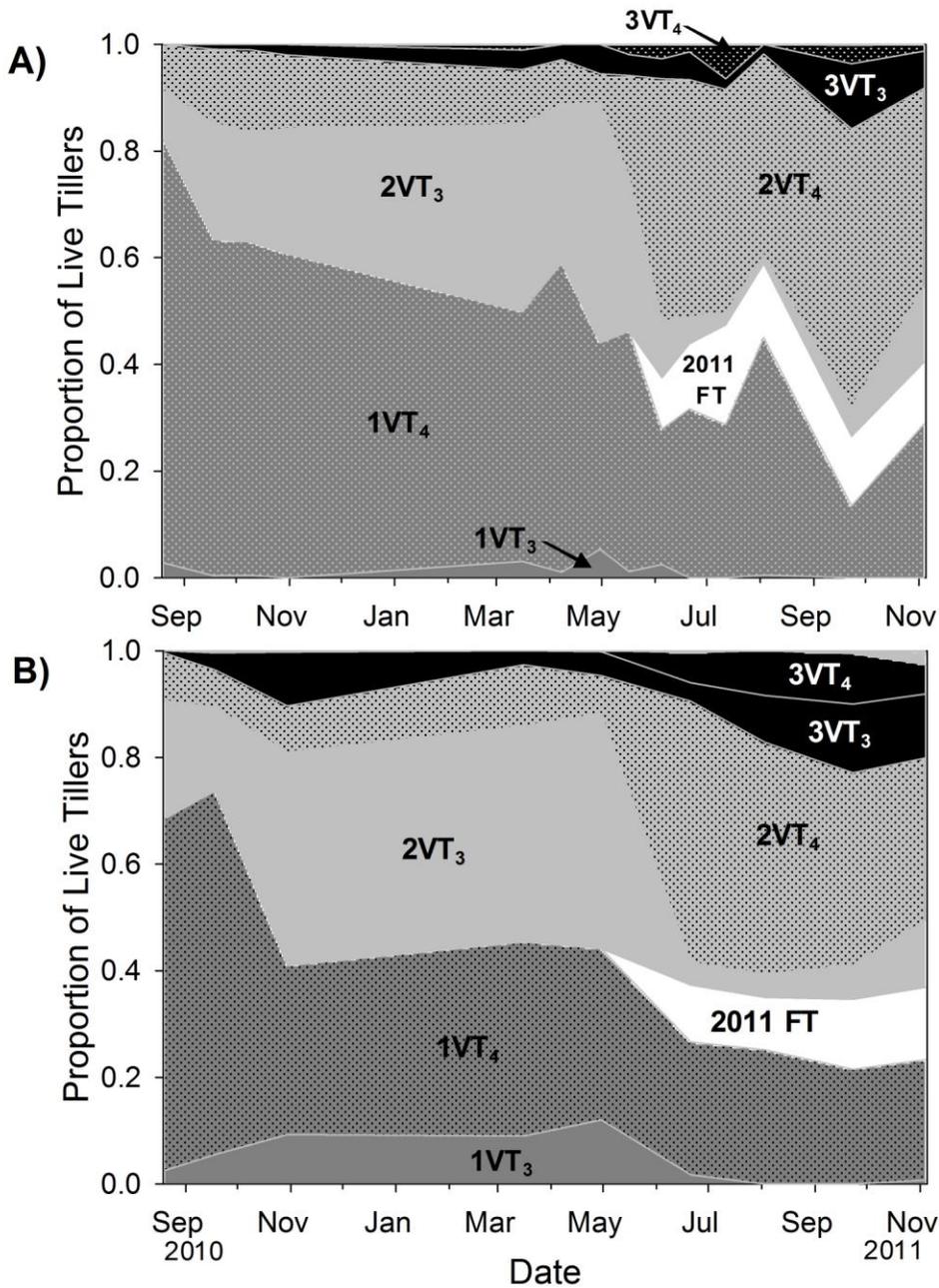
**Figure 2-4. Proportion of live tillers according to size, generation, and flowering status.** A) *H. comata* B) *N. viridula*  The small unlabeled gray area above the $3VT_4$ in each figure corresponds to quaternary tillers ($4VT_{3,4}$) of *H. comata* and quaternary and quinary ($5VT_{3,4}$) tillers of *N. viridula*.
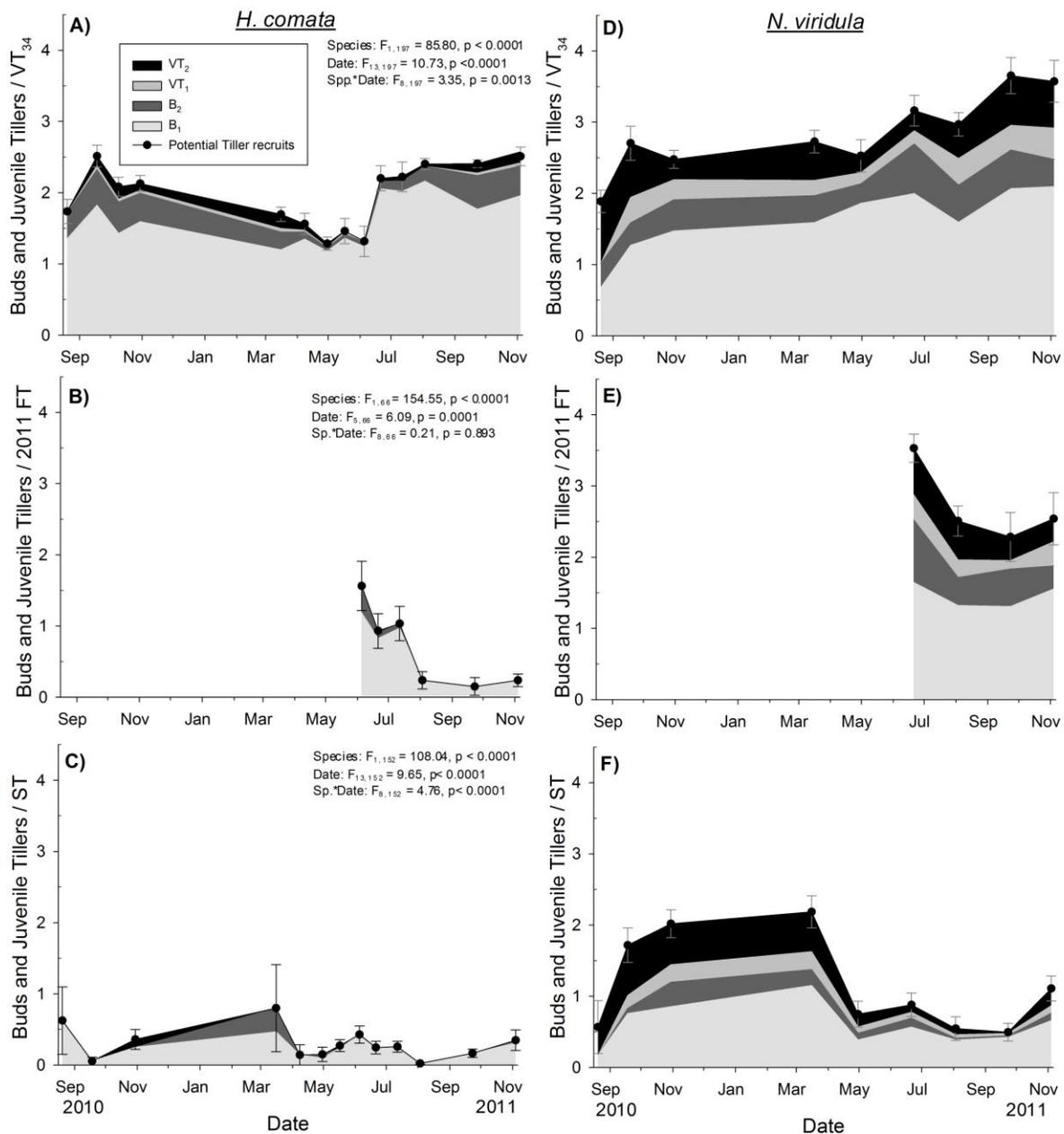
**Figure 2-5. Production of potential tiller recruits of *H. comata* and *N. viridula* on vegetative, flowering, and senesced tillers.** Potential tiller recruits (i.e. buds and juvenile tillers) per tiller were analyzed for each of these tiller classifications in three separate analyses (Table 2-1). *Nassella viridula* maintained more potential tiller recruits than *H. comata* on all these tiller types.

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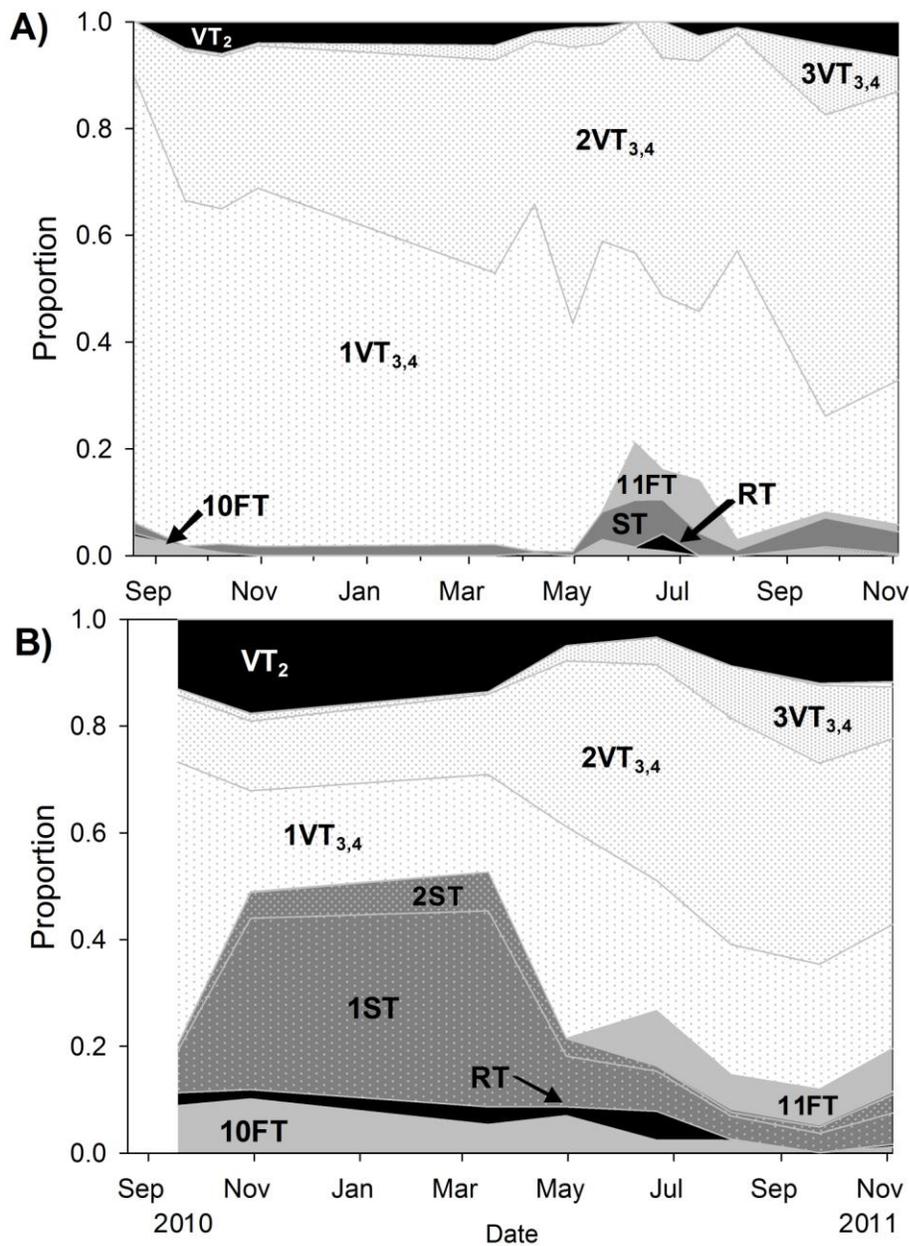
**Figure 2-6. Proportion of entire genet potential tiller recruits according to their tiller sources A) *H. comata* B) *N. viridula*.** Potential tiller recruits could be supported by multiple generations of vegetative ($VT_{2-4}$), flowering (10FT- 2010 flowering tillers and 11FT- 2011 flowering tillers), senesced (ST), and residual (RT) tillers. Generations are indicated with numerals. Note that the small solid white area between $3VT_{3,4}$ and $VT_2$ represents the portion of potential tiller recruits from $4VT_{3,4}$ and $5VT_{3,4}$ and the small solid gray area above 2ST in fall 2011 of *N. viridula* represents 3ST and 5ST.

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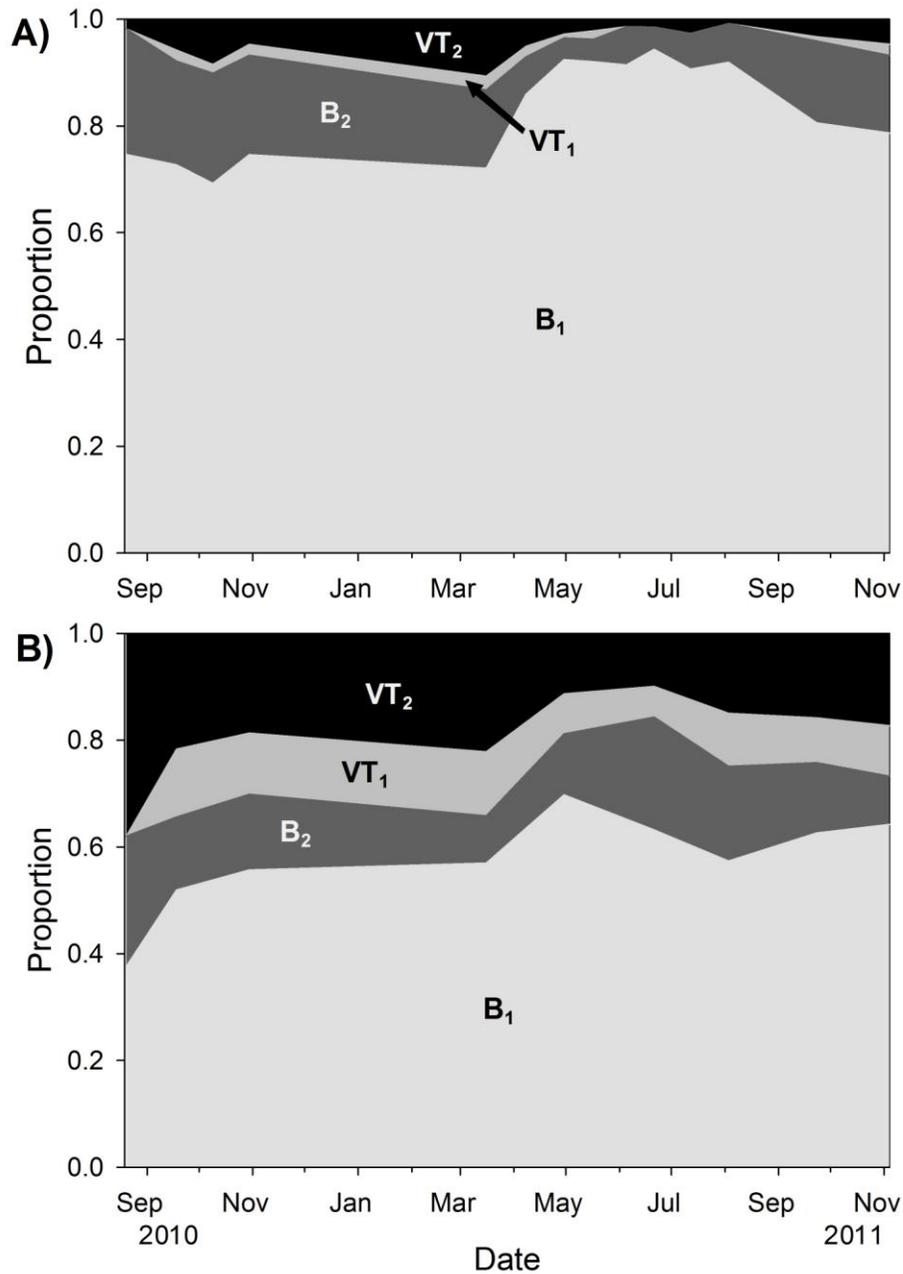
**Figure 2-7. Proportion of entire genet potential tiller recruits according to developmental stage. A)** *H. comata* **B)** *N. viridula*. Buds could be classified as small ($B_1$) or large ($B_2$) and juvenile tillers could be classified as small ($VT_1$) or large ($VT_2$). *Nassella viridula* maintained more potential tiller recruits in higher developmental stages than *H. comata*. Note that $VT_1$ were classified as $VT_2$ for the August 20, 2010 sampling date.
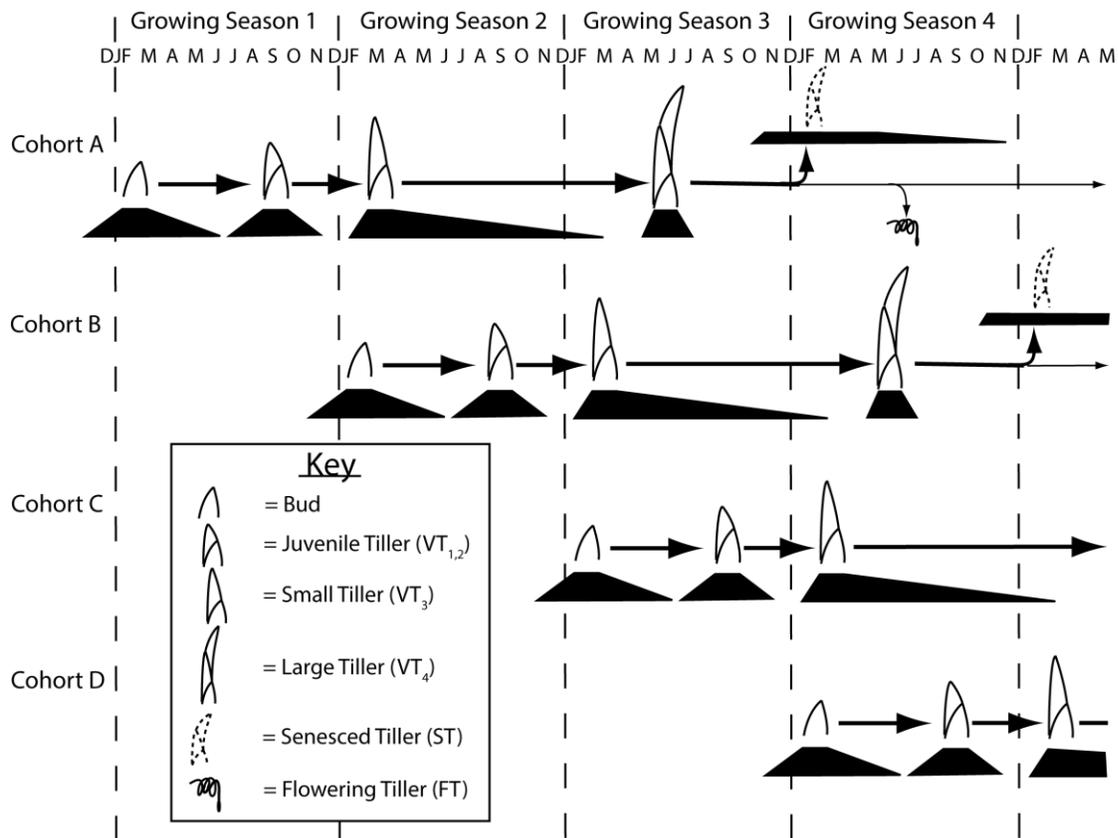
**Figure 2-8. Generalized diagram of the life cycles of a tiller for the C₃ caespitose grasses *H. comata* and *N. viridula*.** Months are indicated by their first letter below the growing season. The stage symbol was placed below the month where approximately 50% of the cohort had transitioned to that stage. The black trapezoids beneath each symbol indicate the span of time when bud natality or the specific transition leading to that stage began and ended. During a single growing season (e.g. growing season 4), four different cohorts can be active. Although the majority of tillers follow the general pattern of Cohort A when ungrazed and unburned, there appeared to be exceptions in which tillers transitioned to stages at alternative times. The bud was assumed to have been borne on a juvenile tiller or a small tiller (VT₃) of the previous cohort (e.g. cohort B's bud was produced by the cohort A's small tiller).

