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Axillary bud banks of two semiarid perennial grasses: occurrence, longevity, and contribution to population persistence

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Abstract The occurrence, longevity, and contribution of axillary bud banks to population maintenance were investigated in a late-seral perennial grass, *Bouteloua curtipendula*, and a mid-seral perennial grass, *Hilaria belangeri*, in a semiarid oak-juniper savanna. Axillary buds of both species were evaluated over a 2-year period in communities with contrasting histories of grazing by domestic herbivores. A double staining procedure utilizing triphenyl tetrazolium chloride and Evan's blue indicated that both viable and dormant axillary buds remained attached to the base of reproductive parental tillers for 18–24 months which exceeded parental tiller longevity by approximately 12 months. Bud longevity of the late-seral species, *B. curtipendula*, exceeded bud longevity of the mid-seral species, *H. belangeri*, by approximately 6 months. Younger buds located on the distal portion of the tiller base were 3.2 and 1.4 times more likely to grow out than older proximal buds of *B. curtipendula* and *H. belangeri*, respectively. The percentage of older proximal buds, which included comparable portions of viable and dormant buds, that grew out to produce tillers following mortality of parental tillers was 6.0% for *B. curtipendula* and 8.4% for *H. belangeri*. In spite of the occurrence of relative large axillary bud banks for both species, the magnitude of proximal bud growth did not appear sufficient to maintain viable tiller populations. We found no evidence to support the hypothesis of compensatory bud growth on an individual tiller basis for either species. Grazing history of the communities from which the buds were collected did not substantially affect the number, status, longevity, or outgrowth of axillary buds on an individual tiller basis for either species. However, long-term grazing by domestic herbivores influenced axillary bud availability by modifying population structure of these two species. Bud number per square meter for *B. curtipendula* was 25% lower in the long-term grazed compared to the long-term ungrazed community based on a reduction in both tiller number per plant and plant number per square meter. In contrast, bud number per square meter for *H. belangeri* was 190% greater in the long-term grazed than in the long-term ungrazed community based on a large increase in plant density per square meter. Minimal contributions of axillary bud banks to annual maintenance of tiller populations in this mid- and late-seral species underscores the ecological importance of consistent tiller recruitment from recently developed axillary buds. Consistent tiller recruitment in grasslands and savannas characterized by intensive grazing and periodic drought implies that (1) bud differentiation and maturation must be remarkably tolerant of adverse environmental conditions and/or (2) tiller recruitment may resume from buds that mature following the cessation of severe drought and/or grazing, rather than from mature buds that survive these disturbances. These scenarios warrant additional research emphasis given the critical importance of this demographic process to tiller replacement in species populations and the maintenance of relative species abundance in grasslands and savannas.

Key words Axillary buds · Bud demography · Population persistence · Population structure · Tiller recruitment

Introduction

Plant and population persistence in perennial grasses requires annual tiller recruitment to offset mortality losses associated with short tiller longevity (≤ 2 years) (White 1980; Briske and Butler 1989). Frequent tiller turnover within species populations presents an opportunity for shifts in relative species abundance to occur. If tiller recruitment was suppressed for a period equivalent to the maximum longevity of existing tillers, all apical

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meristems would be lost, the population would experience a substantial reduction in tiller density, and potentially face local extinction. Yet, numerous perennial grasses demonstrate remarkable persistence to intensive grazing and periodic drought, which comprise the major large scale disturbances, in grasslands and savannas. These disturbances remove existing biomass to varying degrees (Grime 1979, p. 39), but do not completely destroy seed and/or meristematic tissues located at or beneath the soil surface except in the most extreme cases. What mechanisms enable grasses to offset tiller mortality on an annual basis and maintain tiller densities in spite of these disturbances? Mechanisms of population persistence collectively contribute to the stability of grassland and savanna communities by affecting the relative abundance of species populations through time.

In situations where tiller recruitment is constrained by drought and/or intensive grazing, tiller recruitment can potentially resume from axillary buds that survive the disturbance, axillary buds that develop following the disturbance, or by plant establishment from seed in the soil (e.g., Eriksson 1989). Axillary buds are rudimentary apical meristems differentiated from the apical meristems of parental tillers that can potentially grow out to produce juvenile tillers (Sharman 1945; Langer 1963). It is generally recognized that tiller initiation and growth are suppressed by suboptimal environmental conditions (Langer 1963), including drought (Busso et al. 1989; Van Loo 1992) and severe defoliation (Olson and Richards 1988; Murphy and Briske 1992). In addition, the transient nature (< 1 year) of seed banks of temperate perennial grasses is well documented (Thompson and Grime 1979; Pyke 1990). However, relatively little is known about the occurrence, longevity, and ecological significance of axillary bud banks given their potential importance to plant and population persistence in perennial grasses.