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**Table 2-1. Developmental stage classifications and symbols**

| Symbol | Developmental Stage | Description |
|--------|---------------------|-------------|
| $B_1$ | Small buds | < 3.0 mm height |
| $B_2$ | Large buds | ≥ 3.0 mm height |
| $VT_1$ | Small juvenile tillers | Apex elongated < 3.0 mm past prophyll |
| $VT_2$ | Large juvenile tillers | Elongated 3.0 mm – 4.0 cm past prophyll (*H. comata*) <br> Elongated 3.0 mm – 5.0 cm past prophyll (*N. viridula*) |
| $VT_3$ | Small vegetative tillers | 4.0 – 15.0 cm height (*H. comata*) <br> 5.0 – 18.9 cm height (*N. viridula*) |
| $VT_4$ | Large vegetative tillers | > 15.0 cm height (*H. comata*) <br> > 18.9 cm height (*N. viridula*) |
| FT | Flowering tillers | |
| ST | Senesced tillers | Aboveground parts senesced but retaining live residual base with buds |
| RT | Residual tillers | Aboveground parts absent but retaining residual base with buds |

**Table 2-2. ANOVA test results for 8 response variables.** Basal area is denoted as "BA".

Bolded results are significant at α = 0.05. *Was not significant using the balanced model $F_{8, 152}$ = 1.76, p = 0.090

| Response Variable | Species | Date | Species*Date |
|-------------------|---------|------|--------------|
| Buds/BA | **$F_{1, 196} = 18.29$, p < 0.0001** | **$F_{13, 196} = 2.06$, p = 0.018***  | **$F_{8, 196} = 2.18$, p = 0.031** |
| $VT_{1,2}$/BA | **$F_{1, 196} = 83.9$, p < 0.0001** | **$F_{13, 196} = 4.71$, p < 0.0001** | $F_{8, 196} = 1.41$, p = 0.19 |
| $VT_{3,4}$/ BA | **$F_{1, 196} = 52.0$, p < 0.0001** | **$F_{13, 196} = 2.86$, p = 0.0008** | **$F_{8, 196} = 2.67$, p = 0.008** |
| ST/BA | $F_{1, 188} = 1.97$, p = 0.16 | **$F_{13, 188} = 3.04$, p = 0.0004** | **$F_{7, 188} = 5.15$, p < 0.0001** |
| Total $VT_{3,4}$, FT, ST, and RT / BA | **$F_{1,196} = 68.0$, p < 0.0001** | $F_{13, 196} = 1.15$, p = 0.32 | **$F_{8, 196} = 3.16$, p = 0.002** |
| Potential tiller recruits /$VT_{3,4}$ | **$F_{1, 197} = 85.8$, p < 0.0001** | **$F_{13, 197} = 10.7$, p < 0.0001** | **$F_{8, 196} = 3.35$, p = 0.0013** |
| Potential tiller recruits/ST | **$F_{1, 152} = 108$, p < 0.0001** | **$F_{13, 152} = 9.65$, p < 0.0001** | **$F_{8, 152} = 4.76$, p < 0.0001** |
| Potential tiller recruits/2011 FT | **$F_{1, 66} = 155$, p < 0.0001** | **$F_{13, 66} = 6.09$, p = 0.0001** | $F_{3, 66} = 0.21$, p = 0.89 |

**Table 2-3. Flowering tiller density of *H. comata* and *N. viridula*.** Flowering was assessed for the same genets of each species in both 2010 and 2011.  Letters indicate pairwise significant differences.  Error bars ± 1 s.e.

|  | *2010* | *2011* |
|---|---|---|
| *H. comata* | 0.082 ± 0.008[A] | 0.056 ± 0.006[BC] |
| *N. viridula* | 0.042 ± 0.006[B] | 0.025 ± 0.003[C] |
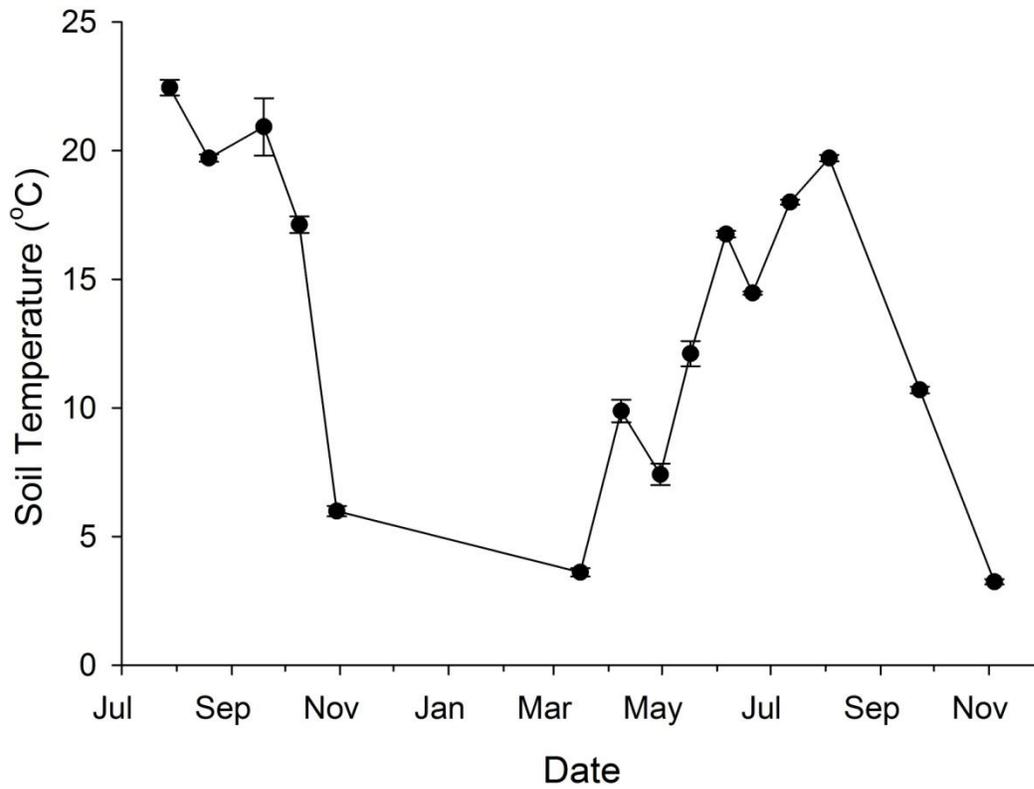
**Appendix Figure 2-1. Soil temperatures taken at 5cm depths at Wind Cave National Park.**
Error bars are ± 1 se.
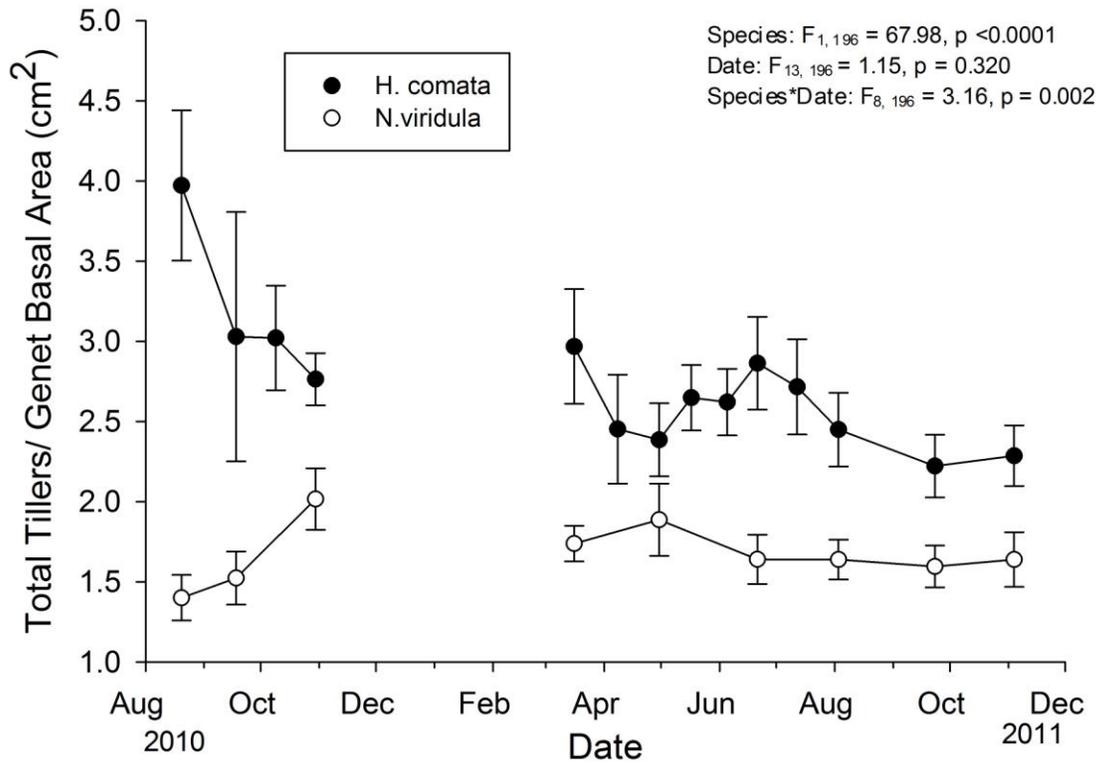
**Appendix Figure 2-2. Number of potential tiller recruits (i.e. buds and juvenile tillers) per genet of *H. comata* and *N. viridula*.** Error bars are ± 1 se.

**H. comata**

A)

Buds and Juvenile Tillers / $1VT_{3,4}$

Legend:
- VT$_2$
- VT$_1$
- B$_2$
- B$_1$
- Potential Tiller Recruits

Spp.: $F_{1, 253} = 140.8$, $p < 0.0001$
Date: $F_{13, 241} = 12.8$, $p < 0.0001$
Gen: $F_{2, 332} = 78.5$, $p < 0.0001$
Spp*Date: $F_{8, 238} = 1.49$, $p = 0.16$
Spp*G: $F_{2, 332} = 22.9$, $p < 0.0001$
Date*G: $F_{24, 220} = 0.99$, $p = 0.48$
Sp*D*G: $F_{13, 338} = 1.51$, $p = 0.11$

B)

Buds and Juvenile Tillers / $2VT_{3,4}$

C)

Buds and Juvenile Tillers / $3VT_{3,4}$

**N. viridula**

D)

Buds and Juvenile Tillers / $1VT_{3,4}$

E)

Buds and Juvenile Tillers / $2VT_{3,4}$

F)

Buds and Juvenile Tillers / $3VT_{3,4}$

Date

2010    2011

**Appendix Figure 2-3. Potential tiller recruits per $VT_{3,4}$ according to species and generation.**
The only significant interaction term was between species and generation indicating that changes
in production of potential tiller recruits (i.e. buds and juvenile tillers) per $VT_{3,4}$ changed across
tiller generation differently for each species. The main effects of species, date, and generation all
significantly affected the potential tiller recruits produced per $VT_{3,4}$. $3VT_{3,4}$ did not have any
potential tiller recruits that were large juvenile tillers ($VT_2$). Error bars are ± 1 se.
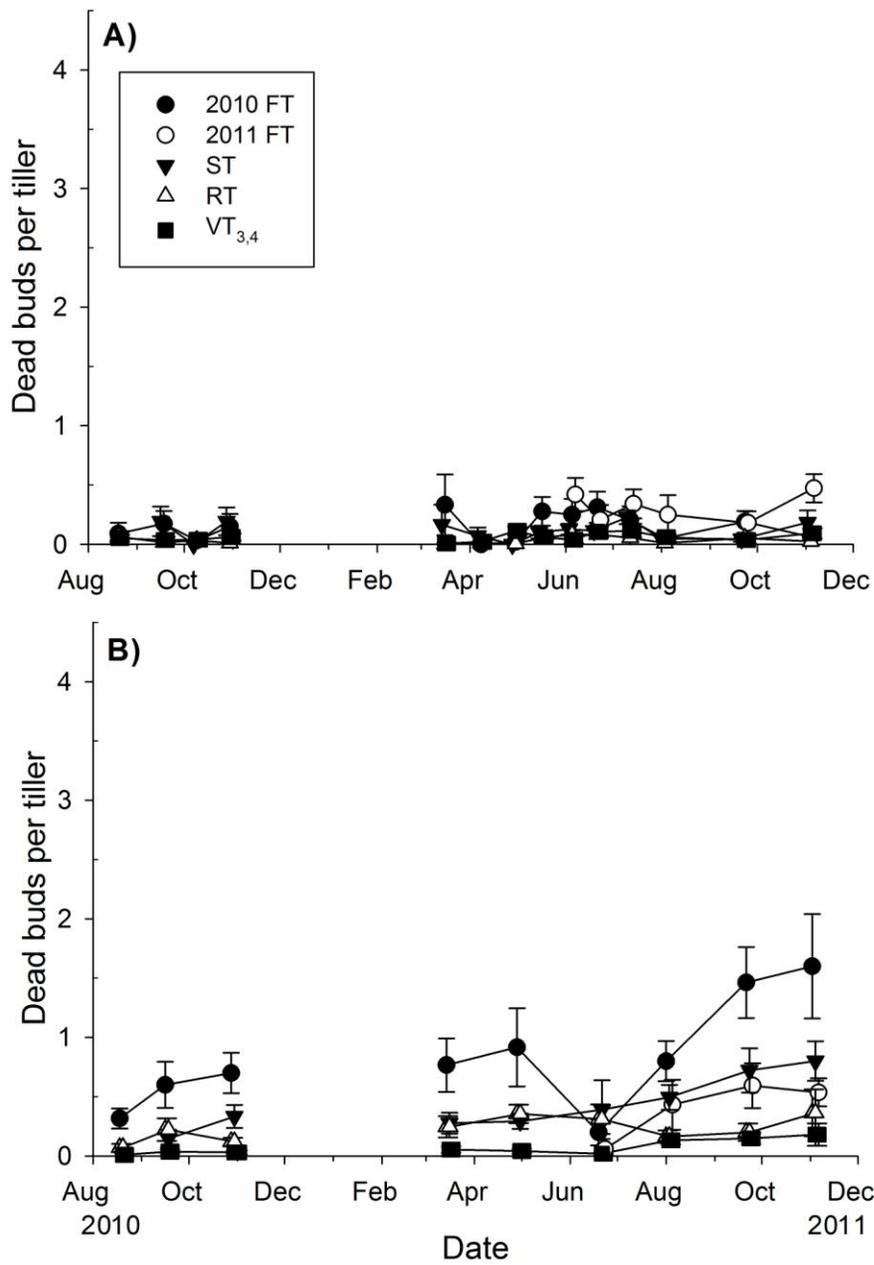
**Appendix Figure 2-4. Dead buds per tiller of A)** *H. comata* **and B)** *N. viridula*. Intact dead buds were counted but bud scars were not counted. Error bars are ± 1 se.
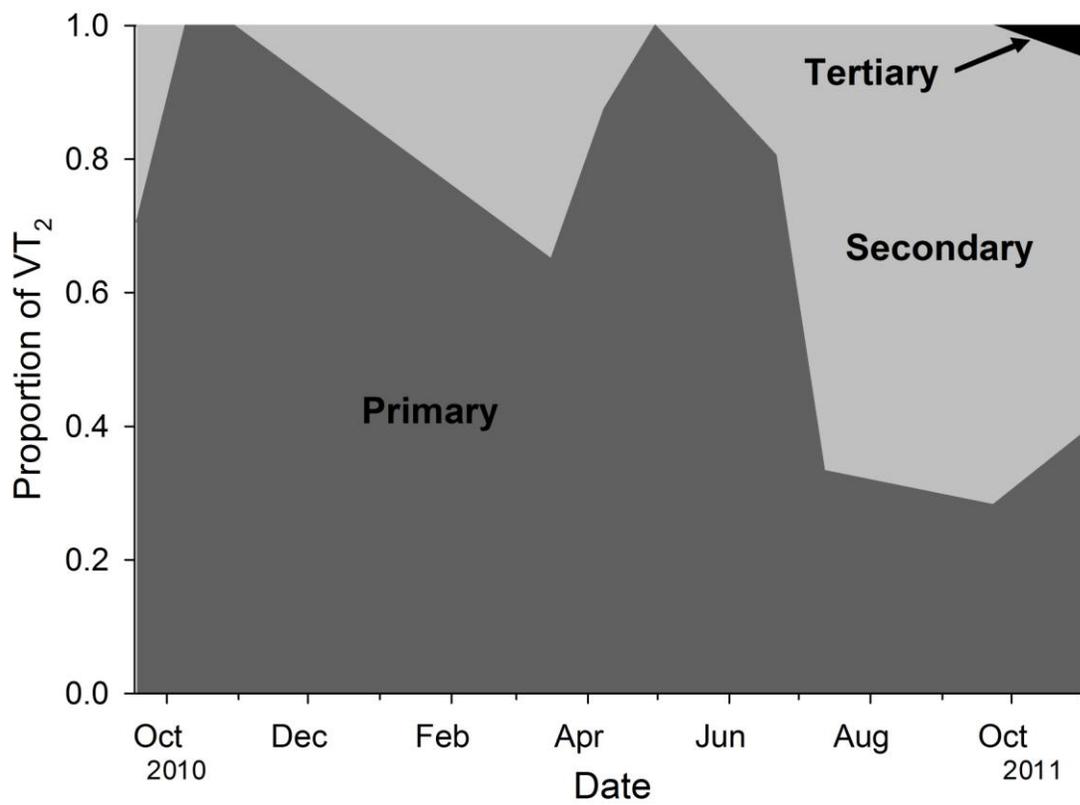
**Appendix Figure 2-5. Proportion of *H. comata* large juvenile tillers (VT$_2$) originating on different generations of live vegetative tillers (VT$_{3,4}$).**
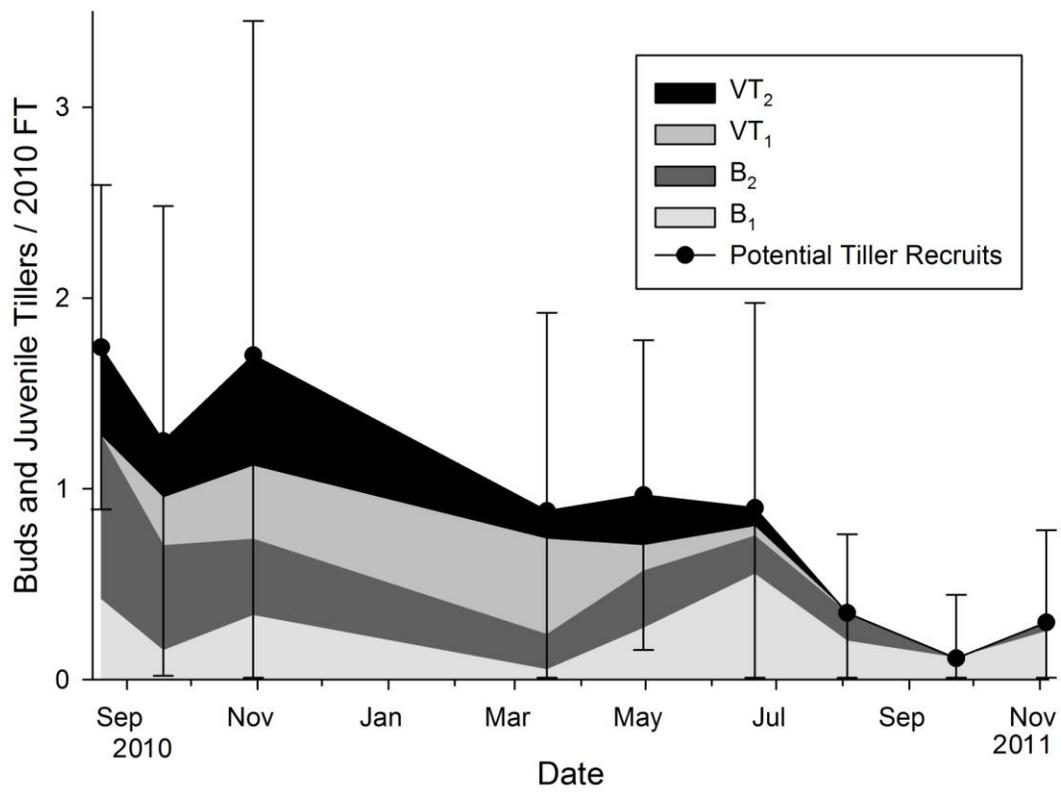
**Appendix Figure 2-6. Potential tiller recruits (i.e. buds and juvenile tillers) per *N. viridula* 2010 flowering tiller.** Error bars are ± 1 s.e.
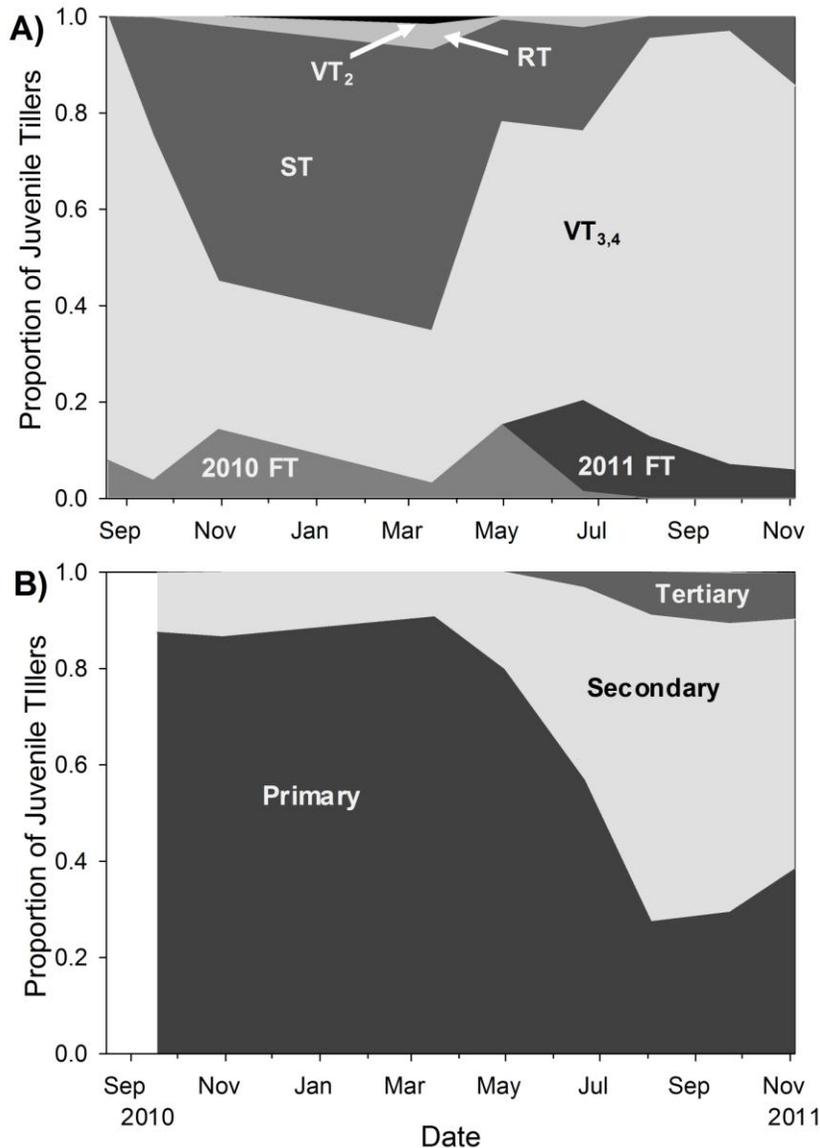
**Appendix Figure 2-7. Proportion of juvenile tillers ($VT_{1,2}$) of *N. viridula* genets A) produced on different tiller types (i.e. flowering status, photosynthesizing status, and size) and B) produced on ST and $VT_{3,4}$ according to generation.** A) Live tillers produced most juvenile tillers during the growing season while senesced tillers maintained most juvenile tillers over the winter season. B) Primary ST and $VT_{3,4}$ maintained the most juvenile tillers into early 2011 but soon secondary ST and $VT_{3,4}$ maintained more juvenile tillers than primary ST and $VT_{3,4}$ in later 2011. Juvenile tillers occurred on quaternary and quinary ST and $VT_{3,4}$ but not in large amounts. Therefore, it is difficult to see their contribution above tertiary tillers in the figure.
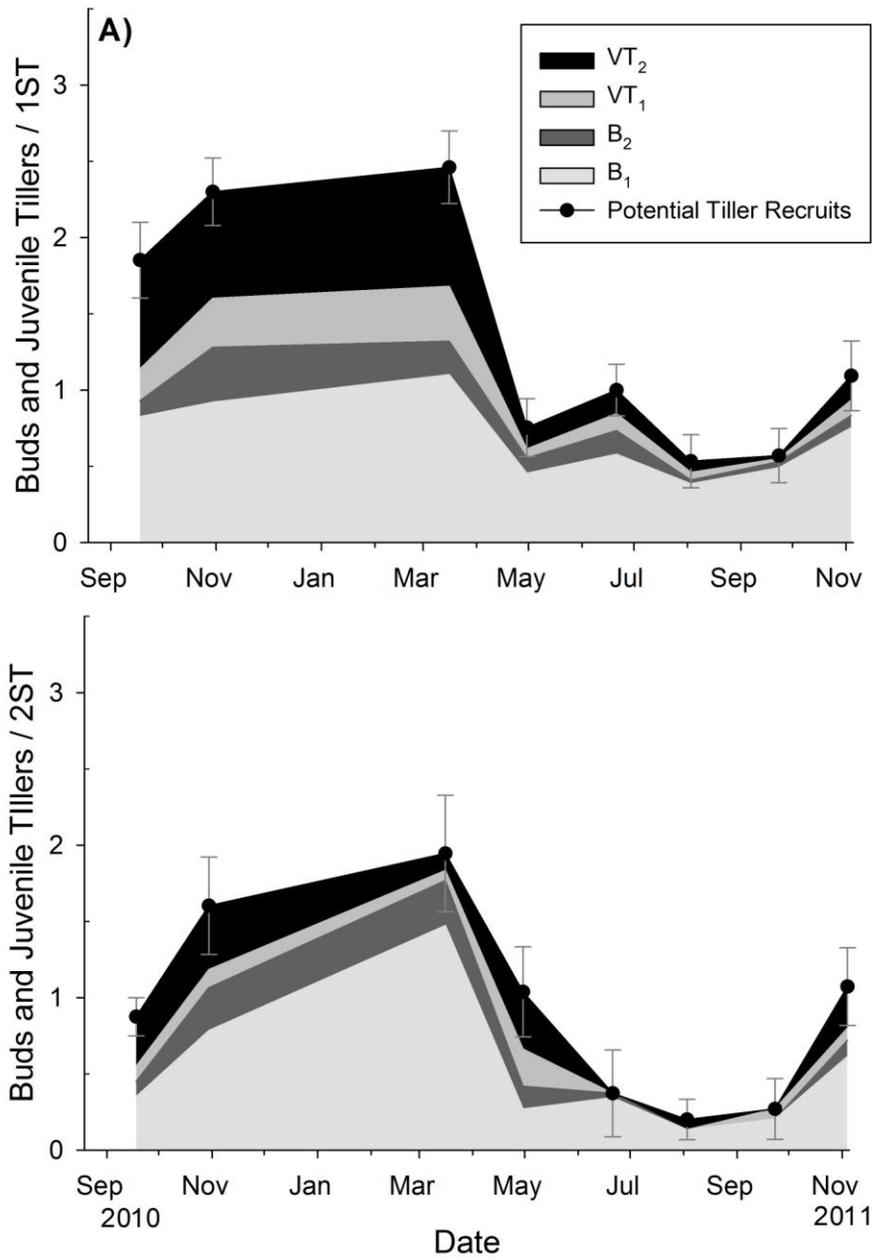
**Appendix Figure 2-8. Potential tiller recruits (i.e. buds and juvenile tillers) per *N. viridula* senesced tiller (ST) according to generation.** Primary and secondary ST had similar temporal trends of potential tiller recruits per tiller but 1ST had more potential tiller recruits per tiller than 2ST. Error bars are ± 1 se.