Two contrasting interpretations exist concerning the longevity and contribution of axillary buds to the maintenance of tiller populations. One interpretation is that longevity of axillary buds exceeds that of parental tillers (e.g., Silsbury 1964; Leakey et al. 1977; McKendrick et al. 1975) while the second interpretation is that buds that do not grow out to produce juvenile tillers following maturation rapidly senesce (e.g., Mitchell 1953; Dahl and Hyder 1977). The first interpretation is supported by observations of 2- to 3-year-old buds in *Agropyron desertorum* and *A. spicatum* (Busso et al. 1989), *Andropogon gerardii* (McKendrick et al. 1975) and *Trichachne californica* (Cable 1971). If this interpretation accurately characterizes most perennial grass species, then axillary buds may accumulate to form a bud bank (*sensu* Harper 1977, p. 108) with the potential to initiate juvenile tillers. Accumulation of dormant axillary buds may potentially form a more persistent meristematic source than seed banks in temperate perennial grasses which seldom retain seed viability for more than 1 year (Thompson and Grime 1979; Pyke 1990; Kinucan and Smeins 1992). The second interpretation is supported by observations that tiller growth most frequently occurs from the youngest, most distal, mature buds along tiller bases (Mitchell 1953; Mueller and Richards 1986; Busso et al. 1989) or rhizomes (Leakey et al. 1977; Harris and Davy 1986) and that juvenile tillers are infrequently initiated from older proximal buds (Mitchell 1953; McKendrick et al. 1975; Hume 1991).

Axillary bud banks would intuitively seem to be a more adaptive trait of species in arid or semiarid environments and/or in systems subjected to long-term intensive grazing (e.g., Tuomi et al. 1994). It is in these systems that disturbances would be more likely to suppress tiller recruitment and jeopardize population persistence. Similarily, highly competitive late-seral species would be anticipated to accumulate greater numbers of axillary buds to maintain site occupation and dominance following disturbance (e.g., De Kroon and Knops 1990).

A series of experiments were conducted with a late-seral perennial grass, *Bouteloua curtipendula* Michx. (Torr.), and a mid-seral perennial grass, *Hilaria belangeri* (Steud.) Nash, to investigate the occurrence, longevity, and contribution of axillary bud banks to population persistence. We investigated three hypotheses:

1. Axillary bud longevity exceeds parental tiller longevity for both species.
2. Axillary bud longevity of the late-seral species exceeds that of the mid-seral species.
3. Tiller recruitment from axillary bud banks represents a substantial contribution to maintenance of tiller populations for both species.

Reproductive tillers of both species were marked and destructively evaluated over a 2-year period in communities with contrasting histories of grazing by domestic herbivores. Tiller selection at the time of flowering provided a developmental reference to ensure that subsequent buds were not differentiated after their initial selection and marking (Sharman 1945; Langer 1972, p. 25). Vegetative tillers were evaluated at the same sampling dates as reproductive tillers to provide an estimate of the number, viability and outgrowth of currently developed axillary buds.

Methods

Study Area

Research was conducted at the Texas A&M University Agricultural Research Station 56 km south of Sonora, Texas USA (31°18′N; 100°28′W). The station is located in the southwestern portion of the Edwards Plateau Land Resource Area at an elevation of 735 m. The climate is classified as sub-tropical and semiarid (Smeins et al. 1976; Smeins and Merrill 1988). Mean temperature is highest in July (30°C) and lowest in January (9°C). Median long-term precipitation is 439 mm, but it is highly erratic both within and between years. May and September are typically the wettest months while November and January tend to be the driest. Mean annual precipitation was 73.6, 98.1, and 94.3% of the long-term mean for 1993, 1994, and 1995, respectively. Mean annual precipitation was 105% of the long-term mean for the 3 years prior to the investigation. Topography of the research station is highly dissected and soils contain large amounts of limestone fragments, stones, and gravel and are underlain by a limestone substratum. Dominant soils are Tarrant stony clays, of the thermic family of Lithic Haplustolls formed over fractured Buda and Edwards limestone. The area is potentially a midgrass dominated grassland with scattered individuals or clumps of woody plants including, *Quercus virginiana*, *Q. pungens* var. *vaseyena*, *Juniperus ashei* and *J. pinchotii* (Smeins et al. 1976; Smeins and Merrill 1988). However, intensive, long-term grazing by domestic herbivores has altered species composition by reducing the abundance of late-seral midgrasses, including *B. curtipendula*, and increasing the abundance of mid-seral shortgrasses, including *H. belangeri*, and several shrub species. The abundance of late-seral midgrasses, including *B. curtipendula,* has increased following long-term (50 years) protection from domestic herbivores (Smeins et al. 1976; Smeins and Merrill 1988).

This investigation was conducted in two communities with contrasting grazing histories. Both communities had been intensively and continuously grazed by domestic herbivores from 1870 to 1948 (Youngblood and Cox 1922; Smeins and Merrill 1988). One of the communities has been protected from grazing by domestic, but not native, herbivores since 1948, while the other has been continuously grazed since that time. The two communities were approximately 2.5 km apart and specific study sites were located on similar soils with comparable topography. The long-term grazed community has a smaller proportion of late-seral grasses, including *B. curtipendula* and *Eriochloa sericea*, and a greater proportion of mid-seral shortgrasses, including *H. belangeri*, *Bouteloua trifida*, and *Erioneuron pilosum*, compared to the ungrazed community (Smeins et al. 1976; Smeins and Merrill 1988)

Procedures

Approximately 150 *B. curtipendula* and 150 *H. belangeri* tillers with inflorescences were located on individual plants and permanently marked with wire loops along transects in the intensively grazed and ungrazed communities. Reproductive tillers were selected to ensure that axillary bud differentiation and maturation had ceased by the time of marking. Axillary buds develop prior to the time of floral induction when differentiation of leaf primordia ceases and inflorescence production begins (Sharman 1945; Langer 1972, p. 25). Immediately following marking in June 1993, 15 marked tillers of each species were harvested from individual plants, and 15 additional tillers were harvested in November 1993, and again at comparable dates in 1994, and in May 1995. Tillers were transported to the Texas A&M University campus where the tiller bases were cleaned by removing soil and senescent plant material prior to assessing bud number and viability.

Axillary buds of *B. curtipendula* were short, ovate structures enclosed by hardened prophylls. Mean bud length was approximately 3.6 mm and prophyll lengths decreased proximally along the crown base. Axillary buds of *H. belangeri* were lancolate structures without hardened prophylls. Mean bud length was approximately 3.0 mm and prophyll lengths were similar along the entire length of the tiller base.

The maximum number of buds per tiller was based on the cumulative sum of four bud categories including (1) buds which had grown out to form tillers, rhizomes or stolons (live or dead), (2) missing buds based on the occurrence of bud scars, or (3) leaf scars, and (4) existing visible buds. Leaf scars, located at the point of sheath attachment to the tiller base, identified the position of potential buds when a bud scar could not be located. Only those axillary buds located on the basal 20 mm of the parental tiller (crown region) were evaluated. We recognize that some species may not possess buds in all leaf axils (Mueller and Richards 1986). The maximum number of buds per tiller were divided into three equal numerical categories based on their position along the tiller base. These categories were designated as distal, mid, and proximal and were used to chronologically evaluate bud viability and outgrowth.

Bud viability was determined with a double staining procedure described by Busso et al. (1989). Buds were stained with a 2,3,5-triphenyl tetrazolium chloride (TTC) solution to determine viability and those that did not stain with TTC were placed in a 0.25% w/v solution of Evan's blue for 20 min at room temperature to verify bud death. Dead buds were readily identified by a deep blue stain (Gaff and Okong'o-ogola 1971). Buds that did not stain with either TTC or Evan's blue, and which were obviously not necrotic, were considered dormant (e.g., Busso et al. 1989).

Fifteen vegetative tillers in the two-to-five-leaf stage were destructively harvested from individual plants for each species and bud numbers and viability were determined as previously described for reproductive tillers. Vegetative tillers were collected at the same sampling dates as reproductive tillers to provide an estimate of current axillary bud numbers and viability in contrast to the older reproductive tillers.

Bud densities for each of the two species were established by determining mean plant density per square meter, subsampling mean tiller density per plant, then multiplying by the mean bud number per tiller in both communities in June 1994. In the ungrazed community, plant densities were estimated in 50 (0.25 m^2) quadrats located along line transects. Tiller numbers were counted in two plants of each species located in opposite corners of the quadrat. Plant density was sampled in a similar manner in the grazed community, but a smaller (0.18 m^2) quadrat was used to efficiently sample the higher density of smaller plants.

Statistical analyses were conducted using chi-square contingency table analysis (Conover 1980, p. 143). Comparisons were made by species, bud position on the tiller base, and bud viability for both reproductive and vegetative tillers. Analyses were conducted by date and data were pooled if no significant date differences were observed. Lack of replication prevented a statistical comparison between communities with contrasting grazing histories (Hurlbert 1984).

Results

A significantly ($P < 0.01$) greater percentage of axillary buds in the distal and mid positions of reproductive tillers grew out to form tillers, rhizomes or stolons compared to proximal buds for *B. curtipendula* in both communities and for *H. belangeri* in the ungrazed community (Fig. 1). Only 5.3 and 6.0% of the proximal buds of *B. curtipendula* and 8.4 and 4.5% of the proximal buds of *H. belangeri* grew out in the grazed and ungrazed communities, respectively. The proportion of buds that grew out averaged across positions was 12 and 10% greater for reproductive tillers of *B. curtipendula* than for *H. belangeri* tillers ($P < 0.05$) in the grazed and ungrazed communities, respectively. Approximately 39 and 36% of the maximum number of axillary buds grew out from all positions along the base of reproductive *B. curtipendula* tillers in grazed and ungrazed communities, respectively, while approximately 24 and 29% of the maximum number of axillary buds grew out from all positions of reproductive *H. belangeri* tillers in grazed and ungrazed communities, respectively. However, lack of replication prevented a direct statistical comparison between communities with contrasting grazing histories.