# Chapter 3 - Bud bank dynamics and clonal growth strategy in the rhizomatous grass, *Pascopyrum smithii*

## Abstract

Persistence of rhizomatous perennial grasses is dependent on tiller and rhizome recruitment from the belowground bud bank. Although the vast majority of perennial grasses maintain a rhizomatous growth form, bud bank dynamics and seasonal tiller recruitment of rhizomatous grasses have been understudied. Bud availability and spatial distribution strongly determine the spatial distribution of ramets and genet growth patterns. The tiller and bud bank dynamics of *Pascopyrum smithii,* a dominant rhizomatous grass of the northern mixed grass prairie, were examined in order to understand its life history pattern, the relationship between bud bank dynamics, tillering, and clonal spread, and the role of different populations within the bud bank in tiller recruitment and rhizome production. In *P. smithii*, buds are borne on both the bases of tillers and on rhizomes, and buds can live for at least two years producing a mixed-age bud bank. Rhizomes and tillers primarily came from the youngest generation of buds borne on tillers with rhizome production occurring first in the summer followed by tiller recruitment in the fall or subsequent spring. Rhizome branching was limited. Approximately one-third of all potential tiller recruits were primarily buds maintained on rhizomes. Although rhizome axillary buds and older tiller axillary buds were rarely used in annual tiller recruitment, they provide a sizable reserve bud bank prepared to respond to plant injury. The size and spatial distribution of rhizomatous grass bud banks and the resulting growth pattern are strongly dependent on a species' inherent rhizome architecture and its plasticity. Upholding its reputation as a good space colonizer and local disperser via rhizomes, *P. smithii* invested substantially in both phalanx and guerilla tiller production in undisturbed conditions. Co-occurring caespitose grasses had similar bud production per tiller as *P. smithii,* indicating that differences in bud bank densities of rhizomatous and caespitose species are due to differences in tiller and rhizome production and distribution within the community. Although rhizomatous grasses lack the dense bud banks of caespitose grasses, the spatial distribution of their buds enable tiller recruitment over a greater area in locations with sufficient resources. Along with its mixed guerilla-phalanx growth pattern, annual tiller recruitment of *P. smithii* was capable of flexible timing, occurring in either spring or fall whenever soil moisture was adequate. With a varied growth pattern and

flexible tiller recruitment timing, *P. smithii* is capable of employing both conservative and foraging growth strategies which will enable it to persist under local neighborhood variability and global climatic change.

Keywords: bud , foraging, guerilla, phalanx, vegetative reproduction, Western Wheatgrass

## **Introduction**

Grass-dominated ecosystems cover 40.5% of the total land area in the world and can be found on every continent except Antarctica (White *et al.,* 2000; Gibson, 2009). Because many grasslands are dominated by perennial grasses, they are dependent on the success of vegetative reproduction via the belowground bud bank (*sensu* Harper, 1977). Although a wide variety of clonal organs produce and maintain belowground buds, rhizomes are prevalent in grassland floras (Klimesova and Klimes, 2008). The architecture of rhizomatous grasses is strongly determined by their branching pattern (monopodial/ sympodial/ amphipodial), diameter (leptomorph/ pachymorph), and rhizome neck (Judziewicz *et al.*, 1999). All rhizomes function to numerically increase aboveground ramets via their bud bank but the size and spatial distribution of their bud bank is dependent on their architecture. Rhizomes may also assist in functions such as ramet dispersal, protection, anchorage, and resource translocation, acquisition, and storage (Grace, 1993). For example, a short-necked sympodial pachymorph may use its thick rhizomes (which lack buds along the neck) for resource storage and a small numerical increase in ramets. Alternatively, a sympodial leptomorph without a neck may use its thin rhizomes and buds for dispersal, resource acquisition, and a large numerical increase in ramets.

The bud bank of perennial grasses consists of both renewal buds used in seasonal tiller recruitment and regenerative buds used to recover following injury or unprogrammed tiller death (Klimesova and Klimes, 2007). It is often impossible to visually identify renewal and regenerative buds (Klimesova and Klimes, 2007). However, a plant's bud bank can be divided into multiple populations distinguished by categories such as age, meristem type (axillary vs apical), or parent organ (tiller vs rhizome). Usually buds within each population have similar developmental trajectories and/or outgrowth sensitivities (Watson *et al.*, 1997). For example, axillary buds of *Trifolium repens* respond individually to their microenvironment while apical buds display a single integrated response to microenvironments encountered by the whole plant (Turkington *et al.*, 1991). Therefore, renewal buds might primarily be associated with certain

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populations of buds within the bud bank. In previous studies of three perennial grasses, the majority of annual tillers were produced by younger annual cohorts of belowground grass buds rather than older buds (Hendrickson and Briske, 1997; Ott and Hartnett, 2012a). Thus, renewal buds of perennial rhizomatous grasses would be expected to be from the youngest cohort of buds. However, ramet dispersal patterns would determine whether most are produced from buds borne on parent tillers or rhizomes (e.g. Zhang *et al.,* 2009).

Ramet dispersal patterns of stoloniferous and rhizomatous species have often been described by the guerilla-phalanx continuum (Lovett Doust, 1981). At one extreme, a species has widely spaced ramets infiltrating the surrounding vegetation (guerilla growth form). At the other extreme, a species has closely spaced ramets which exclude other plants from its territory such that the entire plant (genet) expands as an advancing front (phalanx growth form). Guerilla species are better at exploiting patchily distributed resources quickly while phalanx species are more effective at exploiting temporal resource pulses (Humphrey and Pyke, 1998). Some species exhibit a combination of both guerilla and phalanx growth and may maintain enough architectural plasticity to shift between the two growth patterns in response to habitat and nutrient conditions (Lovett Doust, 1981; Carlsson and Callaghan, 1990; Navas and Arnier, 1990; Ye *et al.*, 2006; Chen *et al.*, 2011). Bud and tiller production on rhizomes as well as differential timing of rhizome and tiller initiation from the bud bank may reveal how a plant prioritizes guerilla versus phalanx growth.

Despite the abundance of rhizomatous grass species, their bud banks have been less studied than those of caespitose grasses. Individuals of rhizomatous grasses can be difficult to identify in the field and enumeration of buds per unit rhizome length requires intensive labwork. Therefore, in rhizomatous grass studies, buds produced by rhizomes have been omitted, reported as a site-specific density, or included in the total buds per tiller (e.g. Mullahey *et al.*, 1991; Hendrickson and Briske, 1997; Zhang *et al.*, 2009; Ott and Hartnett, 2012a). In order to begin to understand how rhizome architecture affects the numerical increase of ramets via the bud bank, detailed and spatially explicit bud bank demography per unit rhizome length should be examined in individual species.

*Pascopyrum smithii,* commonly referred to as western wheatgrass, is a common rhizomatous perennial grass throughout the central and western United States. This grass produces both phalanx and guerilla tillers via its amphipodial leptomorphic growth pattern and is

known to rapidly expand into open habitat (Fig. 3-1; Rogler, 1962; Weaver, 1968; Asay and Jensen, 1996; Judziewicz *et al.*, 1999).  The regional productivity of *P. smithii* is primarily driven by a negative correlation between its growth rate and mean annual temperature, making it a dominant in northern mixed grass prairie although its range extends throughout the Great Plains (Barker and Whitman, 1988; Epstein *et al.*, 1998).  During the great drought of the 1930s, *P. smithii* became a dominant in the more mesic tallgrass prairie (Weaver, 1968).  *Pascopyrum smithii* is also an excellent early season forage and soil stabilizer (Rogler, 1962; Asay and Jensen, 1996).  An understanding of its tiller and bud bank dynamics would increase our understanding of the population ecology of rhizomatous grasses, and knowledge of what factors regulate its clonal growth and dynamics would benefit land managers.

The objective of this study was to quantify bud bank and tiller dynamics throughout an annual cycle of the perennial grass *P. smithii* in order to 1) understand the life history pattern of a dominant rhizomatous $C_3$ grass in the northern Great Plains, 2) characterize its pool of potential tiller recruits, including both the bud bank and supply of juvenile tillers, according to age and parent ramet (rhizome or tiller), 3) determine the relative contributions of various bud populations to tiller and rhizome recruitment, and 4) evaluate the investment in guerilla versus phalanx tillers of *P. smithii* under undisturbed field conditions.

## Methods

### *Site description*

The study was conducted at Wind Cave National Park (WCNP), a 13,699 hectare mixed-grass prairie interspersed with ponderosa pine forest located at the southeastern extent of the Black Hills in western South Dakota (43º33'N, 103º29'W).  The vegetation is dominated by cool-season $C_3$ grasses such as *Hesperostipa comata*, *Pascopyrum smithii*, and *Nassella viridula* with discrete patches of less abundant warm-season $C_4$ grasses including *Andropogon gerardii*, *Bouteloua curtipendula*, and *Bouteloua gracilis*.  Bison (*Bison bison*), elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) are the major large herbivores.  However, bison and elk are the primary consumers of grass due to their grazing habits and population sizes.  The region's semi-arid climate has cool winters (average Jan temp: 27.8ºF) and warm summers (average July temp: 73.2 ºF) with moderate rainfall (499 mm) primarily occurring April through October, especially in

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May and June.  During this study, annual precipitation in 2010 and 2011 was 645.92mm and 574.80mm respectively.  April, May, and June of 2010 and May of 2011 had at least 58mm of rainfall above the long-term average for each month.  WCNP has a hilly topography (elevation ranging from 1113m to 1527m).

For this study, the prairie portion of the 42 hectare Elk Mountain enclosure within WCNP was used.  The enclosure excludes bison but not other herbivores.  Although a seasonal campground is located in the southern forested portion of the enclosure, the large northern portion of the enclosure is undisturbed native mixed grass prairie.  Prescribed fire occurs every 5 to 7 years and the Elk Mountain enclosure was last burned in the fall of 2008.  The enclosure is at an elevation of 1310m and primarily had loamy-skeletal soils (Typic Argiustolls) but included a small area with fine-loamy soil (Fluventic Haplustolls); USDA-NRCS-WSS).

## *Field Sampling*

*Pascopyrum smithii* (Rydb.) Á. Löve (western wheatgrass) is a strongly rhizomatous perennial $C_3$ grass which may flower between May and September.  Due to its rhizomatous growth form and intermingling of different genets,  *P. smithii* genets are very difficult to identify in the field.   Therefore, an individual of *P. smithii* consisted of all interconnected tillers and associated belowground parts within an 8.0 cm radius.

In June and July 2010, ten sites with a *P. smithii* population and separated by an average distance of $74 \pm 7$m were established within the northern grassland portion of the enclosure. Two parallel 15m transects were laid 2m apart from one another in a random direction at each site.  An individual of *P. smithii* was randomly selected and marked with a 16cm diameter ring every 1.5 meters along each transect and its tiller density within the ring was counted.  The 2010 tillers of each individual were counted and flowering tillers were marked using small wire rings. Beginning on August 20, 2010 and continuing until November 4, 2011, an individual from each site was harvested approximately every 3 weeks during the growing season (i.e. while soil temperatures remained consistently above freezing; total of 14 sample dates).  When a set of samples was harvested, soil temperature was measured at a 5cm depth in three consistent locations at every site.  Soil temperatures were taken within the first 2 hours of dawn using a thermocouple (TH-65 Thermocouple Thermometer, Wescor, Inc or T-85154 Microprocessor thermometer Type J-K-T thermocouple Model HH23, Omega Engineering, Inc).  Individuals

were harvested by excavating to a 15 cm depth and washed to remove soil. A voucher specimen was collected from adjacent Custer State Park and is housed at the Kansas State University Herbarium.

### *Bud, tiller, and rhizome classification*

Buds, tillers and rhizomes from each individual plant were examined using a dissecting scope with magnifications between 7 and 40x. Tillers, rhizomes and basal/belowground buds were counted, assessed to be living or dead, and classified by which tiller type (see below) produced them. Although all tillers were counted and classified for the entire individual, a random subsample of five tillers was chosen for assessing bud production of each tiller generation and photosynthesizing status. Ten tillers were used to assess buds on residual tillers.

Tillers were distinguished from buds by their elongation in relation to the prophyll. Buds were contained within the prophyll and tillers had elongated past the prophyll. Live buds were divided into two size classes: small and large (Table 3-1). Dead buds were identified by their soft, spongy or mealy brown interiors and easily distinguished from live buds. Six tiller stages were identified (Table 3-1). Four stages were different size classes of live tillers (Table 3-1). For the first sample date (August 20, 2010), small juvenile tillers ($T_1$) were counted as large juvenile tillers ($T_2$). Juvenile tillers ($T_{1,2}$) typically had not emerged aboveground. Therefore, buds and juvenile tillers were considered collectively as "potential tiller recruits."

Tillers ($T_{3-5}$) were further classified according to generation (primary/1, secondary/2, tertiary/3). The oldest tiller generation present aboveground was considered the primary tiller generation and the youngest was the tertiary tiller generation. Hereafter, tillers may be referred to by their generation, if appropriate, and symbol (e.g. primary small tillers ($1T_3$), secondary live tillers ($2T_{3,4}$), juvenile tillers ($T_{1,2}$), primary tillers ($1T_{3-5}$)). Residual tillers (RT) are older than primary tillers but may be comprised of multiple generations which are indistinguishable from one another. Although RT do not comprise a single generation, they are included in analyses as if they were the generation previous to primary tillers. In previous work (Ott and Hartnett 2012a), $VT_1$ were classified as activated buds in both the $C_3$ grass *D. oligosanthes* and the $C_4$ grass *A. gerardii*. It is proposed that classifying bud and tiller stages in relation to prophyll development as done in this study provides an objective standardized bud and tiller classification system that can be widely applied to many grass species to aid in future comparative studies.

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The length of each rhizome was measured and its parent tiller, overall developmental stage, and apical meristem identity (i.e. developmental stage of the rhizome tip (e.g. bud, horizontal or vertical juvenile tiller, or tiller)) were classified. Three rhizome developmental stages were identified (Table 3-1). $R_1$ were classified as $R_2$ for the first sample date (Aug 20, 2010). Up to approximately 30cm of rhizomes at each developmental stage was assessed for bud production. A rhizome exhibiting multiple developmental stages along its length was classified by the developmental stage found along the majority of its length. This occurred infrequently and using this classification method did not significantly alter results. Unlike tillers which only maintained axillary buds, rhizomes had both axillary buds along their stems and apical buds at their tips.

## *Statistical analysis*

Total bud and juvenile tiller density was evaluated using date as the treatment factor in a RCBD blocking on site (PROC MIXED, SAS9.2). Total bud and juvenile tiller production per tiller was evaluated using a two-way factorial treatment with the factors of date and generation in a RCBD blocking on site with a split-plot (PROC MIXED, SAS9.2). The treatment factor of date was applied to the wholeplot experimental unit (WPEU) of individual genet and the treatment factor of generation was applied to the subplot experimental unit (SPEU) of tiller. Kenward-Roger's method was used to approximate the denominator degrees of freedom. Contrasts compared the total bud and juvenile tiller production of tiller generations in fall 2010 and fall 2011 as well as interannual differences in peak bud and juvenile tiller production of current year tillers. In a RCBD blocking on site with a split-plot, a two-way factorial treatment structure with the factors of date and rhizome age was used to assess total bud and juvenile tiller production per rhizome length (PROC MIXED, SAS9.2). A contingency table analysis was used to test for an overall difference between observed and expected proportions of 2011 tillers produced from four different sources of buds (PROC FREQ, SAS9.2). Observed proportions of individual sources were tested against their expected proportions using the significance test of proportions for large sample sizes (Agresti, 2007).

# Results

## *Tiller dynamics*

*Pascopyrum smithii* produced annual generations of tillers. One tiller generation ($2T_{3,4}$) began recruitment in the spring but the subsequent tiller generation ($3T_{3,4}$) began recruitment in the fall (Fig. 3-2). Although there was less rainfall in 2011 than 2010, soil temperatures were lower during the growing season in 2011 than in 2010. Lower temperatures during the hottest summer months may have advanced new tiller development in 2011 due to the cool-season phenology of *P. smithii*. Thus, *P. smithii* recruited its tertiary tiller generation in the fall rather than the spring. Flowering was rare as < 0.01% of all live tillers were flowering in June and July 2010 and no flowering tillers were observed in 2011. Flowering 2010 tillers only occurred at one site.

A tiller generation was primarily recruited from buds produced by the previous tiller generation rather than from older buds (Table 3-2 and 3-3). At the peak of secondary tiller ($2T_3$) recruitment (April 30, 2011-June 5, 2011), secondary tillers were recruited from four different sources of buds and juvenile tillers (Table 3-2). Assuming that buds and juvenile tillers from each source had equal likelihood of producing a tiller, expected proportions of secondary tillers recruited from each source were based on the bud and juvenile tiller availability of each source. Observed proportions of secondary tillers recruited from each source significantly differed from expected proportions ($X^2_3 = 896$, p<0.0001). Younger buds of tillers and apical rhizome buds produced more secondary tillers than expected while older buds of tillers and axillary rhizome buds produced less secondary tillers than expected (Table 3-2). The beginning of tertiary tiller ($3T_3$) recruitment indicated a similar trend as most tertiary tillers were recruited from secondary tiller buds (Table 3-3).

## *Rhizome dynamics*

*Pascopyrum smithii* produced rhizomes annually. Juvenile rhizomes ($R_1$) were produced in the summer after spring aboveground tiller recruitment had been completed for one month (Fig. 3-2). Juvenile rhizomes were never observed developing from axillary rhizome buds. In 2011, $81.0 \pm 6.8$ % of juvenile rhizomes were produced from buds of secondary tillers ($2T_{3,4}$), the most recently recruited tiller generation. The remaining proportion of juvenile rhizomes developed from buds of residual tillers ($3.8 \pm 3.8\%$), primary tillers ($1T_{3,4}$; $8.7 \pm 4.7\%$), or their

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origin was unknown ($6.5 \pm 4.3\%$). However, $11 \pm 1\%$ of older rhizomes ($R_{2,3}$) examined over the course of this study had grown from axillary rhizome buds. Therefore, rhizome production from axillary rhizome buds can occur but only did to a limited extent.

At this field site on average, $18.32 \pm 0.94$ m of *P. smithii* rhizomes existed per m$^2$ at any point in time during the year. Younger rhizomes ($R_{1,2}$) made up a small proportion of total rhizome length (Appendix Fig. 3-1). Instead, aged rhizomes ($R_3$) comprised the majority ($\sim 79 \pm 1\%$) of total rhizome length. The average rhizome length between tillers was $4.48 \pm 0.27$cm.

### *Potential Tiller Recruits*

*Pascopyrum smithii* maintained a supply of buds and juvenile tillers (i.e. potential tiller recruits) throughout the year at two locations (basal buds on tillers and buds on rhizomes). Total bud and juvenile tiller density of *P. smithii* individuals did not vary by date (Fig. 3-3; Date: $F_{13, 111} = 1.46$, p=0.15). Small buds comprised the majority of potential tiller recruits. Rhizomes contributed fewer potential tiller recruits than tillers. Throughout the study, approximately 35% of all buds and juvenile tillers were located on rhizomes rather than tillers (Fig 3-3).

Buds, juvenile tillers ($T_{1,2}$) and possibly small tillers ($T_3$) overwintered before transitioning to higher developmental stages. Bud natality on tillers and rhizomes occurred as they elongated in the spring and summer respectively. Juvenile tiller recruitment peaked in the fall from both rhizomes and tillers although a few juvenile tillers were recruited from young three month old buds in the summer (Figs. 3-4BC, 5B). Juvenile tiller production peaked in September on the youngest tiller generation (e.g. primary tillers in 2010 and secondary tillers in 2011). Due to the earlier start of tertiary tiller recruitment as compared to the previous tiller generation (i.e. secondary tillers), juvenile tillers began to decrease earlier on secondary tillers in 2011 than they did the previous year on primary tillers (Fig. 3-4BC).

Buds and juvenile tillers were found on all generations of tillers (RT, $1T_{3,4}$, $2T_{3,4}$, $3T_{3,4}$) producing a multi-aged bud bank and supply of potential tiller recruits but most generations varied in their abundance of potential tiller recruits over the annual cycle. Residual tillers maintained similar numbers of potential tiller recruits per tiller throughout the study unlike primary ($1T_{3-5}$) and secondary ($2T_{3-5}$) tillers. In fall 2010 (Sep-Oct), primary tillers ($1T_{3-5}$) had significantly greater numbers of potential tiller recruits per tiller than older residual tillers (Fig. 3-4AB; contrast: $F_{1, 200} = 153.29$, p <0.0001). In spring 2011, juvenile tillers on primary tillers

rapidly transitioned to secondary tillers and this transition produced a notable decline in potential tiller recruits per primary tiller (Fig. 3-4B). In fall 2011, the numbers of potential tiller recruits did not significantly differ between residual and primary tillers (contrast: $F_{1, 205} = 3.61$, p = 0.059) but were significantly lower on primary than secondary tillers (contrast: $F_{1, 201} = 32.58$, p<0.0001). Buds of *P. smithii* can live for at least two years. However, as older buds transitioned to new tiller generations or died, the supply of potential tiller recruits become composed of mostly buds on the youngest tillers ($T_{3-5}$; Fig. 3-6).