B. curtipendula had a mean maximum bud number (sum of all four bud categories) of 8.5 and 7.5 buds per tiller while *H. belangeri* had a mean maximum bud number of 5.7 and 5.4 buds per tiller ($P < 0.10$) in the

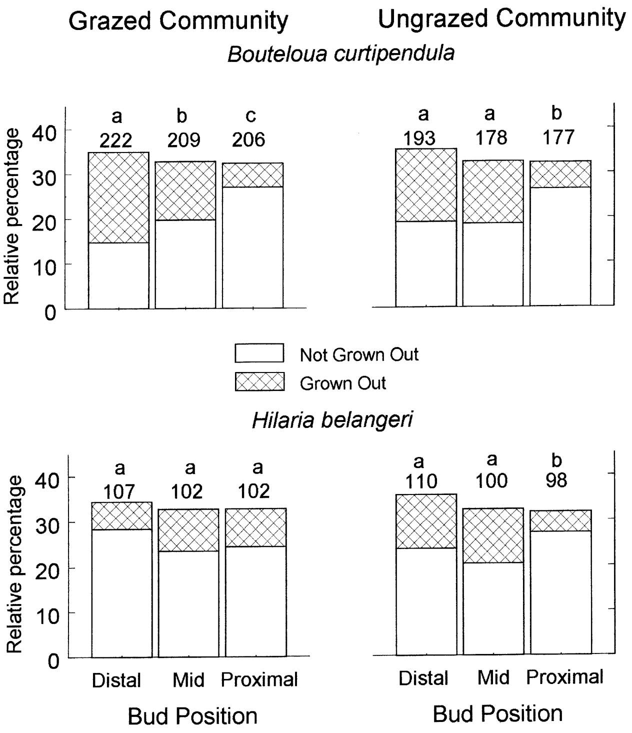

Fig. 1 Mean maximum number of buds by distal, mid, and proximal positions along reproductive tiller bases (*numerals above bars*) and relative percentage of bud outgrowth by position for *Bouteloua curtipendula* and *Hilaria belangeri* in communities with contrasting grazing histories. *Bars* marked with a different *letter* indicate a significant difference for the relative percentage of buds grown out between positions as determined by a χ^2 test; $n = 60$ and 75 tillers per community for *H. belangeri* and *B. curtipendula*, respectively

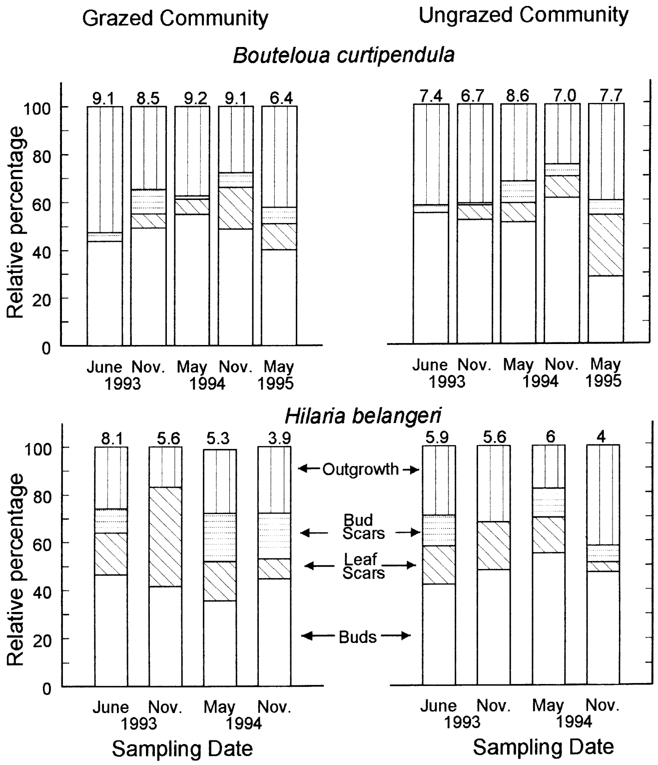

Fig. 2 Mean maximum number of buds per tiller (*numerals above bars*) and relative percentage comprised of buds that had grown out, buds scars, leaf scars, and remaining buds for reproductive tillers of *Bouteloua curtipendula* and *Hilaria belangeri* in communities with contrasting grazing histories. All buds for *Hilaria belangeri* had decomposed prior to may 1995; $n = 15$ tillers per community per sampling date for each species

grazed and ungrazed communities, respectively (Fig. 2). Mean maximum bud number per reproductive tiller decreased by the end of the investigation, except for *B. curtipendula* in the ungrazed community. *B. curtipendula* had a greater number of remaining buds per tiller (3.5–5.1) than did *H. belangeri* (1.9–3.8) at all sampling dates (Fig. 2). The proportion of remaining buds and buds that had grown out was relatively constant throughout the investigation. A smaller percentage of the maximum number of buds was assigned to leaf and bud scar categories in *B. curtipendula* than in *H. belangeri*, which indicates that the fate of buds was more accurately determined in the larger, late-seral species. Leaf scars accounted for up to 40% of the maximum number of buds in *H. belangeri* tillers in the grazed community.

The proportion of viable buds decreased significantly ($P < 0.01$) within the first 12 months following permanent marking of reproductive tillers in both species regardless of grazing history (Fig. 3). The mean number of viable buds per tiller decreased by 25 and 50% in *B. curtipendula* and by 10 and 66% in *H. belangeri* in the ungrazed and grazed communities, respectively, at the final sampling date that viable buds were recorded compared to the initial sampling date. Bud viability within a sampling date generally did not differ between species, with the exception of the ungrazed community in May 1994 when *H. belangeri* had 30% bud viability compared to 20% bud viability for *B. curtipendula*. However, *B. curtipendula* tillers retained viable buds 6 months longer than did *H. belangeri* tillers. The number of dormant *B. curtipendula* buds per tiller remained high and relatively constant throughout the investigation, with the exception of the November 1994 sampling. *B. curtipendula* had one or more dormant buds per tiller and *H. belangeri* had 0.6 dormant buds per tiller after the first year. *B. curtipendula* had greater than 0.5 dormant buds per tiller at the end of the second year when *H. belangeri* had only nonviable buds. The number of dormant buds per tiller was similar to viable bud number at the last sampling date when viable buds were recorded for each species, with the exception of *H. belangeri* in the ungrazed community which had a higher proportion of viable than dormant buds.

In contrast to reproductive tillers, bud outgrowth from vegetative tillers was significantly greater in *H. belangeri* than in *B. curtipendula* ($P < 0.10$) (Fig. 4A). A mean of 0.54 and 0.38 buds per tiller grew out in *H. belangeri* and *B. curtipendula*, respectively. Greater than 70% of the maximum number of buds remained on vegetative tillers, but only 5–10% of the maximum number of buds grew out to form a tiller,

Table 1 Estimated axillary bud number per m^2 for *Bouteloua curtipendula* (BOCU) and *Hilaria belangeri* (HIBE) calculated from the mean (±SE) number of viable and dormant buds per vegetative tiller, number of vegetative tillers per plant, and plants per m^2 in communities with contrasting grazing histories. Number of viable and dormant buds per vegetative tiller represents a mean of all sampling dates (see Fig. 4). Tiller number per plant and plant number per m^2 were estimated in both communities in June 1994

Grazing History	Species	Axillary buds tiller^{-1}				
		Viable	Dormant	Tillers plant^{-1}	Plants m^{-2}	Buds m^{-2}
Ungrazed	BOCU	3.8 ± 0.19	0.6 ± 0.17	20.4 ± 3.7	8.0 ± 1.3	718
	HIBE	3.1 ± 0.16	0.3 ± 0.08	22.6 ± 3.9	18.9 ± 4.4	1452
Grazed	BOCU	4.0 ± 0.18	0.5 ± 0.11	4.4 ± 0.8	27.0 ± 3.8	535
	HIBE	2.8 ± 0.15	0.1 ± 0.05	13.1 ± 1.4	111.0 ± 8.4	4217

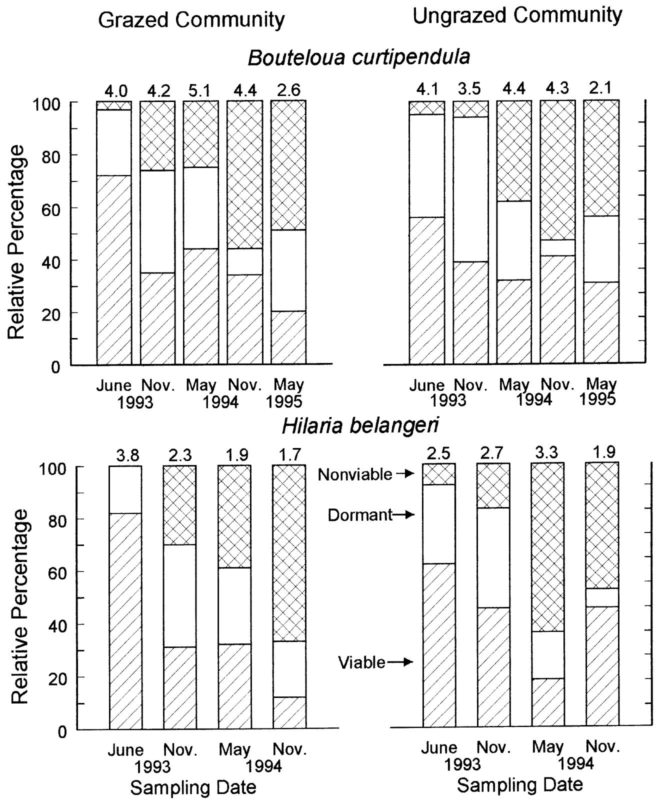

Fig. 3 Mean number of buds per tiller (*numerals above bars*) and relative percentage of viable, dormant, and nonviable buds for reproductive *Bouteloua curtipendula* and *Hilaria belangeri* tillers in communities with contrasting grazing histories. All buds for *Hilaria belangeri* had decomposed prior to May 1995; $n = 15$ tillers per community per sampling date for each species