Both primary and secondary tillers produced a similar peak number of potential tiller recruits per tiller (contrast: Oct 30, 2010 for $1T_{3-5}$ vs Sep 23, 2011 for $2T_{3-5}$: $F_{1, 321} = 0.69$, p= 0.41). Each tiller typically produced between two and three buds. On average over the entire study, $0.41 \pm 0.07$ buds were produced per large juvenile tiller. Therefore, bud production primarily occurred on tillers ($T_{3-5}$) rather than juvenile tillers ($T_{1,2}$).

Potential tiller recruits per rhizome length was significantly greater on younger ($R_{1,2}$) rhizomes rather than older rhizomes ($R_3$). However, potential tiller recruits per rhizome length significantly varied similarly by date for younger and older rhizomes (Fig. 3-5; Date: $F_{1, 97.5} = 1.91$, p = 0.048; Age: $F_{1, 107} = 102.07$, p<0.0001; Date*Age: $F_{11, 106} = 0.80$, p= 0.64). Because younger rhizomes had more buds and juvenile tillers per length than older rhizomes but younger rhizomes were less abundant, younger and older rhizomes contributed similar numbers of buds and juvenile tillers to each individual (Fig. 3-7). Tillers recruited from rhizomes primarily came from young rhizomes ($R_{1,2}$) as older rhizomes ($R_3$) did not maintain juvenile tiller stages even though they maintained buds (Fig. 3-5). The lowest number of potential tiller recruits per rhizome length occurred following new rhizome growth from tiller buds in June and July. However, juvenile rhizome development from axillary rhizome buds was not observed. At that time, younger rhizomes were about to transition to older rhizomes as they had been recruited in the previous growing season and had already lost buds to spring tiller recruitment and natural senescence. Older rhizomes must have experienced a period of bud mortality. Newly recruited rhizomes had not yet begun to produce enough buds to compensate for these bud losses. Together, these factors would create the observed decline in the number of buds and juvenile tillers on rhizomes ($R_{1-3}$) in July.

## Discussion

Both tillers and rhizomes of *P. smithii* were recruited annually. A tiller generation may begin recruitment in either the fall or spring but will senesce by the following fall. Rhizomes and tillers developed primarily from the youngest generation of buds borne on tillers, with rhizome development occurring first in the summer followed by tiller recruitment in the fall or subsequent spring. No new rhizomes were produced from axillary rhizome buds although there was history of limited rhizome development from axillary rhizome buds. Thus, there was limited rhizome branching in *P. smithii* and their buds remained dormant so this grass did not employ a space-filling strategy like many clonal forbs that have a branching rhizome system.

A bud of *P. smithii* can live for at least two years thereby creating a multi-aged bud bank. Because the youngest rhizomes and tiller generation produced the greatest numbers of tiller recruits per rhizome length and per tiller respectively, the majority of potential tiller recruits were less than one year old. Approximately two-thirds of all potential tiller recruits in an individual of *P. smithii* were maintained on tillers rather than rhizomes. The year-round supply of potential tiller recruits consisted of both buds and juvenile tillers with juvenile tillers comprising a large proportion of the overwintering population.

### *Bud bank spatial dynamics and clonal growth patterns*

Although tillers were recruited from buds of different ages and borne on different parent organs, these sub-populations of buds contributed disproportionately to annual tiller recruitment. Bud bank size and bud availability for tiller recruitment is a function of bud natality, longevity, and dormancy (Watson *et al.*, 1997). Similar to seeds, bud dormancy can be imposed by a combination of endogenous factors from within the solitary bud, exogenous factors from the parent tiller, and environmental factors (Harper, 1957; Nikolaeva, 1977; Baskin and Baskin, 1998). Although buds may be present in the bud bank, they may not be available for tiller recruitment due to dormancy. The exogenous factor of apical dominance, which involves the suppression of axillary buds produced by the apical meristem, is commonly observed in grasses and was evident in *P. smithii* (Murphy and Briske, 1992). Axillary buds on rhizomes of *P. smithii* were much less likely to grow out into tillers than apical rhizome buds. Similar to other grasses, most tillers of *P. smithii* were recruited from the most recently produced cohort of buds (Hendrickson and Briske, 1997; Ott and Hartnett, 2012a). Older cohorts of buds on rhizomes

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and tillers consist of individuals that did not grow out in previous seasons.  Because the most distal buds, closest to the apical meristem are the largest and most likely grow out, the collection of older buds consist of small buds with a historically high degree of dormancy (McIntyre, 1967; Mueller and Richards, 1986; Busso *et al.*, 1989).  Thus, renewal buds of *P. smithii* are most likely to be apical rhizome buds and young axillary tiller buds.  Buds with a greater degree of dormancy, such as axillary rhizome buds and older axillary tiller buds, primarily function as a reserve or regenerative bud bank of *P.smithii* that have a primary role of recover after disturbance.

   *Pascopyrum smithii* heavily invested in a guerilla growth pattern as ~40% of its 2011 annual tillers were produced from rhizome buds away from the parent tiller.  In addition, a third of its bud bank was maintained on rhizomes rather than on tillers.  *Pascopyrum smithii* produced twice as many spreading tillers in undisturbed conditions as *Leymus chinensis*, a Eurasian $C_3$ rhizomatous grass which often forms mono-specific stands in China (Zhang *et al.*, 2009).  Although both species had maintained similar proportions of buds on rhizomes during the winter, this proportion widely fluctuated throughout the growing season in *L. chinensis* but was relatively consistent year-round in *P. smithii* (Zhang *et al.*, 2009).  The rhizome bud supply is dependent on the bud production of new rhizomes and the maintenance of buds on old rhizomes.  Although most guerilla tiller recruitment of *P. smithii* came from buds of younger rhizomes, older rhizomes can provide nutritional support and a reserve of buds for a plant (Jonsdottir and Callaghan, 1988).  The consistent rhizome bud supply of *P. smithii* maintained by rhizomes of all ages would enable immediate response to plant injury or environmental alterations over a wide spatial area throughout the year.  *Pascopyrum smithii* recruits most new tillers from younger-aged tillers and apical rather than axillary rhizome buds, which would be near the genet periphery.  In combination with little rhizome branching, these traits result in *P. smithii* having a strong guerilla growth pattern.

   Consideration of ramet dispersal patterns have led to extensive literature dedicated to clonal plant foraging behavior as stimulated by the environment, especially resource heterogeneity (Sutherland and Stillman, 1988; Hutchings, 1988; MacDonald and Lieffers, 1993; Kleijn and van Groenendael, 1999; Louapre *et al.*, 2012).  de Kroon and Schieving (1990) extended the guerilla-phalanx growth pattern concept to include a suite of traits describing three clonal growth strategies. The foraging growth strategy explores a patch habitat opportunistically,

the conservative growth strategy uses resources efficiently, and the consolidation growth strategy spatially and temporally monopolizes available resources. Although every species has a basic clonal growth pattern (i.e. clonal architecture), the plasticity of this pattern in response to resource availability shifts is considered its clonal growth strategy (de Kroon and Knops, 1990; de Kroon and Schieving, 1990). As a trait of clonal growth patterns, bud banks and their spatio-temporal dynamics are the key mechanism through which clonal architecture and growth strategies are determined. Clonal growth patterns which produce long rhizomes with long-lived buds would benefit the conservative growth strategy. In this case, buds positioned throughout the habitat are prepared to respond to increases in resource levels. Clonal growth patterns which have no rhizomes or short rhizomes and long-lived buds characterize the consolidation growth strategy as a dense bud bank promotes local persistence (de Kroon and Schieving, 1990; Briske and Derner, 1998). Species, such as *P. smithii*, with mixed growth patterns of both short and long rhizomes, or phalanx and guerilla ramets, would enable a mixture of conservative and foraging growth strategies.

## *Comparison with other grasses*

*Pascopyrum smithii* produced similar or lower numbers of buds per tiller than $C_3$ caespitose grasses in the Great Plains. Because caespitose grasses are characterized by a dense grouping of tillers and thus a dense bud bank, tillers of caespitose grasses might be expected to invest less in bud production than tillers of rhizomatous grasses. Two widespread $C_3$ caespitose grasses of temperate semi-deserts in the western United States (*Agropyron desertorum* and *Pseudoroegneria spicata*) and a sub-dominant $C_3$ caespitose grass of mesic tallgrass prairie (*Dichanthelium oligosanthes*) produced at least twice as many buds per tiller than *P. smithii* (Mueller and Richards, 1986; Busso *et al.*, 1989; Ott and Hartnett, 2012b). But another subdominant $C_3$ caespitose grass of tallgrass prairie, *Koeleria macrantha*, produced fewer buds per tiller than *P. smithii* (Dalgleish *et al.*, 2008). However, co-dominant $C_3$ caespitose grasses within the same mixed-grass community as *P. smithii* produced similar numbers of buds per tiller as *P. smithii* (chapter 1). Therefore, in the mixed grass prairie community at WCNP, the spatial distribution of the grass community's bud bank was strongly driven by the spatial distribution of tillers and bud-bearing rhizomes rather than bud production per tiller differences among species. In a mid-grass Texas grassland, grazing altered bud densities via alteration in

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plant and tiller densities more than alteration of bud production per tiller (Hendrickson and Briske, 1997).

The concept that caespitose grasses generally produce more buds per tiller than rhizomatous grasses is also supported by comparisons of $C_4$ species from the southern Great Plains. Caespitose $C_4$ grasses *Schizachyrium scoparium* and *Sporobolus heterolepis* produced similar or more buds per tiller than the rhizomatous grass *B. curtipendula* but not the rhizomatous grass *A. gerardii* (Hendrickson and Briske, 1997; Dalgleish *et al*., 2008; N'Guessan and Hartnett, 2011; Ott and Hartnett, 2012a). Interestingly, *A. gerardii* has a different clonal growth architecture than *B. curtipendula*. *Bouteloua curtipendula*, similar to *P. smithii*, produces long rhizomes potentially with additional buds to supplement the buds produced by their tillers. With its short-neck sympodial pachymorph architecture, *A. gerardii* produces few to no buds along its rhizomes and obviously compensates with high bud production of its tillers. Classification of grasses according to the rhizomatous architecture of Judziewicz *et al*. (1999) would enable general characterization of differences in spatial bud distributions of rhizomatous grasses. In turn, this classification could facilitate comparisons between coexisting grasses that would benefit studies using clonality traits to examine plant community assembly and structure (Klimesova and Klimes, 2008; Rusch *et al.,* 2011).

### *Potential meristematic constraints on tradeoffs between growth patterns*

Competition for limiting resources is a valid explanation for any tradeoff observed between guerilla and phalanx growth within a plant. Guerilla ramets often involve greater carbon costs than phalanx ramets, as more biomass is required to create long rhizomes (Carlsson and Callaghan, 1990). Tradeoffs between growth patterns can also be driven by tradeoffs of grazing avoidance versus grazing resistance or tolerance. The guerilla growth pattern in grasses results in widely spaced tillers that would provide grazing resistance to the genet. A smaller proportion of a genet with a guerilla growth pattern is consumed per bite than a genet with a phalanx growth pattern. However, bud availability can constrain a plant's capacity to produce new ramets (Geber, 1990; Watson *et al.*, 1997). From its bud supply, a parent grass tiller can produce either daughter tillers (phalanx tillers) or rhizomes with axillary and apical buds which produce daughter tillers (guerrilla tillers). Tradeoffs between two processes, such as rhizome and phalanx tiller production, can be a result of competition for a limited supply of meristems

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(i.e. buds) rather than resources (Watson, 1984). For example, each tiller of *Carex arenaria* is limited to producing two daughter ramets because it only produces two buds at its tiller base. Typically, one bud of *C. arenaria* becomes a new rhizome and the other bud remains dormant or transitions to a tiller.

*Pascopyrum smithii,* which only produces two to three buds per tiller, could encounter some meristematic limitations leading to tradeoffs between rhizome growth and local tiller recruitment from a parent tiller. Rhizomes were initiated before tillers from the same *P. smithii* parent tiller, as was also observed in *L. chinensis* (Zhang *et al.*, 2009). This initial investment in rhizome growth may reflect a plant prioritization of guerilla over phalanx growth. Recruitment of a bud to rhizome leaves fewer buds with potentially high dormancy-breaking requirements for subsequent tiller recruitment. For species that maintain a large number of available buds, this meristematic constraint may be insignificant. However, investing in rhizome growth first could be part of a bet-hedging strategy that ensures local persistence of a plant. Rhizome elongation occurs while the *P. smithii* parent tiller is assimilating carbon. Rhizome initiation before tiller initiation allows the seasonal conditions to determine rhizome length and the distance its tillers are from the parent tiller. If assimilation is low and rhizome elongation is minimal, tiller recruitment directly from the parent tiller may be unlikely but a tiller produced from the rhizome apical meristem would be still close to the parent tiller (i.e. a phalanx-type tiller) ensuring local persistence. By initiating a rhizome first, a parent tiller still maintains the option of producing guerilla and phalanx tillers under good growing conditions. Environmental conditions, such as increased nitrogen or humidity, and positional effects along the tiller base can play a strong role in determining the trajectory of buds as rhizomes or tillers (McIntyre, 1967; 1976). Therefore, environmental conditions and positional effects need to be examined in conjunction with timing of rhizome and tiller initiation in future examinations of potential meristematic constraints on tradeoffs between tiller and rhizome production.

### *Temporal flexibility in tiller recruitment*

Several $C_3$ perennial grasses begin tiller recruitment in the fall with tillers continuing growth during the subsequent spring (Lamp, 1952; Mueller and Richards, 1986; Zhang *et al.*, 2009). However, tillering of *A. desertorum* and *P. spicata* was delayed until spring under drought conditions (Busso *et al.*, 1989). Tiller recruitment timing of *Agropyron dasystachyum*

also appeared dependent on soil water availability.  As a result, annual tiller recruitment of *A. dasystachyum* occurred in either the fall or the subsequent spring similar to *P. smithii* (Zhang and Romo, 1995).  Although *P. smithii* has increased exponentially during harsh drought in mesic tallgrass prairie (Weaver, 1968), it may be sensitive to soil moisture in more arid grasslands.  A slight decline in productivity of *P. smithii* following fall and spring burning was correlated with lower soil moisture on burned plots in eastern Montana (White and Currie, 1983).  Lower water use efficiency (WUE) of *P. smithii* as compared to *B. gracilis, Thinopyrum intermedium,* and *Agropyron cristatum* may partially explain its prevalence on lowland sites of the shortgrass steppe and its distribution within other semi-arid grasslands (Frank and Karn, 1988; Monson *et al*., 1986).  In addition to precipitation, higher temperatures during the summer may slow bud development in cool-season grasses, subsequently altering their tiller recruitment timing (Ott and Hartnett 2012a).  As climate change is expected to alter temperature, precipitation patterns, and growing season length, the capacity to advance or delay vegetative reproduction until soil moisture is adequate may enable the persistence of *P. smithii* in semi-arid grasslands.

## *Conclusion*

The bud bank of a rhizomatous grass clone ensures local persistence while also enabling opportunities for expansion via vegetative reproduction.  Buds on tillers contribute to local persistence while buds on rhizomes are prepared to respond to injury and enable tiller dispersal away from the parent plant.  The size and spatial distribution of rhizomatous grass bud banks are strongly dependent on a species' inherent rhizome architecture and its plasticity.  Although rhizomatous grasses lack the dense bud banks of caespitose grasses, the spatial distribution of their buds enable tiller recruitment over a greater area in locations with sufficient resources.

Flexibility in both clonal architecture and clonal phenology enables a species to employ multiple growth strategies to successfully respond to changes within its environment. *Pascopyrum smithii* recruited new tillers from buds near the previous year's tillers as well as near its genet periphery and also limited rhizome branching.  Thus, coupled with flexible tiller recruitment timing, the strong guerilla growth pattern of *P. smithii* produces a mixture of both foraging and conservative growth strategies.  Additional studies of rhizomatous grass bud banks and their contribution to clonal growth patterns will assist in further understanding of clonal growth strategies involving rhizomes.

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# Figures and Tables



Basal Tiller Bud

Axillary Rhizome Bud
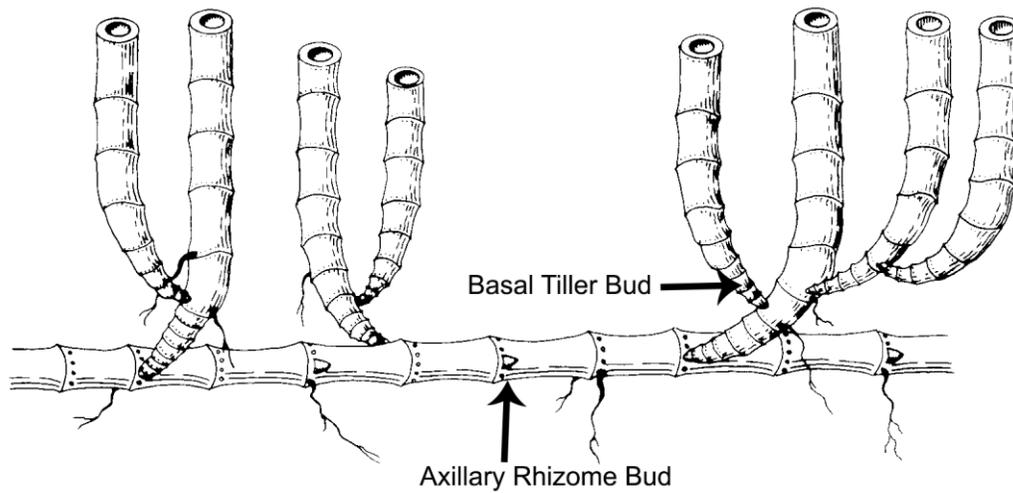
**Figure 3-1.  Conceptual drawing of a tillering amphipodial leptomorph (adapted from Judziewicz *et al*., 1999).**  Tillers can be recruited from axillary buds borne on rhizomes or tiller bases as well as apical rhizome buds (not pictured).   Tillers produced from basal tiller buds produce phalanx tillers while tillers produced from axillary or apical rhizome buds produce guerilla tillers.
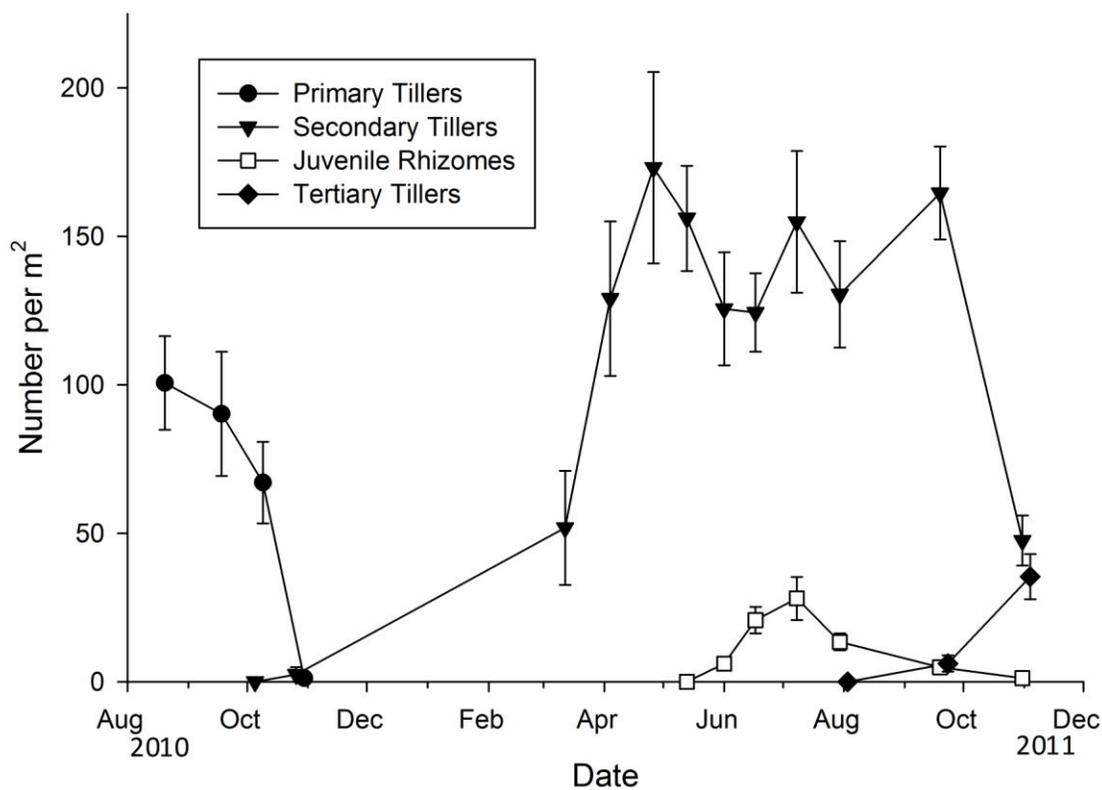
**Figure 3-2. Live tiller ($T_{3,4}$) density according to annual generation and juvenile rhizome ($R_1$) density.** Tertiary live tillers ($3T_{3,4}$) only consisted of small tillers ($T_3$). Error bars are $\pm$ 1 s.e.
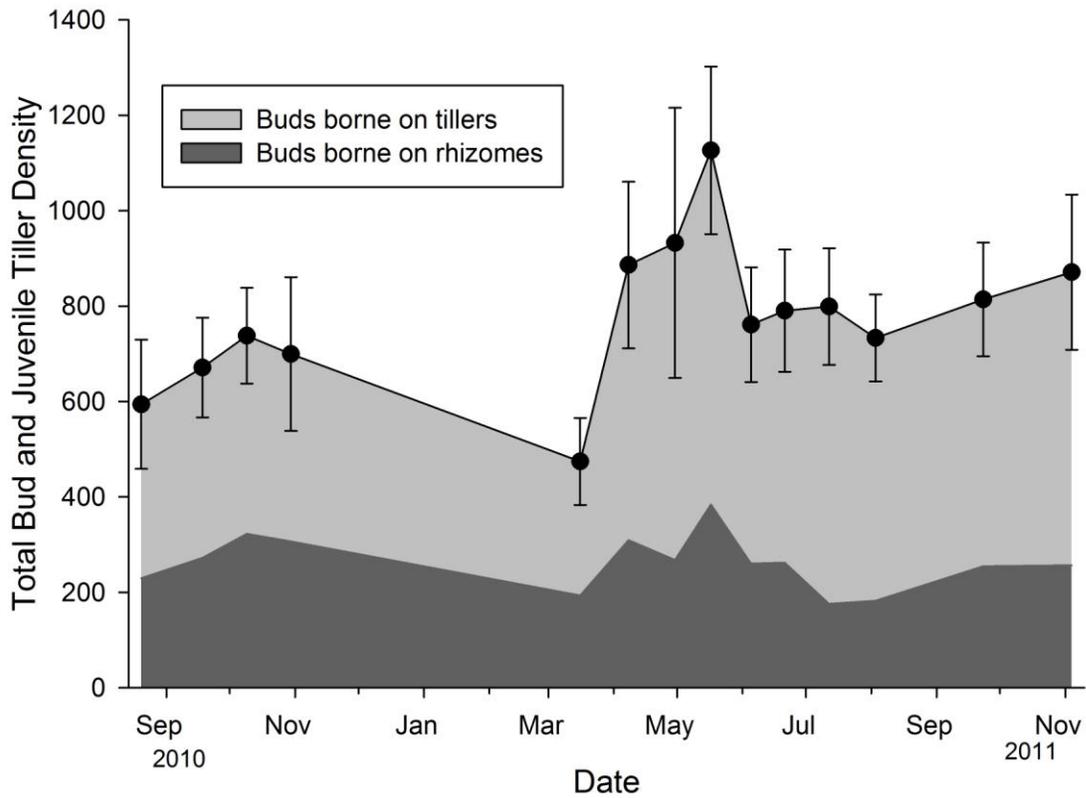
**Figure 3-3. Density and source of potential new tiller recruits (buds and juvenile tillers/m$^2$ area).** Buds borne on rhizomes included both axillary buds along the rhizome and their apical bud. Tiller axillary buds are borne at the base of the tiller.
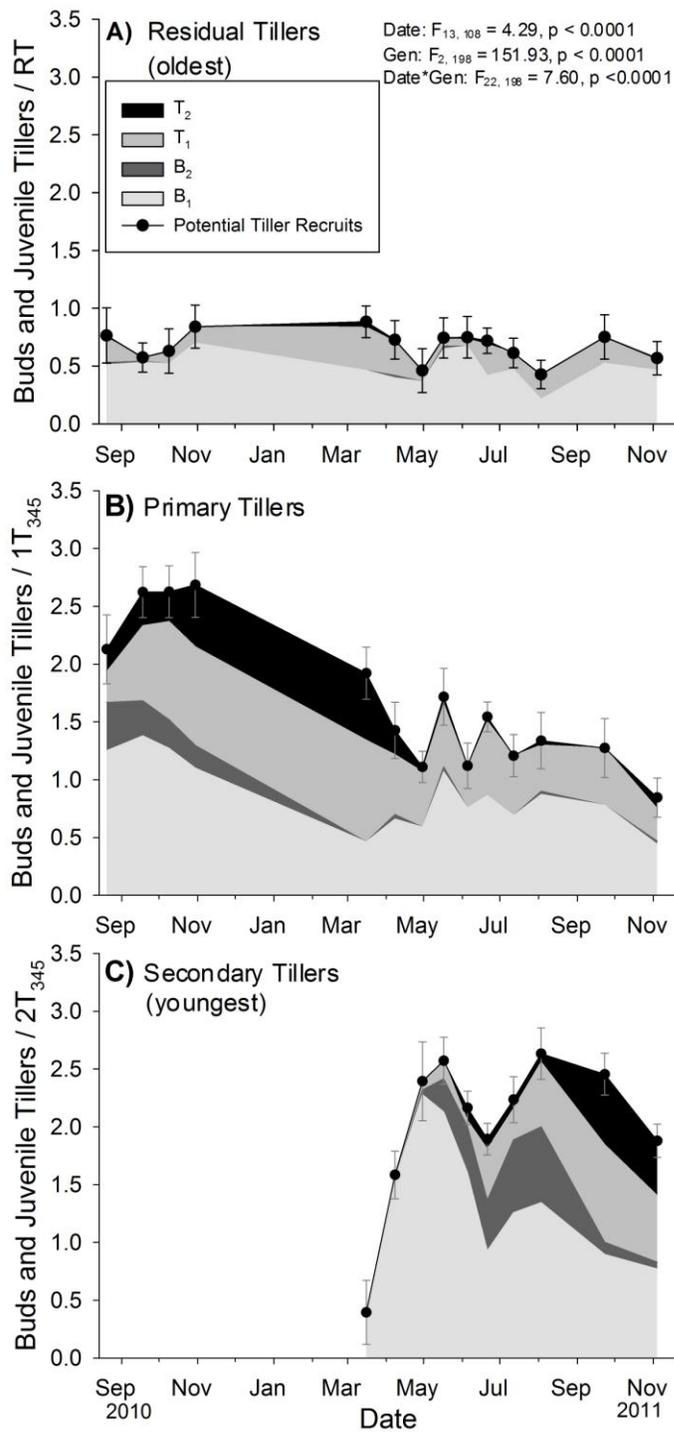
**Figure 3-4. Bud and juvenile tiller production of three tiller (T$_{3-5}$) generations.** Although tillers may senesce (T$_5$), they still maintained potential tiller recruits (i.e. buds and juvenile tillers). Error bars are ± 1 s.e.