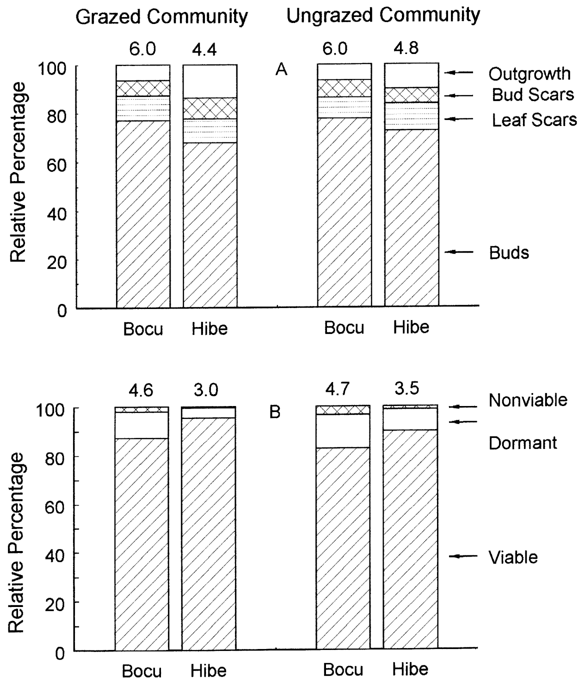

Fig. 4 **A** Mean maximum number of buds per tiller (*numerals above bars*) and relative percentage of buds that had grown out, bud scars, leaf scars, and remaining buds, and **B** mean number of buds per tiller (*numerals above bars*) and relative percentage of viable, dormant, and nonviable buds for vegetative tillers of *Bouteloua curtipendula* (*Bocu*) and *Hilaria belangeri* (*Hibe*) in communities with contrasting grazing histories; $n = 75$ tillers per community for each species

rhizome or stolon. The maximum number of buds was 30% greater for *B. curtipendula* than for *H. belangeri*, but the proportions of buds in each category remained relatively constant for each species regardless of grazing history. A smaller proportion of the maximum number of buds was assigned to leaf scars and missing buds in vegetative than in reproductive tillers indicating that tiller age influenced bud availability and the accuracy of interpretation. Bud viability was uniformly high, exceeding 85%, in vegetative tillers of both species (Fig. 4B). Dormant buds comprised the second largest category in both species regardless of grazing history. Few nonviable buds occurred in the vegetative tillers compared to the older reproductive tillers within both species. Grazing history of the communities from which the buds were collected did not substantially modify the number, status, longevity, or outgrowth of axillary buds per tiller for either species. However, long-term grazing affected axillary bud number per square meter by modifying both tiller number per plant and plant density per square meter. Estimated bud density per square meter was 25% lower for *B. curtipendula* while estimated bud density was 190% greater for *H. belangeri* in the long-term grazed compared to the long-term ungrazed community, respectively (Table 1).

Discussion

Both viable and dormant axillary buds existed on the base of reproductive tillers for 18–24 months, which surpassed parental tiller longevity of both perennial grass species. Bud longevity of the late-seral species, *B. curtipendula*, exceeded bud longevity of the mid-seral species, *H. belangeri*, by at least 6 months. This is a conservative estimate of bud longevity because the oldest proximal buds were differentiated several months prior to reproductive development when the tillers were initially marked. However, the maximum percentage of older proximal buds, which consisted of similar proportions of viable and dormant buds, that grew out to produce tillers, rhizomes or stolons was 6.0% for *B. curtipendula* and 8.4% for *H. belangeri*. Consequently, we were unable to reject the initial two hypotheses that axillary bud longevity exceed parental tiller longevity for both species and that axillary bud longevity of the late-seral species exceeded that of the mid-seral species. However, the third hypothesis that tiller recruitment from axillary bud banks represents a substantial contribution to maintenance of tiller populations must be rejected based on the minimal number of older proximal buds that grew out. Although this magnitude of tiller recruitment from the bud bank may contribute to genet survival, it does not appear to be of sufficient magnitude to maintain viable tiller populations on an annual basis. For example, even 10% outgrowth of a maximum of 3.9 and 1.2 buds, including the dormant and viable bud categories combined for *B. curtipendula* and *H. belangeri* tillers, respectively, 1 year after inflorescence development, would not be sufficient to offset parental tiller mortality. The potential contribution of the bud bank to tiller population maintenance is reduced by approximately 50%, if only the dormant bud category is considered.

Older proximal buds were less likely to grow out than younger, distal buds affirming the previous interpretation of Mitchell (1953). Approximately 3.2 and 1.4 times more distal than proximal buds grew out on reproductive tillers of *B. curtipendula* and *H. belangeri*, respectively. Comparable patterns of bud outgrowth have been documented in *Agropyron cristatum*, *A. spicatum* (Mueller and Richards 1986; Busso et al. 1989) and *Stipa tenuis* (Busso et al. 1993). This hierarchical pattern of bud outgrowth is difficult to interpret because our knowledge of the mechanisms regulating axillary bud growth in grasses is largely speculative and of a correlative, rather than a causal nature (Cline 1991; Murphy and Briske 1992). Greater outgrowth of distal than proximal buds is inconsistent with the “hormonal” theory of apical dominance because distal buds are closest to the source of growth inhibition in the apical meristem region (Cline 1991; Murphy and Briske 1992). Decreasing nitrogen concentrations from distal to proximal portions of tiller bases or rhizomes has been proposed as an explanation for this pattern of bud outgrowth (McIntyre 1970; Leakey et al. 1977). It has recently been suggested that the hierarchy of bud outgrowth may be established by the rate of bud development, rather than the size or developmental history of buds (Novoplansky 1996). This interpretation also implies that buds that have been inhibited for the shortest period of time will have the greatest potential for outgrowth.

The proportion of bud outgrowth differed between reproductive and vegetative tillers of the late- and mid-seral species. Bud outgrowth from reproductive *B. curtipendula* tillers was significantly higher than from reproductive *H. belangeri* tillers, but the response was reversed in vegetative tillers. This pattern of bud outgrowth suggests that a greater proportion of buds grew out during the earlier stages of tiller development in the mid-seral species than in late-seral species. A greater proportion of bud outgrowth during the early stages of tiller development suggests that buds of *H. belangeri* experienced less correlative inhibition than did buds of *B. curtipendula*. Greater bud inhibition would contribute to the accumulation of a larger number of proximal buds per tiller in the late-seral compared to the mid-seral species.

A relatively large and constant proportion of dormant axillary buds were evident in both species regardless of grazing history or sampling date. Dormant buds have previously been observed to comprise a large (60%) and consistent proportion of the bud bank in *Carex arenaria* (Noble et al. 1979). The concept of dormancy implies that buds cannot be activated regardless of prevailing environmental conditions based on innate properties of the dormant organ (Vegis 1964) or that an appropriate set of environmental conditions must be met for growth to occur (Villiers 1972; Vleeshouwers et al. 1995). Unfortunately, neither the environmental conditions nor physiological processes required to break dormancy in axillary buds are known (Vegis 1964; Villiers 1972; Murphy and Briske 1992). Dormancy within the context of the double staining procedure was based on the observation that buds did not stain with either TTC or Evan’s blue (e.g., Busso et al. 1989) which indicates that membrane integrity remained intact, but that respiratory activity was minimal. Shoots of all of the initially marked parental tillers had completely senesced by the end of the 2-year investigation, so it is difficult to envisage how dormant buds would perceive environmental stimuli to break dormancy and initiate growth. Dormant buds of *A. desertorum* and *A. spicatum* did not break dormancy and initiate growth following parental tiller senescence regardless of the environmental conditions to which they had been exposed (Busso et al. 1989).

The occurrance of a large proportion of viable and dormant buds in the proximal position that did not growth out raises the possibility that proximal buds exist as vestigial organs which have surpassed their opportunity for outgrowth (e.g., Mitchell 1953; Dahl and Hyder 1977). Continued bud existence may be a consequence of the inability of parental tillers to abort them (e.g., absence of an abscission zone) and the apparent low cost associated with bud maintenance. However, axillary buds that were assumed to have had undergone a period of dormancy have been reported to develop into tillers in several perennial grasses (Heidemann and Van Riper 1967; Haslam 1969). Yet the development of smaller, less vigorous tillers from older proximal buds compared to those developed from more distal buds supports the supposition that bud viability decreases with increasing age (Mueller and Richards 1986).

The mechanism capable of sustaining viable and/or dormant buds on senescent parental tillers for more than 1 year is not known. It has previously been hypothesized that proximal buds may import resources from one or more daughter tillers that had previously grown out from the more distal buds of the parental tiller (Busso et al. 1989). Small quantities of basipetally allocated resources between younger and older tiller generations has previously been documented (Welker et al. 1987, 1991) which may be sufficient to maintain bud viability following shoot senescence of parental tillers. However, only 12% of the *H. belangeri* tillers and none of the *B. curtipendula* tillers that retained viable buds possessed a live daughter tiller 18 and 24 months after marking, respectively. An alternative interpretation is that buds may be capable of storing sufficient energy and nutrients to maintain minimal metabolic activity provided that parental root systems retain the ability to absorb small quantities of water following shoot senescence.

Axillary bud numbers of two to five per tiller, in *B. curtipendula* and *H. belangeri*, were comparable with previous investigations reporting three to nine buds per tiller in *A. desertorum* and *A. spicatum* (Mueller and Richards 1986) and 3.3 buds per tiller in *Trichachne californica* (Cable 1971). Bud densities for *B. curtipendula* (535–718 m^{-2}) were higher than those reported for *Calamovilfa longifolia* (101 m^{-2}), but comparable to those reported for *Andropogon gerardii* (413 m^{-2}) (Mullahey et al. 1991) and *Carex arenaria* (160–590 m^{-2}) (Noble et al. 1979). Bud densities for *H. belangeri* (1452–4217 m^{-2}) were much higher than those previously reported which is primarily associated with the higher tiller densities characteristic of stoloniferous species.