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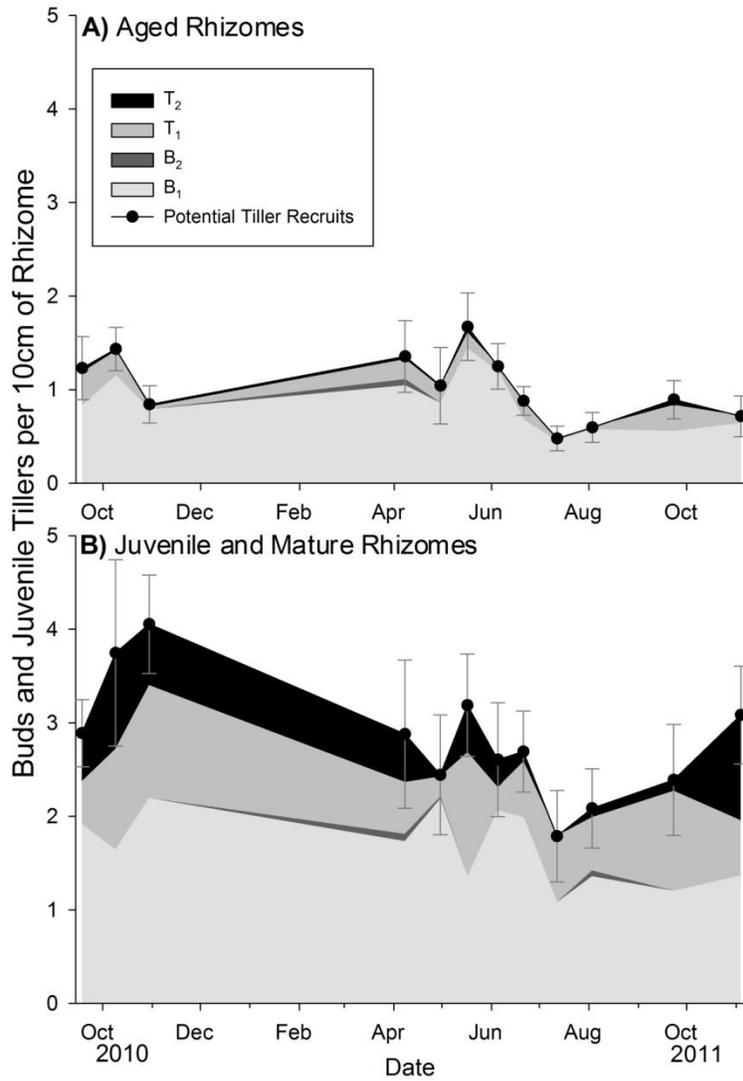
**Figure 3-5. Potential tiller recruits (i.e. buds and juvenile tillers) per 10cm of rhizome.** A) Aged Rhizomes ($R_3$) and B) Juvenile and mature rhizomes ($R_{12}$). Error bars are ± 1 s.e.
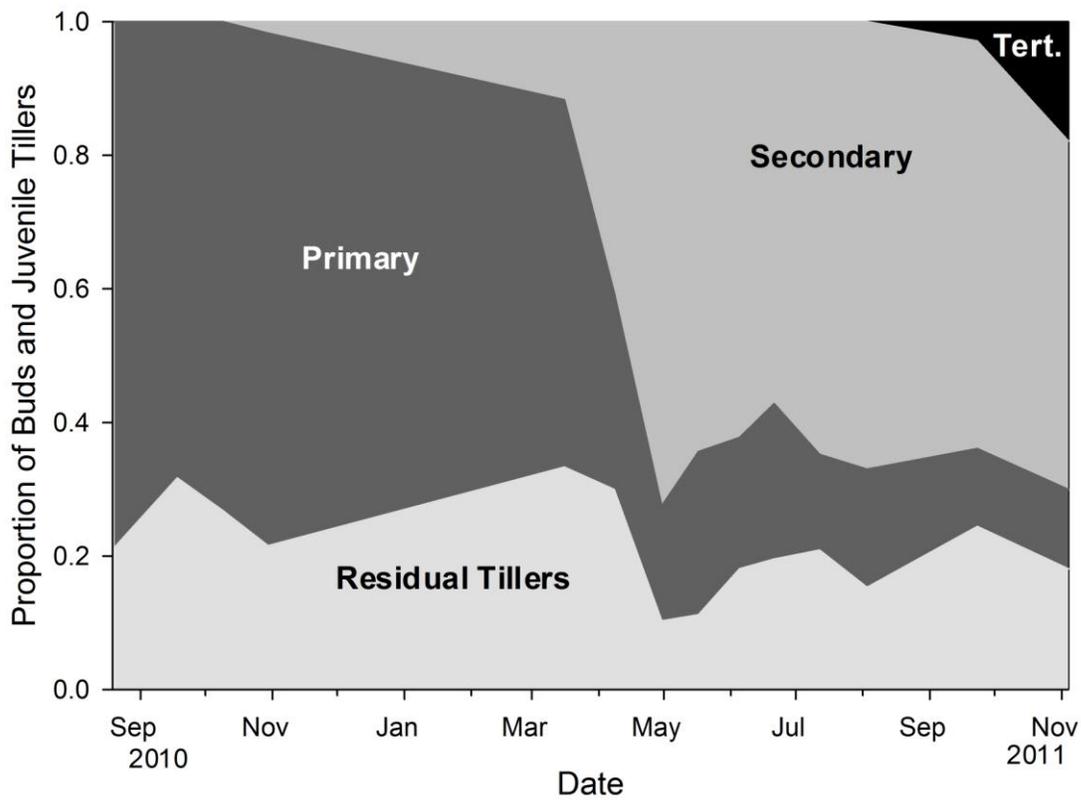
**Figure 3-6. Proportion of buds and juvenile tillers on tillers ($T_{345}$) according to tiller generation.** Residual tillers are the oldest generation followed by primary, secondary, and tertiary tiller generations.
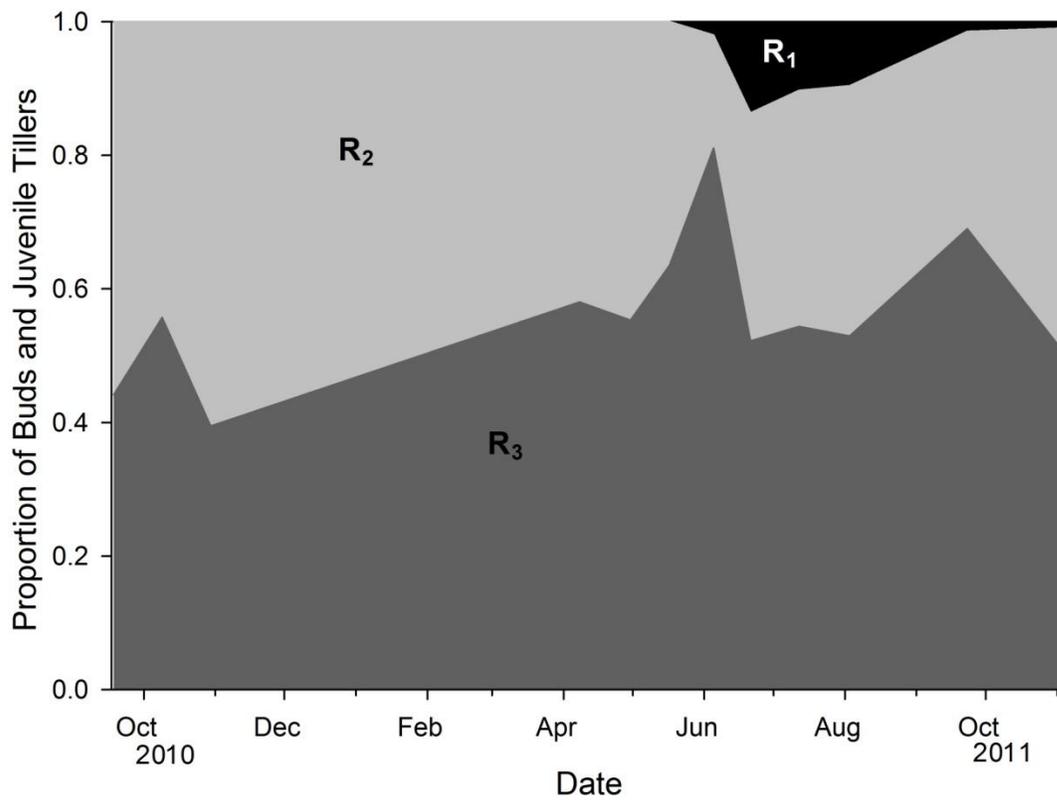
**Figure 3-7. Proportion of buds and juvenile tillers on rhizomes according to rhizome age.**
Rhizomes are either juvenile ($R_1$), mature ($R_2$), or aged ($R_3$).

**Table 3-1. Bud and tiller developmental stages.** The recorded vegetative tiller height of *P. smithii* was obtained from Flora of the Great Plains (Great Plains Flora Association, 1986). *Pascopyrum smithii* often maintained small juvenile tillers ($VT_1$) at < 3mm in height and with the tiller barely protruding beyond its prophyll.

| Symbol | Developmental Stage | Description |
|---|---|---|
| $B_1$ | Small buds | < 3.0 mm height |
| $B_2$ | Large buds | $\geq$ 3.0 mm height |
| $T_1$ | Small juvenile tillers | < 1.0 cm height; (< 2% of recorded vegetative tiller height) |
| $T_2$ | Large juvenile tillers | 1.0 mm – 4.5 cm height; (2-9% of recorded vegetative tiller height) |
| $T_3$ | Small tillers | <4.5 – 16.5 cm height; ( 9-33% of recorded vegetative tiller height) |
| $T_4$ | Large tillers | > 16.5 cm height; (>33% of recorded vegetative tiller height) |
| $T_5$ | Senesced tillers | Aboveground parts senesced but retaining live residual base with buds |
| RT | Residual tillers | Aboveground parts absent but retaining residual base with buds |
| $R_1$ | Juvenile rhizomes | White actively elongating rhizome with a white rhizome sheath (or bracts); pliable; (~0-3 months old) |
| $R_2$ | Mature rhizomes | Yellow, hardened rhizome with senesced rhizome sheath (or bracts); (~3-12 months old) |
| $R_3$ | Aged rhizomes | Brown, senesced rhizome and rhizome sheath (or bracts); (typically > 1 year old) |

**Table 3-2. Observed and expected proportions of bud sources from which secondary tillers ($2T_3$) were recruited during their peak recruitment period (April 30, 2011- June 5, 2011).** N=336. Expected proportions were based on the number of buds present from each source at the time of tiller recruitment. Buds from each source were expected to have similar outgrowth probabilities.

| Source of Tiller | Expected | Observed | z-score |
|---|---|---|---|
| Residual Tiller Bud | 0.16 | 0.04 | z = -6; p<0.0001 |
| Primary Tiller Bud | 0.26 | 0.57 | z = 13; p<0.0001 |
| Axillary Rhizome Bud | 0.56 | 0.17 | z = -14; p<0.0001 |
| Apical Rhizome Bud | 0.02 | 0.22 | z = 26; p<0.0001 |

**Table 3-3. Observed and expected proportions of bud sources from which tertiary tillers ($3T_3$) were beginning recruitment in November 2011.** N=28 Inadequate counts for each source prevented statistical analysis.

| Source of Tiller | Expected | Observed |
|---|---|---|
| Secondary Tiller Bud | 0.59 | 0.79 |
| Axillary Rhizome Bud | 0.34 | 0.14 |
| Apical Rhizome Bud | 0.07 | 0.07 |

# Appendix
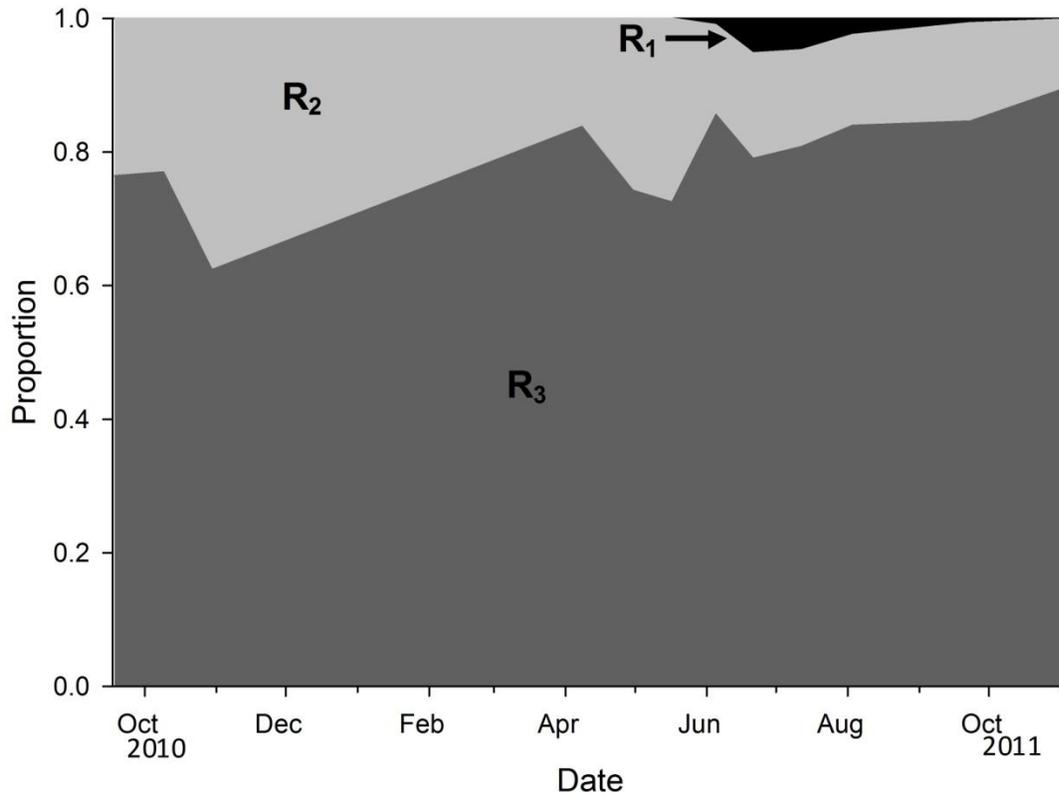


**Appendix Figure 3-1. Proportion of rhizome length according to rhizome age.** Approximate age ranges of rhizomes are 1) Juvenile rhizomes ($R_1$): 0 - 3 months, 2) Mature rhizomes ($R_2$): 3-12 months, and 3) Aged rhizomes ($R_3$): usually >1 year.

# Chapter 4 - Central and peripheral populations of the perennial grass *Andropogon gerardii* persist via vegetative reproduction

## Abstract

1. Successful sexual reproduction often declines in a plant species near its range limit and vegetative reproduction may play a more significant role in determining its distributional range and population dynamics. The vegetative reproduction of *Andropogon gerardii*, a prominent $C_4$ perennial grass of the Great Plains of North America, was compared between its tallgrass prairie range center and its range edge in northern $C_3$-dominated mixed grass prairie.

2. Bud production and tiller recruitment in ten populations were examined throughout an annual growing cycle in the northern mixed grass prairie of western South Dakota. Bud bank characteristics and both individual and population performance were compared with previous work conducted in eastern Kansas tallgrass prairie. Stage-structure matrix models were used to examine population growth rates.

3. *Andropogon gerardii* tillers produced lower numbers of buds and had a lower flowering probability in peripheral populations. The annual phenology of bud and tiller development was also contracted to fit within the shorter growing season at the range periphery. Bud longevity and bud bank age structure were similar between regions.

4. Mean population growth rates ($\lambda$) of each region were positive and not significantly different from one another. In both regions, bud production of vegetative tillers and changes in annual tiller recruitment from young buds had the largest potential influence on future changes in $\lambda$.

5. Reduced regional productivity of *A. gerardii* in northern mixed grass prairie does not appear to be due to differences in the population growth rate of vegetative reproduction. Instead, a greater patchiness of suitable habitat and/or reduction in tiller size may offer an explanation for this reduction in productivity.

6. The response of *A. gerardii* populations to climate change and disturbance are largely dependent on how these drivers alter the cycle of bud production of vegetative tillers and subsequent young bud to vegetative tiller transitions.

7. Synthesis: Despite declines in individual performance of both sexual reproduction and vegetative reproductive capacity (i.e. bud production) in peripheral populations, vegetative reproduction via the belowground bud bank enabled population persistence of a perennial grass at both the center and periphery of its range.

Keywords: bud bank, matrix model, mixed grass prairie, phenology, population growth rate, range limit, tallgrass prairie

## **Introduction**

Successful sexual reproduction of a plant species generally occurs under a narrower range of environmental conditions than its vegetative growth and reproduction (Baker's Law; Baker 1959; Hengeveld 1990; Philbrick & Les 1996). At the distribution range limit of a species, favorable environmental conditions deteriorate especially if the range limit depicts the edge of the fundamental niche (Pulliam 2000; Samis & Eckert 2009). As a result, seed production and seedling recruitment are expected to decline (e.g. Iversen 1944; Pigott & Huntley 1981; Jump & Woodward 2003; Tsaliki & Diekmann 2009 but see Sexton *et al.* 2009). An annual plant population at its species' range limit that fails to maintain a self-sustaining level of seed production is dependent on metapopulation processes, particularly the "rescue effect" of seed dispersal from nearby source populations. Instead of becoming completely dependent on seed immigration, peripheral perennial plant populations may persist primarily via vegetative reproduction, only requiring seeds to establish new populations (Minnick & Coffin 1999). A shift from primarily sexual to vegetative reproduction at range boundaries can negatively impact a population's long-term survival and adaptive potential due to a reduction in outcrossing resulting in lower genetic variation (Dorken & Eckert 2001). However, the shift would enable range boundary populations to persist over short time scales and could contribute to their long-term resistance to extirpation (Nantel & Gagnon 1999).

Dominant perennial grass populations in the Great Plains of North America primarily reproduce vegetatively rather than sexually throughout their range. Although these grasses can put forth a sizable flowering effort (e.g. Fay *et al.* 2003), seedling recruitment of these grasses in undisturbed habitat is rare (Fair *et al*. 1999; Peters 2000; Benson & Hartnett 2006). Therefore, most tiller recruitment occurs via vegetative reproduction from belowground axillary buds (i.e.

the bud bank *sensu* Harper 1977; Benson & Hartnett 2006). Dominant and subdominant perennial grasses within the same grassland can vary in their timing of annual bud production and in their bud bank size and age structure (Ott & Hartnett 2012). This local interspecific variation in bud bank characteristics suggests the possibility of smaller regional intraspecific variation in bud bank characteristics. Vegetative reproduction of a perennial grass could change near its range limit similar to changes observed in the flowering effort and seed production of some annual species near their range limits.

In peripheral perennial grass populations, population persistence and expansion could be assisted or inhibited by vegetative reproduction characteristics depending on whether populations have reached their physiological limits (e.g. Arris & Eagleson 1989) or have adapted to local conditions (e.g. Volis *et al.* 2004). If a species is at the edge of its niche limit and has failed to adapt, a decline in bud production, survival, and recruitment to tiller may contribute to population extinction. Although tillers are primarily recruited from young buds (< 1 year), older buds are capable of producing up to a third of annual tiller recruitment in dominant $C_4$ perennial grasses (Hendrikson & Briske 1997; Ott & Hartnett 2012). In peripheral populations, reduction or complete loss of tiller recruitment from older buds due to reduced bud longevity could produce a declining population growth rate. However, peripheral populations may be locally adapted to environmental and disturbance regime conditions or removed from common predators (Alexander *et al.* 2007; Gaston 2009). As a result, a perennial species may be capable of maintaining or increasing bud production and longevity as compared to core populations and consistently recruit tillers from all annual bud cohorts at a favorable time. Potential factors constraining range limits of plants are numerous (Holt *et al.* 2005; Gaston 2009; Sexton *et al.* 2009; Geber 2011). Therefore, a species may also experience no change in vegetative reproductive characteristics if factors such as seed dispersal, habitat suitability, or temporal climatic variability are limiting range expansion.

If range limits coincide with niche limits, both individual and population performance can shift near the range limit (Angert 2009; Samis & Eckert 2009). Individuals may alter their fecundity, growth, survival, or phenology from their central range tendencies (e.g. Carey *et al.* 1995; Lonn & Prentice 2002). However, population growth rates may not always reflect changes in individual performance across a species' range. A change in phenology may not alter demographic parameters. A decrease in one fitness component may be compensated by a change

in another demographic component (Angert 2006). Therefore, both population and individual performance should be considered when striving to understand population persistence in different portions of a species' range (Pulliam 2000).

Central-peripheral plant population comparisons often neglect the specific contributions of belowground clonal organs to aboveground ramet populations. Instead, they have focused on demographic differences in aboveground growth and sexual reproduction. Incorporating vegetative reproductive (i.e. clonality) traits has benefitted studies examining plant community assembly and structure (Klimesova & Klimes 2008; Rusch *et al.* 2011). Therefore, the study of perennial plant distributions may also benefit from considering the potential mechanistic roles of vegetative reproduction in determining or maintaining current perennial plant distributions. The perennial grass *Andropogon gerardii* Vitman offers an excellent opportunity to examine this as previous work has examined its belowground dynamics (Ott & Hartnett 2012) and this species is present throughout the Great Plains.

Regional productivity distributions of the dominant perennial grasses of the Great Plains are determined by their response to the north-south gradient in mean annual temperature (MAT) and east-west gradient in mean annual precipitation (MAP; Epstein *et al.* 1998). Because of these gradients in the Great Plains, $C_3$ grasses (i.e. cool-season phenology) dominate in the northwest and $C_4$ grasses (i.e. warm season phenology) dominate in the south and east (Teeri & Stowe 1976; Epstein *et al*. 1997). *Andropogon gerardii* is most abundant at high values of MAP and intermediate values of MAT, which are found geographically in the tallgrass prairies of eastern Kansas and Oklahoma (Epstein *et al*. 1998). Although *A. gerardii* has the $C_4$ photosynthetic pathway, the edge of its range extends into the northwestern Great Plains where the northern mixed grass community is dominated by $C_3$ perennial grasses. Populations of *A. gerardii* at this edge of its range experience lower temperatures and 60% of the average annual precipitation normally received in its optimal tallgrass prairie habitat. Thus, the phenology and/or the demographic rates of *A. gerardii* could be altered due to the contracted cooler growing season and lowered water availability.

The objective of this study was to compare vegetative reproduction of *A. gerardii* at its range center in tallgrass prairie and its range edge in northern mixed grass prairie. Specifically, vegetative reproduction of populations from these two regions will be compared by considering differences in: 1) phenology of bud and tiller development and bud bank age structure, 2)

individual tiller performance (e.g. bud production, daughter tiller initiation and establishment), 3) vital rates within the vegetative life cycle, and 4) retrospective and prospective population performance based on the finite population growth rate ($\lambda$).

## Methods

### *Site description and field sampling*

Previous bud bank research in tallgrass prairie at Konza Prairie Biological Station (KPBS) provided us appropriate demographic data of *A. gerardii* in the center of its range (Ott & Hartnett 2012). Therefore, demographic data of *A. gerardii* was only collected from the field in northern mixed grass prairie. This location offered the opportunity to examine shifts in vegetative reproduction of *A. gerardii* due to differences in climate and also between central and peripheral populations. Ideally, to fully examine the vegetative reproduction of *A. gerarii* throughout its range, this study should have included analyses of replicate populations at multiple locations of the range periphery (i.e. north, northwest, eastern edge of the prairie peninsula) and multiple central locations (i.e. Kansas, Missouri, Oklahoma). The extremely labor intensive lab processing and frequent sampling during an annual cycle made this impossible. However, this study can provide the basis for more extensive study of vegetative reproduction throughout a perennial plant species' range.

The field component of this study was conducted at Wind Cave National Park (WCNP), a 13,699 hectare mixed-grass prairie interspersed with ponderosa pine forest with hilly topography (elevation ranging from 1113m to 1527m) located at the southeastern extent of the Black Hills in western South Dakota (43º33'N, 103º29'W). Within this northern mixed-grass prairie, the vegetation is dominated by cool-season grasses such as *Hesperostipa comata*, *Pascopyrum smithii*, and *Nassella viridula* with discrete patches of less abundant warm-season grasses including *A. gerardii*, *Bouteloua curtipendula*, and *Bouteloua gracilis*. Bison (*Bison bison*), elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) are the major large herbivores. However, bison and elk are the primary consumers of grass due to their grazing habits and population sizes. For this study, the prairie portion of the 42 hectare Elk Mountain enclosure within the park, which excludes bison but not other herbivores, was used. Although a seasonal campground is located in the southern forested portion of the enclosure, the large northern portion of the

enclosure is undisturbed native mixed grass prairie. Prescribed fire occurs every 5 to 7 years. The Elk Mountain enclosure was last burned in the fall of 2008. The region's semi-arid climate has cool winters (average Jan temp: -2.3ºC) and warm summers (average July temp: 22.9ºC) with moderate rainfall (499 mm) primarily occurring April through October, especially in May and June.

In October 2010, ten sites separated by at least an average distance of $74 \pm 7$m were established within the grassland portion of the campground enclosure. Study sites occurred at an approximate elevation of 1310m with primarily loamy-skeletal soils (Typic Argiustolls) with the exception of one site in fine-loamy soil (Fluventic Haplustolls; USDA-NRCS-WSS). At each site, a population of *Andropogon gerardii* was located from which ten individuals were randomly selected and marked using a metal tag and a wire ring. *Andropogon gerardii* Vitman (big bluestem) is a short-rhizomatous $C_4$ perennial grass that produces tillers annually and flowers in the Great Plains from July to September. Due to the rhizomatous growth form and intermingling of different genets of *A. gerardii*, genets are very difficult to identify in the field. Therefore, an "individual" of *A. gerardii* consisted of all interconnected tillers and associated belowground parts within an 8.0 cm radius. A voucher specimen was collected from adjacent Custer State Park and deposited at the Kansas State University herbarium.

Beginning on March 16, 2011 until November 4, 2011, an individual from each site was harvested approximately every 3 weeks during the growing season (i.e. while soil temperatures remained consistently above freezing; 10 sample dates). At each sampling time, soil temperature was measured at a 5cm depth in three consistent locations at every site (Chapter 1 Appendix A1). Soil temperatures were taken within the first 2 hours of dawn using a thermocouple (TH-65 Thermocouple Thermometer [Wescor, Inc] or T-85154 Microprocessor thermometer Type J-K-T thermocouple Model HH23 [Omega Engineering, Inc]). Plants were harvested by excavating to a 15 cm depth and were washed to remove soil.

Although the demographic data from tallgrass and northern mixed grass prairie were collected in different years, both examined *A. gerardii* under similar field conditions. Large grazers were excluded and it had been two to three years since fire at both sites. Although KPBS has a higher average annual precipitation (835mm) than WCNP (499mm), precipitation was between 115 and 138% of the research site-specific long-term average in both the year of

(KPBS: 1012mm, WCNP: 646mm) and the year preceding (KPBS: 1153mm, WCNP: 575mm) the study at each site.

### *Lab analysis and bud, tiller, and rhizome classification*

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

Two bud developmental stages were used in this study, characterized by their prophyll development.  (1) "Developing buds" are white, deltoid to lanceolate in shape, with a live developing prophyll and with their adaxial surface tightly appressed to the base of the tiller.  (2) "Mature buds" are larger in basal girth and conical or plano-convex in shape and are surrounded by a manila or brown (i.e. senesced) prophyll.  Dead buds were easily identified by their soft, spongy or mealy brown interiors.  Collectively, developing and mature buds are referred to as "buds".

A bud transitions to a tiller when the bud elongates past its protective prophyll.  Two developmental stage classes of tillers were identified.  (1) "Initiated tillers" turn a deep fuchsia color and elongate beyond the tip of the prophyll no more than 6.0mm.  (2) "Adult tillers" were classified as those which elongated past the prophyll and had turned green.  Adult tillers were further classified as vegetative or flowering and according to annual cohort.  Three adult tiller cohorts were identified: (1) current year, (2) one year old and (3) ≥ 2 year old.  Current year adult tillers were identified by the presence of their aboveground leaves. Senesced aboveground tillers which had lost all aboveground plant material were classified as residual tillers (RT).  One year old RT were distinguishable from ≥ 2 year old RT by their color and leaf remains.  Initiated tillers were classified as activated buds in previous work (Ott & Hartnett 2012).  Changing the name of this developmental category introduces a bud and tiller development classification system that can be more widely applied as it distinguishes a bud from a tiller based on its

development in relation to the prophyll.  See Ott (2009) and Ott & Hartnett (2012) for more detailed descriptions of buds and tiller classifications.

The length of each rhizome was measured and each was classified by developmental stage.  Rhizomes were defined by having at least two elongated internodes and a horizontal trajectory in the soil.  Two rhizome developmental stages were identified. (1) "Mature rhizomes" had yellow, hardened horizontal stems with senesced scales that were typically brown and were typically associated with actively growing tillers.  Mature rhizomes also included any rhizomes currently elongating with actively growing scales.  (3) "Aged rhizomes" had browned senesced internodes and scales.

## *Data Analysis*

### *Individual Performance*

Regional and tiller cohort effects on initial spring bud numbers per tiller, peak new tiller initiation per tiller, and end-of-year bud and tiller production per tiller were tested using two-way factorial treatment structure with region and tiller cohort as fixed factors in a completely randomized design (CRD; PROC MIXED, SAS 9.2).  Kenward-Roger's method (KR) was used to approximate denominator degrees of freedom.  Heterogeneous variances were necessary in all ANOVAs according to the Brown-Forsythe test except for initial spring bud numbers per tiller. Two variance groups were used in the analyses when heterogeneous variances were necessary. One variance group consisted of the $\geq 2$ year old tiller cohort at both sites and the other consisted of all other cohorts at both sites.  When significant interactions involved more than two levels of each factor, appropriate contrasts as denoted in the results were used to explore the source of the interaction's significance.

### *Population Performance*

#### *Matrix Model*

Bud and tiller demography was cohesively examined using a stage-structured matrix population model of a plant's population of ramets (i.e. buds and tillers) over an annual time step from February to February.  The developed projection matrix:

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

had four discrete life stages including buds less than one year old (b1), buds greater than one year old (b2), vegetative tillers (v), and flowering tillers (f), and stage-specific transition rates for axillary bud survival (S), belowground axillary bud production (i.e. vegetative bud production/fecundity, V), and growth (G) (Fig. 4-1). The projection matrix assumed no density dependence and was linear and deterministic.

### *Model parameterization and assumptions*

Projection matrices, one for each population within each region, were parameterized to determine population growth rates and to use in retrospective and prospective analyses. Vital rates were calculated using per tiller estimates of buds and current year tillers of three tiller cohorts (current year (V and F), one year old ($RT_1$), and ≥ two year old ($RT_2$); Table 4-1). Although the abundance of each tiller cohort drives the overall bud bank composition of an individual, the transitions between stages is controlled at the tiller level (i.e. apical dominance). 'Per tiller' estimates also help control for differences, such as tiller number, among individuals within a population. Vital rate calculations often involved two different individuals within a population destructively harvested on different sample dates. Therefore, it is beneficial to use 'per tiller' estimates to calculate transition rates. Fecundity and growth transition rates included both the production or growth and the subsequent survival at that stage over the annual time step.

Individual growth and survival rates should not exceed 1 nor should growth and survival rates transitioning from the same node sum to greater than one. In these data, five cases occurred where the sum of rates from the same node exceeded 1 and one case occurred where a $G_{b2-v}$ transition rate exceeded 1. These overestimates were assumed to be due to high variability of buds per residual tiller, especially per $RT_2$, between dates within a population rather than incorrect estimates of bud transition to tiller. Therefore, $S_{b2}$ and/or $G_{b1}$ were corrected in order to obtain reasonable transition rates coming from the same node that summed to 1 and $G_{b2-v}$ was set to 1. Estimates of $V_f$ were unavailable for seven of the WCNP populations. The WCNP average of $V_f$ was used in the projection matrices of these populations.

In order to produce each of the eight transition rates for each region, several assumptions were made. (1) No buds produced in the current year recruit to tiller before the end of the growing season. Tiller recruitment from current year buds is rare and is mainly observed in years of extreme drought (Ott, unpublished data). (2) Axillary buds produced by flowering and vegetative tillers have equivalent outgrowth probabilities. Differences in bud outgrowth probabilities of flowering versus vegetative tillers are unknown at WCNP and for older buds. Although a short-term field study at KPBS indicated that one year old axillary buds of *A. gerardii* flowering tillers have greater outgrowth probabilities than buds of its vegetative tillers (Ott & Hartnett 2011), this trend may not occur at WCNP. Therefore, buds of flowering and vegetative tillers are assumed to have equivalent outgrowth probabilities. Flowering tillers of *A. gerardii* make up a considerably smaller proportion of the tiller population than vegetative tillers. Because data were obtained in a growing season conducive to high flowering effort and thus a larger contribution of buds to the bud bank by flowering tillers, bud outgrowth estimates may be slightly overestimated at KPBS. (3) Bud death is minimal over the winter months. For each *A. gerardii* tiller cohort, bud numbers per tiller did not change over the winter at KPBS (Ott & Hartnett 2012). (4) Tillers that fail to establish and rhizomes do not contribute to the bud bank. Rhizome buds of *A. gerardii* were low in number and never transitioned to tiller (Ott & Hartnett 2012). Tillers that do not survive to the end of the growing season due to causes such as herbivory or drought produce low numbers of buds (Ott 2009). The overall contribution of these non-establishing tillers in relation to the contributions of established tillers to the bud bank is small and can be excluded. (5) Residual tiller density does not change during the growing season. Residual tiller density was variable but there was no notable change in its density over time at WCNP. However, because older residual tillers likely decompose within the growing season, $S_{b2}$ could be an overestimate. (6) Recruitment from seed does not occur. In tallgrass prairie, tiller recruitment from seed occurs rarely as less than 1% of all established shoots in annually and infrequently burned prairie came from seed (Benson & Hartnett 2006). Seedlings of *A. gerardii* were never observed at WCNP or KPBS during these studies.

*Matrix parameter and model analyses*

Regional effects on each matrix element were tested using either a one-way treatment structure ANOVA or contrasts within two-way factorial treatment structure ANOVA. For $G_{b1}$ and $S_{b2}$, one-way treatment structure with the fixed factor of region in a CRD with KR were used

(PROC MIXED, SAS 9.2).  Based on the Brown-Forsythe test, homogeneous variances and heterogenous variances were necessary for $G_{b1}$ and $S_{b2}$ respectively.  Regional and bud age effects on bud to vegetative tiller transitions and bud to flowering tiller transitions were each tested with a two-way factorial treatment structure with the fixed factors of region and bud age class in a CRD.  Due to non-normality of the data, data were aligned rank-transformed (PROC MIXED, SAS 9.2; Higgins 2004).  Regional effects within bud age class and bud age class effects within region on bud transition to tiller were tested with contrasts of rank-transformed data controlling for the familywise error rate (FWER) by using the permutation min-p adjustment (PROC MULTTEST, SAS 9.2).  Bud production matrix elements were evaluated using a two-way factorial treatment structure with the fixed factors of region and tiller developmental status in a CRD with homogeneous variances using KR (PROC MIXED, SAS 9.2).  The FWER of pairwise differences was controlled using Bonferroni's adjustment.

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

Estimates of the variance around the fixed effect LTRE contribution values and regional element elasticities, loop elasticities, stable stage distributions, and $\lambda$s were obtained using a bootstrap approach.  Appropriate distributions were fitted to each regional vital rate to obtain bootstrapped distributions of these values.   Normal distributions were fitted to fecundity vital rates and beta distributions were fitted to all other vital rates (Appendix Table 4-1).  Every distribution was assessed for goodness-of-fit (GOF; Shapiro-Wilks or Kolmogorov-Smirnov at $\alpha$ =0.05; PROC UNIVARIATE, SAS 9.2).  If fitted distributions were rejected due to GOF tests or fitted beta distributions were U-shaped due to one observational value being greatly different

from the rest of the observations in the data, distributions were not assigned to these matrix elements. Instead, their values were resampled with replacement from among the values of the 10 populations of the given region in the following bootstrapping analysis (Appendix Table 4-1). Growth and survival rates transitioning from the same node were constrained to sum $\leq 1$. From the bootstrapped distributions (10,000 iterations) of regional matrix element elasticities, loop elasticities, stable stage distribution elements and $\lambda$s, 95% bootstrapped confidence intervals were extracted and randomization tests were conducted to obtain p-values comparing each of these parameters between regions (Brault & Caswell 1993; Gotelli & Ellison 2004). P-values were insensitive to using either the vital rates of the regional mean matrices or the bootstrapped means as the observed value (Gotelli & Ellison 2004). Bootstrapped 95% confidence intervals were also obtained for the contribution values produced in the fixed effect LTRE comparing regions. LTRE analyses and bootstrapping were conducted in R (R Foundation for Statistical Computing 2013).

## Results

### *Bud bank characteristics and vegetative reproduction phenology*

Both bud development and transition to tiller at WCNP were synchronous across all bud cohorts (Fig. 4-2, Appendix Fig. 4-1). Bud longevity at WCNP exceeded 2 years creating a multi-age bud bank primarily composed of buds $\leq$ one year old (Fig. 4-3). These characteristics were similar to those of *A. gerardii* populations at KPBS (Ott & Hartnett 2012). In the spring, mature buds began transitioning to initiated tillers at a similar time but more rapidly at KPBS than at WCNP (Fig. 4-4B). Although adult tiller production was delayed at WCNP by 5-6 weeks (Fig. 4-4C), bud production on these adult tillers began at both sites within two weeks of each other (Fig. 4-4D). Bud production was completed within 8 and 12 weeks at WCNP and KPBS respectively. Bud production at WCNP occurred at a consistent rate while bud production at KPBS occurred rapidly for the first four weeks and then more slowly for the remaining 8 weeks (Ott & Hartnett 2012).

### *Individual tiller performance*

Individual tiller performance varied with region and tiller cohort. In the spring, tillers from KPBS had significantly more buds than those from WCNP and one-year old tillers ($RT_1$)

had significantly more buds than two-year old tillers ($RT_2$; Fig. 4-4A). Peak tiller initiation was significantly greater from KPBS $RT_1$ than WCNP $RT_1$ but did not differ by region on $RT_2$ (Fig. 4-4B). Overall $RT_1$ had significantly greater peak bud outgrowth than $RT_2$ (Fig. 4-4B). Buds of $RT_1$ produced $89 \pm 2\%$ and $65 \pm 3\%$ of current year tillers at WCNP and KPBS, respectively (Ott 2009). Final current year tiller production was significantly greater on $RT_1$ than $RT_2$ but did not significantly differ between regions (Fig. 4-4C). By the end of the growing season, current year tillers had significantly more buds than $RT_1$ ($t_{94}= 19.02$, p <0.0001) and $RT_1$ had significantly more buds than $RT_2$ ($t_{129} = 35.49$, p<0.0001). At that time, KPBS had significantly more buds than WCNP only on current year tillers but not on older tiller cohorts (contrast: $RT_1$ vs $RT_2$ across region, $F_{1, 129} = 0$, p = 0.97; contrast: $RT_1$ and $RT_2$ vs Current tillers across region, $F_{1,103} = 25.9$, p<0.0001). Although fewer buds were maintained on $RT_2$ than on $RT_1$, $RT_2$ were more abundant than $RT_1$ over the entire time of the study in each region (KPBS: $5.3 \pm 0.4$ $RT_2/R_1$, WCNP: $4.2 \pm 0.4$ $RT_2/R_1$). In summary, on a per tiller basis, *A. gerardii* at KPBS produced more buds and initiated more tillers than WCNP. Adult tiller production and the amount of buds on older tiller cohorts ($RT_1$ and $RT_2$) in the fall were similar at both sites. Younger tillers ($RT_1$) maintained more buds and parented more new tillers than did older tillers ($RT_2$).

Rhizome buds made small contributions to the bud bank and none of them transitioned to tiller at either site (Fig. 4-3, Ott & Hartnett 2012). Rhizomes at WCNP averaged $2.00 \pm 0.05$ cm in length and maintained $0.13 \pm 0.02$ and $0.17 \pm 0.04$ buds per cm of rhizome for aged and mature rhizomes respectively. Rhizomes were formed when axillary buds elongated and became the apical meristem of the rhizome. The apical meristem of the rhizome always rapidly transitioned into an aboveground tiller or died.

### *Regional vital rates*

Consideration of vital rates offers a broader perspective of the regional differences in *A. gerardii* ramet demography. Flowering tillers produced significantly more buds than vegetative tillers at each site (Region: $F_{1, 30} = 34.45$, p<0.0001, Tiller Development: $F_{1,30} = 16.90$, p = 0.0003, R*TD: $F_{1,30} = 0.39$, p = 0.54). Vegetative fecundity (i.e. bud production) was lower at WCNP than at KPBS. Both flowering and vegetative tillers at WCNP had significantly lower bud production than tillers of comparable flowering status at KPBS (Table 4-2). Vital rates

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within the bud bank (bud survival [$G_{b1}$ and $S_{b2}$]) did not significantly vary between regions (Table 4-2).

Tiller recruitment was significantly affected by region and bud age class. In general, buds at WCNP had significantly higher probabilities of transitioning to vegetative tillers than at KPBS (Region Main Effect (ME): $F_{1,36} = 5.95$, p = 0.020). Younger buds transitioned to vegetative tiller at higher rates than older buds at both sites (Bud Age Class ME: $F_{1,36} = 26.69$, p < 0.0001, Region*Bud Age Class: $F_{1,36} = 0.10$, p = 0.76). Although older bud outgrowth to vegetative tillers did not significantly differ between regions (Table 4-2), this difference is primarily responsible for the significance of the region ME on vegetative tiller recruitment. More younger buds transitioned to flowering tillers at KPBS than WCNP but both sites transitioned similar amounts of older buds to flowering tillers (Region ME: $F_{1,36} = 67.78$, p < 0.0001, Bud Age Class ME: $F_{1,36} = 21.57$, p < 0.0001, Region*Bud Age Class: $F_{1,36} = 18.81$, p = 0.0001; Table 4-2).

### *Retrospective population performance analysis*

Retrospective analyses suggest that *A. gerardii* has relied upon similar vital rates in both regions to maintain increasing populations. Finite population growth rates did not vary significantly by region ($\lambda_{wcnp} = 1.485$, $\lambda_{kpbs} = 1.514$, p = 0.94). Overall, most vital rates provided similar contributions to λ in each region (Fig. 4-5). However, all contributions of flowering tillers (i.e. $V_f$, $G_{b1-f}$, and $G_{b2-f}$) contributed significantly more to λ at KPBS than WCNP but contributions from $V_f$ and $G_{b2-f}$ were small. Bud production of vegetative tillers also tended to contribute more to $\lambda_{kpbs}$ than to $\lambda_{wcnp}$. To offset these contributions to $\lambda_{kpbs}$, vegetative tiller recruitment from the second bud age class tended to contribute more to $\lambda_{wcnp}$.

Due to a larger variance around $\lambda_{wcnp}$, 95% bootstrapped confidence intervals of $\lambda_{wcnp}$ included 1 unlike $\lambda_{kpbs}$ (var($\lambda_{wcnp}$) = 0.116, $CI_{wcnp}$ = [0.930, 1.947]; var($\lambda_{kpbs}$) = 0.053, $CI_{kpbs}$ = [1.140, 1.877]). Variances and covariances involving the transition of buds to vegetative tillers from either bud age class ($G_{b1-v}$ and $G_{b2-v}$) at WCNP contributed to ~90% of the variance in $\lambda_{wcnp}$. At KPBS, variances and covariances associated with the transition of young buds to vegetative and flowering tillers ($G_{b1-v}$ and $G_{b1-f}$) contributed to ~85% of the variance in $\lambda_{kpbs}$ (Appendix Table 4-2). Therefore, transitioning of buds to tillers, especially younger buds to vegetative tillers, is responsible for a large portion of the observed variability in each region's λ.

*Prospective population performance analysis*

A proportional perturbation of each vital rate would have a similar effect on λ in both regions (Table 4-3). A change in the vital rates of vegetative tiller recruitment from young buds or bud production of vegetative tillers would initiate the largest potential change in λ (Δλ). Therefore, perturbations of the cycle of vegetative tillers recruiting from young buds and subsequently producing buds would have an exceedingly large impact on λ (Table 4-4). Alterations in vital rates involving older buds and flowering tillers only would create small changes in λ. During the study, all known possible biological transitions between stages were observed except for older buds transitioning to flowering tillers at WCNP. Based on the sensitivities of demographic parameters at WCNP (Appendix Fig. 4-2), adding this transition to this population's demography would have a moderate to large positive effect on λ. However, increases in tiller recruitment from young buds would have greater effects on λ and may be more biologically feasible.

Predicted stable stage distributions did not differ significantly by region and favored maintaining a large bud bank with a large proportion of buds less than one year old. (Table 4-5). Observed stable stage distributions did not differ significantly from predicted stable stage distributions for either region implying that these populations are at equilibrium (Table 4-5).

## Discussion

Although individual performance of vegetative reproduction was lower in peripheral than central populations and the phenology of individuals shifted in peripheral populations, population performance of vegetative reproduction was similar in both peripheral and central *A. gerardii* populations. Individual *A. gerardii* tillers produced lower numbers of buds and had a lower flowering probability in peripheral populations. The annual phenology of bud and tiller development was contracted to fit within the shorter growing season at the northwestern periphery of its range. However, mean population growth rates of each region indicated positive growth and were similar to one another. A decline in population performance in peripheral plant populations does not always occur (Stokes *et al.* 2004; Angert 2009; Villellas *et al.* 2013). The rarity of sexual reproduction in peripheral *A. gerardii* populations did not limit their ability to persist and expand via vegetative reproduction. Therefore, persistence of peripheral *A. gerardii*

populations is not dependent on metapopulation dynamics but are dependent on consistent tiller recruitment from the bud bank.

Sexual reproduction and seed dispersal still play a role in determining the broad scale distribution of perennial grasses (Brown & Gersmehl 1985). For example, local persistence of two *Bouteloua* species with very low seedling establishment dominate their respective North American grasslands, desert grassland and shortgrass steppe, via vegetative reproduction (Lauenroth *et al.* 1994; Peters 2000). However, spatial patterns in soil water availability and temperature determined seed germination and establishment of each species and explained the location of the ecotone between desert grassland and shortgrass steppe (Minnick & Coffin 1999). Tallgrass $C_4$ perennial grasses are still slowly expanding westward since the 1800's at speeds that require seed dispersal, especially in the southern prairies (Brown 1993). Only when vegetative reproduction fails to maintain a population will perennial grass expansion reach its physiological range limit. At that point, edge populations will become sink populations dependent on seed immigration from more central source populations.

The local population persistence ability of *A. gerardii* in northern mixed grass prairie does not explain its reduction in regional productivity as compared to tallgrass prairie (Epstein *et al.* 1998). Assuming that the range center is the niche center of a species and that these optimal conditions are spatially autocorrelated, overall habitat is expected to decline in its suitability at the edge of its range (Brown 1984). However, at the edge of its range, habitat may not just decline in suitability but suitable habitat may have a more patchy distribution across the landscape. The cool-season and warm-season elements of northern mixed grass prairie in South Dakota occur in distinctive topographic positions with warm-season grasses occupying warmer, open sites and cool-season grasses occupying cooler, more shaded sites (Tiezson 1970; Teeri 1979; Barnes *et al.* 1983; Steuter 1987). In the nearby Nebraska sandhills, $C_3$ and $C_4$ prairie elements were spatially segregated depending on the seasonal timing of soil moisture (Barnes & Harrison 1982). Local separation of $C_3$ and $C_4$ grasses along environmental gradients would be expected at the latitude of this study due to the difference in temperature effect on $C_3$ and $C_4$ quantum yields (Ehleringer 1978; Barnes *et al.* 1983). Therefore, reduced regional productivity of *A. gerardii* in northern mixed grass prairie is likely a result of greater patchiness of suitable habitat rather than a large difference in population persistence ability. Reduction in tiller size in

mixed-grass prairie due to climate, competition, and genotype could also reduce regional productivity of *A. gerardii*.

Evidence of *A. gerardii* nearing its range limit where vegetative reproduction is unable to sustain populations in the northern mixed grass prairie was subtle. Both central and peripheral populations of *A. gerardii* were evaluated under high precipitation years. Even with these good growing conditions, a few peripheral populations of *A. gerardii* could have declining population growth rates. Probability of population extinction increases as λ decreases and the variance of λ increases (Lande & Orzack 1988; Lande 1993). The population growth rate of a peripheral population could decline in years with less favorable growing conditions or have a high interannual variability due to variable climatic conditions. Increased demographic variability in populations located closer to the margin of their species' distribution could be a factor limiting their species' range limits (Nantel & Gagnon 1999). Extreme climatic events may determine range limits more frequently than mean environmental conditions (Klok *et al.* 2003).

Current variability in annual rates of bud transition to tiller made the largest contribution to within-region variation in λ. Future changes in λ of both regions will be most strongly influenced by changes in vegetative tiller recruitment from young buds and bud production on vegetative tillers. Therefore, the response of *A. gerardii* populations to climate (e.g. drought) and disturbances such as grazing are largely dependent on how these disturbances alter the cycle of bud production of vegetative tillers and subsequent vegetative tiller recruitment from young buds.

Tiller recruitment may be more easily altered than bud production per tiller. Grazing reduced the number of tillers per plant but not bud production per tiller in three perennial $C_4$ grasses (Hendrikson & Briske 1997; N'Guessan & Hartnett 2011). Drought in tallgrass prairie only altered annual bud production per *A. gerardii* tiller by one to two buds (Ott, unpublished data). *Andropogon gerardii* bud production per tiller may remain relatively unchanged unless a disturbance occurs during the one month period of rapid bud development (VanderWeide 2013). Insuring adequate population performance of key forage grasses may depend on a minimum level of tiller recruitment if bud production per tiller remains largely unaltered by grazing or climatic shifts. Therefore, the key to understanding how future tiller recruitment can influence population performance depends on understanding the environmental and hormonal controls of

apical dominance, sustained bud outgrowth, and individual bud characteristics (Tomlinson & O'Connor 2004; Waldie *et al.* 2010; Williamson *et al.* 2012).

Bud bank characteristics were conserved between peripheral and central populations. Bud longevity and vital rates within the bud bank were similar between regions leading to bud banks with similar age structure. Annual tiller populations were primarily recruited from younger buds. The contributions of older buds to annual tiller production may be small and would be insufficient to offset parent tiller mortality without additional tiller recruitment from younger buds (Hendrikson & Briske 1997; Ott & Hartnett 2012). However, older buds contribute to *A. gerardii* population stability as they comprised a large proportion of the stable stage distribution population. Older buds are often the most proximal buds of those originally produced on an individual tiller and usually yield tillers with reduced vigor (Mitchell 1953; McIntyre 1972; Mueller and Richards 1986). Therefore, older buds have been proposed to be vestigial organs which have missed their primary outgrowth opportunity and continue to exist due to the developmental constraints of bud abortion and their low maintenance costs (Hendrikson & Briske 1997). Buds within the bud bank can be used for renewal (i.e. annual tiller recruitment) or regeneration (i.e. recovery following disturbance) and buds destined for each purpose may be indistinguishable from one another (Klimesova & Klimes 2007). The decreased probability of older bud outgrowth may facilitate their population stabilizing role as regeneration buds or their ability to buffer population dynamics against unfavorable climatic conditions similar to soil seed banks (Ott & Hartnett 2012, Pake & Venable 1996).

Vegetative reproduction via the belowground bud bank can enable population persistence of perennial grasses at both the center and periphery of their ranges. Range distributions may expand or contract depending on the effects of climate change on vegetative and sexual reproduction as evidenced by changing population growth rates at range boundaries (Eckhart *et al.* 2011). The effect of climate change at the range boundary may vary among different edges as each edge is likely determined by a different suite of ecological and historical factors (Sagarin *et al.* 2006). As a mediator of grassland population and community responses to climate change and disturbance, vegetative reproduction of perennial grasses needs to be understood throughout their ranges in order to predict their population persistence and future range limit shifts.

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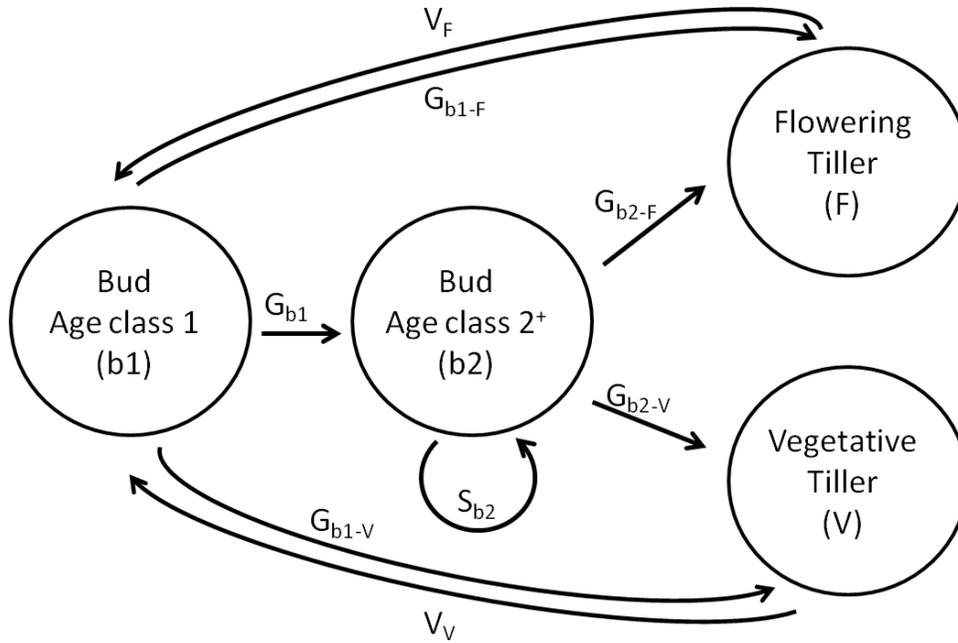
**Figure 4-1. Vegetative reproduction life cycle diagram of *A. gerardii*.** Collectively, buds from both age classes form the bud bank.
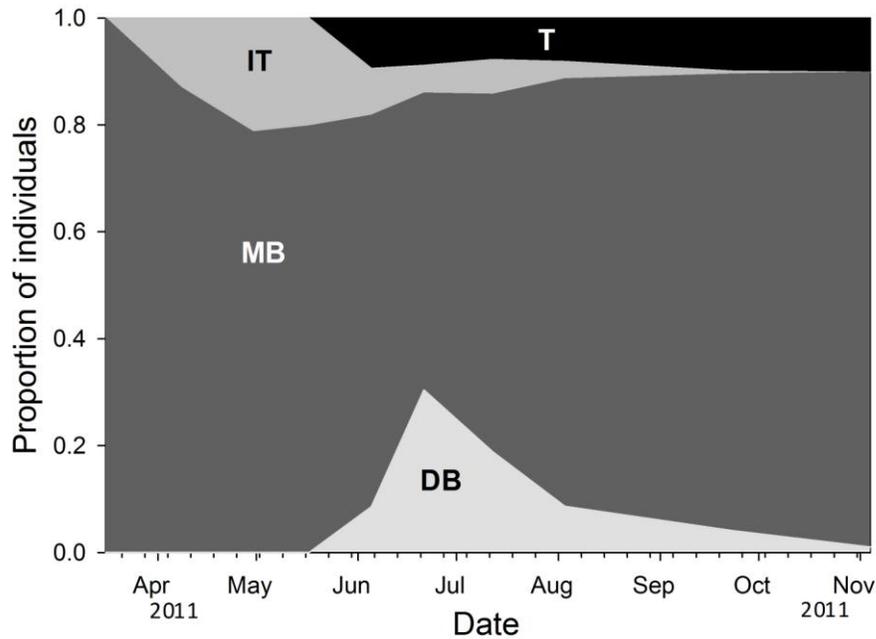
**Figure 4-2. Overall proportion of live ramets according to developmental stage at WCNP.** Developing (DB) and mature (MB) buds comprised the majority of individuals throughout the annual cycle. Initiated tillers (IT) were synchronously recruited from MB in the early spring. IT transitioned synchronously to adult tillers (T) in late spring.
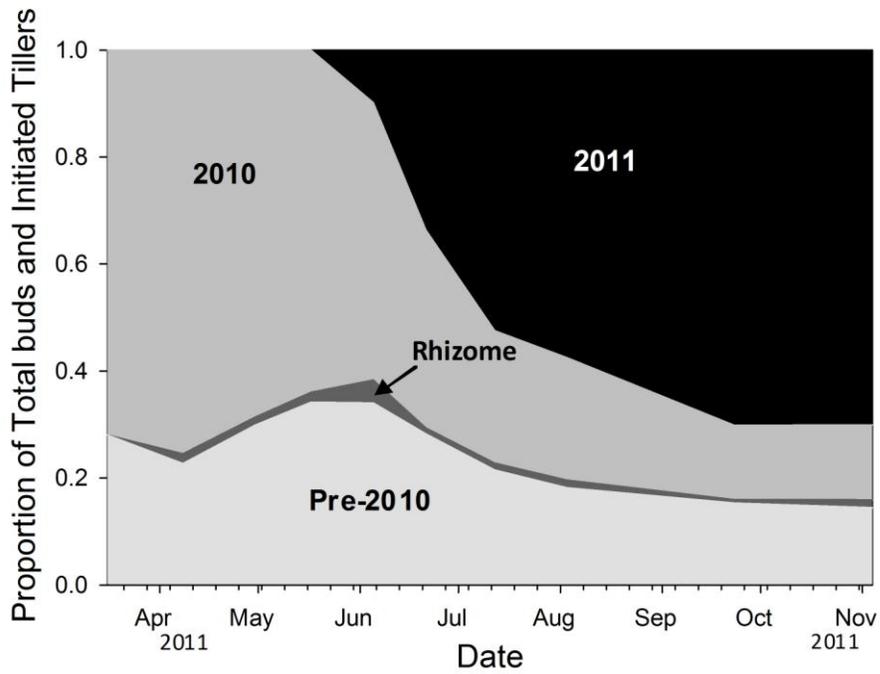
**Figure 4-3. Overall proportion of buds and initiated tillers according to cohort.** Rhizome buds were either from pre-2010 or 2010. Rhizome buds from 2011 were included with the 2011 tiller cohort. At any given point in an annual cycle, multiple ages of buds were present.
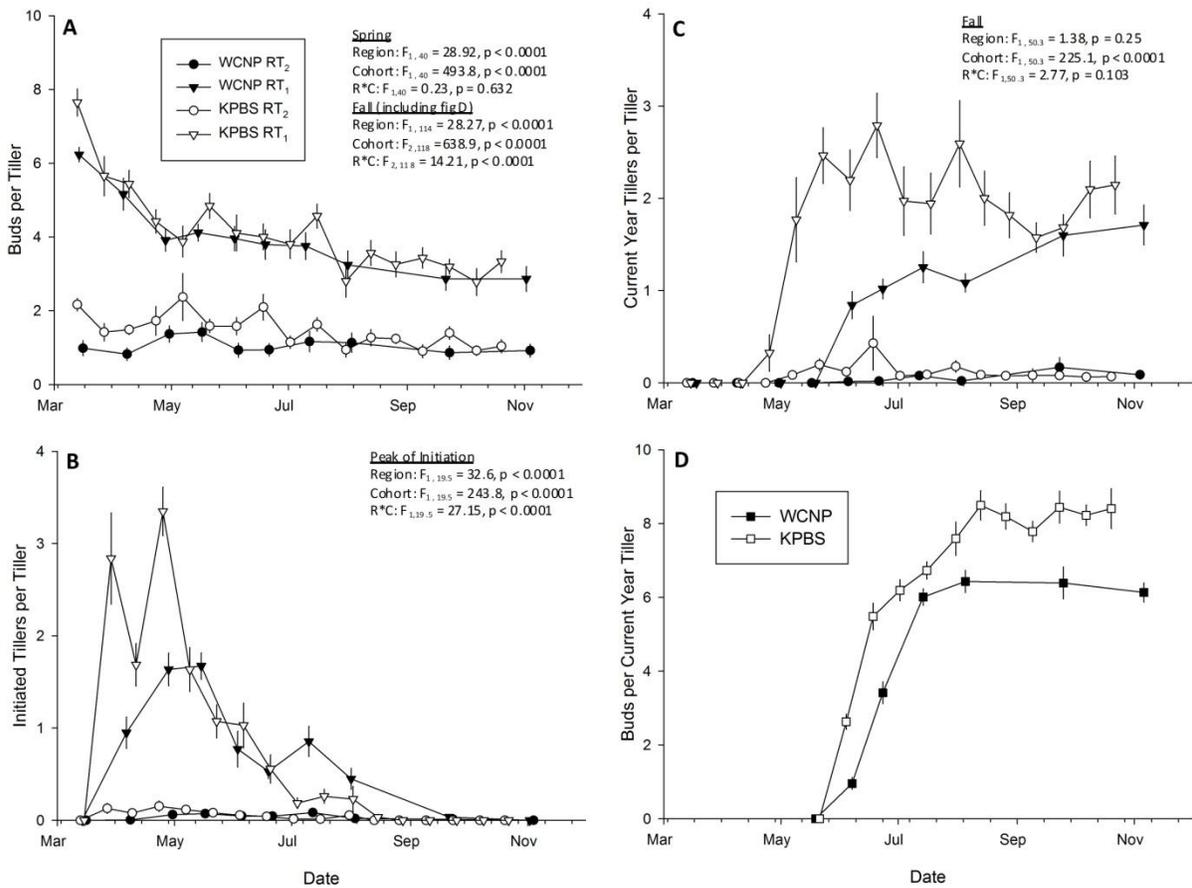
**Figure 4-4. Regional comparison of buds, initiated tillers, and new tillers supported per tiller according to cohort from Wind Cave NP (WCNP) and Konza Prairie Biological Station (KPBS).** Tiller cohorts include one year old and two year old residual tillers ($RT_1$ and $RT_2$, respectively) and current year tillers (panel D).

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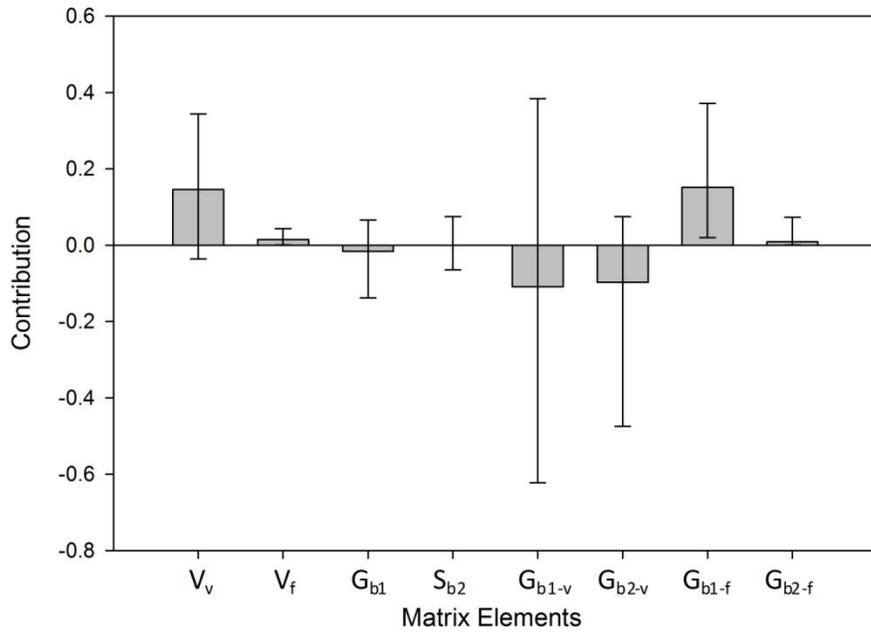
**Figure 4-5. Contributions values to the difference in λ between regions.** Positive contributions of demographic parameter indicate that KPBS had a greater contribution than WCNP and vice versa for negative contributions. Error bars indicate 95% bootstrapped confidence intervals. The lower confidence intervals of $V_f$ and $G_{b2-f}$ are greater than zero.

**Table 4-1. Matrix element parameterization of projection matrices.** B = buds, V = vegetative tiller, F= flowering tiller, RT=residual tiller; Numerical subscripts indicate age with "0" being the current year, etc.; Additional subscripts indicate from which sampling date data were used. If only a season is listed, then the average of all sampling dates from that season was used. If "peak" or "base" is listed, the sampling date within the season with the highest or lowest average value was used. It should be noted that estimates for $V_f$ at WCNP were based on data from both 2010 and 2011 as only one 2011 tiller flowered.

| Matrix element | Definition | Equation |
|---|---|---|
| $G_{b1}$ | Survival probability of a 1 year old bud | $\dfrac{(B_1/RT_1)_{fall\ base}}{(B_1/RT_1)_{spring\ peak}}$ |
| $G_{b1\text{-}v}$ | Outgrowth probability of a 1 year old bud to vegetative tiller | $\dfrac{(V/RT_1)_{fall}}{(B_1/RT_1)_{spring\ peak}}$ |
| $G_{b2\text{-}v}$ | Outgrowth probability of a $2^+$ year old bud to vegetative tiller | $\dfrac{(V/RT_2)_{fall}}{(B_2/RT_2)_{spring\ peak}}$ |
| $G_{b1\text{-}f}$ | Outgrowth probability of a 1 year old bud to a flowering tiller | $\dfrac{(F/RT_1)_{fall}}{(B_1/RT_1)_{spring\ peak}}$ |
| $G_{b2\text{-}f}$ | Outgrowth probability of a $2^+$ year old bud to a flowering tiller | $\dfrac{(F/RT_2)_{fall}}{(B_2/RT_2)_{spring\ peak}}$ |
| $S_{b2}$ | Survival probability of a $2^+$ year old bud | $\dfrac{(B_2/RT_2)_{fall\ base}}{(B_2/RT_2)_{spring\ peak}}$ |
| $V_v$ | Axillary bud production of a vegetative tiller | $\left(\dfrac{B_0}{V}\right)_{fall}$ |
| $V_f$ | Axillary bud production of a flowering tiller | $\left(\dfrac{B_0}{F}\right)_{fall}$ |

**Table 4-2. Matrix elements for *A. gerardii* from tallgrass and mixed-grass prairie.** Values display the regional mean ± 1SE and are boldfaced when there is a significant difference between regions at α = 0.05 with statistical details listed under Region Effect. Developmental effect considers either the effect of bud age class or tiller developmental stage within a region on the matrix elements. Significant developmental effects at α = 0.05 are indicated by gray shading of the statistical details. Perm indicates a permutation contrast was used.

| Matrix element | Tallgrass (KPBS) | Dev. Effect at KPBS | Mixed-grass (WCNP) | Dev. Effect at WCNP | Region Effect |
|---|---|---|---|---|---|
| $G_{b1}$ | 0.364 ± 0.047 | | 0.455 ± 0.047 | | $F_{1,18} = 1.9$, p = 0.18 |
| $G_{b1-v}$ | 0.209 ± 0.018 | Perm, | 0.266 ± 0.031 | Perm, | Perm, p = 0.869 |
| $G_{b2-v}$ | 0.024 ± 0.007 | p = 0.034 | 0.197 ± 0.096 | p = 0.78 | Perm, p = 0.056 |
| $G_{b1-f}$ | 0.059 ± 0.014 | Perm, | 0.002 ± 0.002 | Perm, | Perm, p < 0.0001 |
| $G_{b2-f}$ | 0.008 ± 0.004 | p < 0.0001 | 0 | p = 1.0 | Perm, p = 0.871 |
| $S_{b2}$ | 0.409 ± 0.040 | | 0.412 ± 0.113 | | $F_{1,11.2} \approx 0$, p = 0.98 |
| $V_v$ | 8.02 ± 0.30 | $t_{30} = 2.89$, | 6.27 ± 0.22 | $t_{30} = 2.97$, | $t_{30} = 5.38$, p < 0.0001 |
| $V_f$ | 8.97 ± 0.19 | p = 0.007 | 7.54 ± 0.21 | p = 0.035 | $t_{30} = 3.29$, p = 0.015 |

**Table 4-3. Element elasticities according to region.** No element elasticities varied significantly by region. Bootstrapped estimates ± 1 s.d. and 95% bootstrapped CI. Element elasticities from the observed mean regional matrices were similar to bootstrapped estimates and are included in the appendix (Appendix Fig. 4-3).

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

**Table 4-4. Loop elasticities according to region.** No loop elasticities varied significantly by region. Bootstrapped estimates ± 1 s.d. and 95% bootstrapped CI.

| Loop | Tallgrass (KPBS) | Mixed-grass (WCNP) | Bootstrapped p-value |
|---|---|---|---|
| B1-B2-F-B1 | 0.152 ± 0.0004 (0.00007, 0.135) | N/A | |
| B1-B2-V-B1 | 0.036 ± 0.0006 (0.00009, 0.225) | 0.231 ± 0.002 (0.023, 0.659) | 0.31 |
| B1-F-B1 | 0.224 ± 0.001 (0.047, 0.475) | 0.006 ± 0.0002 (0, 0.072) | 0.45 |
| B1-V-B1 | 0.717 ± 0.001 (0.448, 0.924) | 0.710 ± 0.002 (0.234, 0.974) | 0.81 |
| B2 | 0.007 ± 0.012 (0.00003, 0.041) | 0.053 ± 0.086 (0, 0.310) | 0.38 |

**Table 4-5. Predicted and observed stable stage distributions according to region.**
Bootstrapped estimates ± 1 s.d. and 95% bootstrapped CI for predicted stable stage distributions (SSD). Observed SSD are based on fall averages from each site and are ± 1 s.d. No stable stage proportion varied significantly by region. Bootstrapped p-values in the right column compare the proportions of individuals in each stable stage between regions. Bootstrapped p-values listed underneath the observed SSD of each stage compare the proportion of individuals in the predicted versus observed stable stage distributions for each stage within region. Predicted SSD from the observed mean regional matrices were similar to bootstrapped estimates and are included in the appendix (Appendix Fig. 4-4).

| Stage | Tallgrass (KPBS) | | Mixed-grass (WCNP) | | Regional Predicted SSD p-value |
| | Predicted | Observed | Predicted | Observed | |
|---|---|---|---|---|---|
| B1 | 0.660 ± 0.063 (0.530, 0.776) | 0.636 ± 0.074 p = 0.81 | 0.579 ± 0.093 (0.357, 0.718) | 0.635 ± 0.071 p = 0.62 | 0.63 |
| B2 | 0.219 ± 0.077 (0.079, 0.382) | 0.287 ± 0.081 p = 0.62 | 0.289 ± 0.119 (0.116, 0.573) | 0.267 ± 0.079 p = 0.87 | 0.78 |
| V | 0.094 ± 0.020 (0.056, 0.133) | 0.057 ± 0.013 p = 0.51 | 0.131 ± 0.035 (0.063, 0.198) | 0.097 ± 0.017 p = 0.54 | 0.41 |
| F | 0.027 ± 0.014 (0.006, 0.059) | 0.020 ± 0.012 p = 0.71 | 0.0007 ± 0.002 (0, 0.008) | 0.0003 ± 0.001 p = 0.19 | 0.45 |
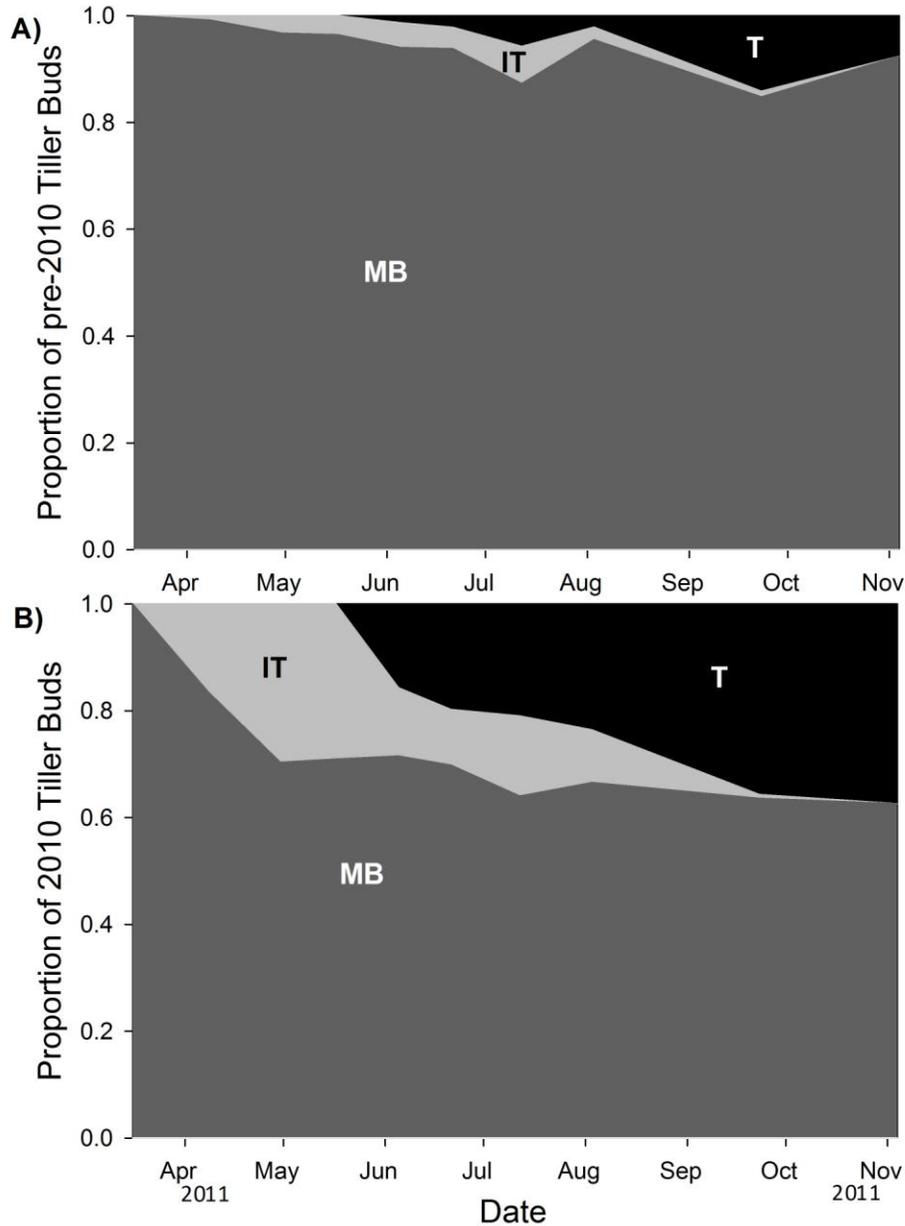
**Appendix Figure 4-1. Proportion of live ramets (i.e. buds and tillers) according to developmental stage at WCNP by A) pre- 2010 cohort and B) 2010 cohort.** Although a higher percentage of 2010 buds recruit to tiller than pre-2010 buds, both cohorts have similar recruitment phenology.

**Appendix Figure 4-2. Sensitivities of matrix elements for regional mean matrices of KPBS and WCNP.**

$$sensitivity\ of\ \lambda_{KPBS} = \begin{bmatrix} 0.487 & 0.161 & 0.070 & 0.020 \\ 0.077 & 0.025 & 0.011 & 0.003 \\ 2.581 & 0.850 & 0.370 & 0.105 \\ 2.887 & 0.951 & 0.414 & 0.117 \end{bmatrix}$$

$$sensitivity\ of\ \lambda_{WCNP} = \begin{bmatrix} 0.430 & 0.182 & 0.101 & 0.0006 \\ 0.333 & 0.141 & 0.078 & 0.0004 \\ 1.813 & 0.768 & 0.427 & 0.002 \\ 2.180 & 0.924 & 0.513 & 0.003 \end{bmatrix}$$

**Appendix Figure 4-3. Elasticities of matrix elements for regional mean matrices of KPBS and WCNP.**

$$elasticity\ of\ \lambda_{KPBS} = \begin{bmatrix} 0 & 0 & 0.370 & 0.118 \\ 0.019 & 0.007 & 0 & 0 \\ 0.356 & 0.013 & 0 & 0 \\ 0.113 & 0.005 & 0 & 0 \end{bmatrix}$$

$$elasticity\ of\ \lambda_{WCNP} = \begin{bmatrix} 0 & 0 & 0.427 & 0.003 \\ 0.102 & 0.039 & 0 & 0 \\ 0.325 & 0.102 & 0 & 0 \\ 0.003 & 0 & 0 & 0 \end{bmatrix}$$

**Appendix Figure 4-4. Stable Stage Distributions of regional mean matrices of KPBS and WCNP.**

$$w_{KPBS} = \begin{bmatrix} b_1 \\ b_2 \\ v \\ f \end{bmatrix} = \begin{bmatrix} 0.66 \\ 0.22 \\ 0.09 \\ 0.03 \end{bmatrix}$$

$$w_{WCNP} = \begin{bmatrix} b_1 \\ b_2 \\ v \\ f \end{bmatrix} = \begin{bmatrix} 0.60 \\ 0.26 \\ 0.14 \\ 0.0008 \end{bmatrix}$$

**Appendix Table 4-1. Fitted distributions with location and shape parameters for each matrix element for each region separately and for the overall study.** N= normal, B = Beta

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

**Appendix Table 4-2. Demographic parameters scaled contributions to within regional variability of λ.** The sum of the raw contributions approximates the variance in λ. Contributions were obtained from the random effect LTRE for each region and are scaled by Var(λ) to sum to 1.

| Mat. Element | Tallgrass (KPBS) | Mixed-grass (WCNP) |
|---|---|---|
| $G_{b1}$ | -0.018 | 0.034 |
| $G_{b1-v}$ | 0.502 | 0.342 |
| $G_{b2-v}$ | 0.025 | 0.558 |
| $G_{b1-f}$ | 0.359 | -0.003 |
| $G_{b2-f}$ | 0.028 | 0 |
| $S_{b2}$ | 0.001 | -0.023 |
| $V_v$ | 0.097 | 0.092 |
| $V_f$ | 0.005 | <0.001 |
| Var(λ) | 0.053 | 0.116 |

# Chapter 5 - Conclusion

Bud and tiller dynamics are strongly tied with one another. Grass species can vary in their bud longevity, bud development synchrony and phenology, bud production per tiller, and degree of bud dormancy. All these bud bank characteristics can strongly influence a species' tiller life history and vice versa. In every grass species, consistent tiller recruitment is vital for maintaining a healthy bud bank that is sufficient in size with buds that can readily break dormancy to produce the next generation of tillers. Although older buds can contribute considerably to seasonal tiller recruitment, most tillers are recruited from the most recently formed cohort of buds (Chapter 2,3,4, Hendrickson and Briske 1997; Ott and Hartnett 2012a).

Climate and disturbances, such as grazing, have the potential to greatly alter bud bank characteristics, especially bud development phenology and bud production per tiller. Although bud longevity and bud development synchrony and phenology were consistent at both the range center and periphery of *A. gerardii*, bud production per tiller was reduced at its cooler, more arid range periphery (Chapter 4). Tillers experiencing drought or defoliation may also experience a reduction in bud production per tiller (Busso et al. 1989). However, current year bud production per tiller was not impacted by drought or grazing history of an individual plant (Hendrickson and Briske 1997; N'Guessan and Hartnett 2011).

Bud bank demography appears to differ between grass species with $C_3$ and $C_4$ photosynthetic pathways (Table 5-1). $C_3$ and $C_4$ grasses varied in the synchrony and phenology of their bud development but could have similar bud production per tiller and bud longevity. $C_3$ grasses consistently maintain multiple developmental stages of buds and activated buds (i.e. juvenile tillers that have not emerged aboveground) throughout much of the year (Chapter 2,3; Ott and Hartnett 2012a). Because $C_3$ grasses are more dominant in the cooler portion of the Great Plains, asynchronous bud development may be an adaptation enabling plant growth to occur in small increments whenever temperatures are at levels where $C_3$ photosynthesis operates efficiently (Badger and Collatz 1977; Ehleringer and Bjorkman 1977; Collatz et al. 1998). This ongoing bud development of $C_3$ grasses whenever temperature allows would be similar to the small growth increments observed in a perennial grass following small rainfall events in a semi-arid grassland (Sala and Lauenroth 1982). Bud production and development of $C_3$ grasses slows or ceases during the late warm summer months, especially in tallgrass prairie when soil

temperatures exceed 22ºC, and new tiller recruitment typically occurs after the summer dormant period (Chapter 2, 3; Collatz et al 1998; Ott 2009; Ott and Hartnett 2012a). $C_3$ grasses have been observed recruiting their seasonal aboveground tillers in the fall, the following spring, or both (Chapter 2,3 and citations therein). Aboveground $C_3$ tiller recruitment phenology is dependent on the rate of belowground bud development, which is dependent on rainfall and temperature. Therefore, the flexibility in the seasonal tiller recruitment timing of perennial grasses appears to be a strongly associated with the $C_3$ photosynthetic pathway. Although studies of $C_4$ grass bud banks are more limited, buds appear to be developmentally dormant over the winter and have a synchronous tiller recruitment event in the spring with continued recruitment throughout the summer occurring in some species (McKendrick et al. 1975; Ott and Hartnett 2012a). Based on the current climatic variables determining current distributions and relative abundances of $C_3$ and $C_4$ grasses, global climate change models predict an increase in $C_4$ grass abundance and decrease in $C_3$ grass abundance in the northern Great Plains (Epstein et al. 2002). Future changes in $C_3$ and $C_4$ grass abundance will be mediated by the bud bank. The response of asynchronous bud development of $C_3$ grasses to changes in climate may play a large role in determining future $C_3$ grass abundance in northern semi-arid grasslands.

The bud banks of co-occurring $C_3$ caespitose and rhizomatous grasses varied more in the spatial distribution of their bud banks rather than bud production per tiller, bud longevity, bud development, and bud bank dynamics (Table 5-1; Chapter 2,3). The dense belowground bud banks of caespitose grasses are due to their high tiller density and higher-order bud production (Chapter 2,3; Ott and Hartnett 2012b). Rhizomatous grasses exhibit a wide range of rhizomatous growth patterns and architecture which strongly influence the spatial distribution of their buds and the functions they perform for the plant (Grace 1993; Judziewicz et al. 1999). Rhizomes of *Pascopyrum smithii* were used for the numerical increase of ramets more than rhizomes of *Andropogon gerardii* (Chapter 3, Ott and Hartnett 2012a). The separate timing of rhizome outgrowth and tiller recruitment in *P. smithii* did not introduce any notable asynchrony into the bud development and bud bank dynamics of individual plants (Chapter 3).

In both tallgrass and mixed grass prairie, the bud longevity of the dominant grasses ≥2 years (Table 5-1). Dominant grasses of the two grasslands varied in their other bud bank characteristics, such as bud production per tiller and bud development synchrony and phenology. *Andropogon gerardii* had bud longevity exceeding two years even when it was a subdominant in

mixed grass prairie. However, expansion of *A. gerardii* in mixed grass prairie may be limited by habitat suitability rather than its vegetative reproductive capabilities (Chapter 4). Greater bud longevity does not confer dominance upon a species but could assist a species in maintaining dominance by buffering population dynamics. For example, bud longevity was greater in the late-seral species *Bouteloua curtipendula* than in the mid-seral species *Hilaria belangeri* (Hendrickson and Briske 1997).

Tiller longevity can affect bud longevity. The relationship between tiller and bud longevity determines the turnover within the bud bank (i.e. whether it is transient or persistent) and the dependency of the bud bank on live aboveground tillers (i.e. whether buds are required to be attached to a live parent tiller in order to live; Table 5-2; also note the critical period of bud dormancy in Table 5-1). The type of bud bank a grass species has could determine how it responds to removal of aboveground tillers. Species with transient bud banks would be highly susceptible during the period of annual tiller and bud bank turnover and may experience reduced survival if disturbed at that time (e.g. *D. oligosanthes*; Ott and Hartnett 2012a). Genets with independent persistent or assisted-independent persistent bud banks could easily regrow following complete destruction of aboveground tillers. Both *H. comata* and *N. viridula* maintained dependent persistent bud banks which provide age structure within the bud bank but not bud persistence beyond a year after tiller senescence. This framework would allow for a classification of bud banks similar to seed banks (Thompson and Grime 1979; Ott and Hartnett 2012a).

Understanding of grass bud banks offers insight into the control of grass population dynamics and production, and ultimately grassland structure and function. Future research should seek to elucidate the bud and tiller dynamics of additional key species in a variety of grasslands as well as their response to altered climatic and disturbance scenarios.

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# Tables

**Table 5-1. Comparison of perennial grass bud bank characteristics in tallgrass and mixed-grass prairie.** Shaded and unshaded columns indicate species examined in tallgrass prairie and mixed-grass prairie respectively. Synchrony in bud development is characterized by the majority of buds transitioning from one stage to the next at approximately the same time. The critical period of bud dormancy refers to the time period when all aboveground tillers have senesced and the recruitment of the next generation of tillers is dependent on the belowground population of buds and juvenile tillers. Tallgrass values obtained from Ott and Hartnett (2012a, 2012b).

|  | *Andropogon gerardii*<br><br>Rhizomatous<br>C$_4$<br>dominant | *Andropogon gerardii*<br><br>Rhizomatous<br>C$_4$<br>subdominant | *Dichanthelium oligosanthes*<br><br>Caespitose<br>C$_3$<br>subdominant | *Hesperostipa comata* and *Nassella viridula*<br>Caespitose<br>C$_3$<br>dominant | *Pascopyrum smithii*<br><br>Rhizomatous<br>C$_3$<br>dominant |
|---|---|---|---|---|---|
| **Bud longevity** | $\geq 2.5$ years | $\geq 2.5$ years | $\leq 1$ year | $\geq 2$ years | $\geq 2.5$ years |
| **Tiller longevity** | 1 year | 1 year | 1 year | $2^+$ years | 1 year |
| **Bud development** | Synchronous | Synchronous | Asynchronous | Asynchronous | Asynchronous |
| **Critical period of bud dormancy** | Winter | Winter | Summer (overwintered juvenile tillers and buds) | None | Fall or winter (dependent on tiller recruitment timing) |
| **Buds/Tiller** | 8.2 | 6.4 | 4.6 (20.9 with higher order buds) | 2.0-2.9 | 2.5 (5.25 including rhizome buds) |

**Table 5-2. Types of grass bud banks.** A bud bank can experience a complete turnover annually forming a transient bud bank. Otherwise, multiple annual bud cohorts comprise the persistent bud bank. These persistent bud banks vary on the degree to which bud longevity depends on having live parent tillers.

|  |  | **Bud Longevity** | |
|---|---|---|---|
|  |  | **≤ Tiller Longevity** | **> Tiller Longevity by 1+ years** |
| **Tiller Longevity** | **1 Year** | **Transient** | **Independent Persistent** |
|  | **> 1 Year** | **Dependent Persistent** | **Assisted-Independent Persistent** |