Grazing history of the communities from which the buds were collected, although not statistically evaluated because of the lack of replication, did not substantially affect the number, status, longevity, or outgrowth of axillary buds on an individual tiller basis for either species. However, frequent defoliation under drought conditions has been shown to decrease bud number per tiller in two *Agropyron* species (Busso et al. 1989) and severe defoliation has been documented to decrease bud viability in *Trifolium repens* (Newton and Hay 1996). Bud viability of *T. repens* was only reduced at the nodes where axillary bud development was occurring at the time defoliation was imposed (Hay and Newton 1996). In this investigation, axillary bud number per square meter for *B. curtipendula* was 25% lower in the long-term grazed compared to the long-term ungrazed community based on a reduction in both tiller number per plant and plant number per square meter. In contrast, bud number per square meter for *H. belangeri* was 190% greater in the long-term grazed compared to the long-term ungrazed community based on a large increase in plant density per square meter. These data demonstrate that the long-term effects of herbivory on axillary bud density are predominantly expressed at the plant and population levels, rather than at the individual tiller level. This is an important distinction when invoking axillary bud growth as a potential mechanism of herbivory resistance (e.g., Murphy and Briske 1992) or compensatory growth in grasses (e.g., Tuomi et al. 1994). We found no evidence to support the hypothesis of compensatory bud outgrowth on an individual tiller basis in long-term grazed compared to long-term ungrazed communities for either the mid- or late-seral species.

Our experimental data indicate that mid- and late-seral species retain substantial numbers of dormant and viable buds that exceed parental tiller longevity by at least 12 months to comprise a meristematic source with greater longevity than the seed bank of numerous perennial grasses (Thompson and Grime 1979; Pyke 1990; Kinucan and Smeins 1992). However, the vast majority (≥ 90%) of buds in the bud bank did not initiate growth in the 2-year period following reproductive tiller development regardless of the grazing history of the community from which they were collected. A limited contribution of axillary bud banks to maintenance of tiller populations in both the mid- and late-seral species underscores the ecological importance of annual tiller recruitment from recently developed axillary buds. Two scenarios could explain how tiller populations are maintained in grasslands and savannas characterized by frequent and/or intense drought and/or grazing which can potentially disrupt annual tiller replacement. First, bud differentiation and maturation may be remarkably tolerant of adverse environmental conditions (e.g., Briske and Wilson 1980; Barlow et al. 1980; Van Loo 1992) and second, tiller recruitment may resume from axillary buds that mature following the cessation of severe drought and/or grazing, rather than from mature buds that survive these disturbances. These scenarios warrant additional research emphasis given the critical importance of this demographic process to tiller replacement in species populations and the maintenance of relative species abundance in grasslands and savannas.

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References

Barlow EWR, Munns RE, Brady CJ (1980) Drought responses of apical meristems. In:Turner NC, Kramer PJ (eds) Adaptation of plants to water and high temperature stress. Wiley, New York, pp 191–205

Briske DD, Butler JL (1989) Density-dependent regulation of ramet populations within the bunchgrass *Schizachrium scoparium*: interclonal versus intraclonal interference. J Ecol 77:963–974

Briske DD, Wilson AM (1980) Drought effects on adventitious root development in blue grama seedlings. J Range Manage 33:323–327

Busso CA, Mueller RJ, Richards JH (1989) Effects of drought and defoliation on bud viability in two caespitose grasses. Ann Bot 63:477–485

Busso CA, Boo RM, Pelaez DV (1993) Fire effects on bud viability and growth of *Stipa tenuis* in semiarid Argentina. Ann Bot 71:377–381

Cable DR (1971) Growth and development of Arizona cottontop (*Trichachne californica* [Benth.] Chase) Bot Gaz 132:119–145

Cline MG (1991) Apical dominance. Bot Rev 57:318–358

Conover WJ (1980) Practical nonparametric statistics. 2nd edn. Wiley, New York

Dahl BE, Hyder DN (1977) Developmental morphology and management implications. In: Sosebee RE (ed) Rangeland plant physiology. Society for Range Management, Denver, pp 257–290

De Kroon H, Knops J (1990) Habitat exploration through morphological plasticity in two chalk grassland perennials. Oikos 59:39–49

Eriksson O (1989) Seedling dynamics and life histories in clonal plants. Oikos 55:231–238

Gaff DF, Okong'o-ogola O (1971) The use of non-permeating pigments for testing the survival of cells. J Exp Bot 22:756–758

Grime PG (1979) Plant strategies and vegetation processes. Wiley, New York

Harper JL (1977) Population biology of plants. Academic Press, New York

Harris D, Davy AJ (1986) Regenerative potential of *Elymus farctus* from rhizome fragments and seed. J Ecol 74:1057–1067

Haslam SM (1969) The development and emergence of buds in *Phragmites communis* Trin. Ann Bot 33:289–301

Hay MJM, Newton PCD (1996) Effect of severity of defoliation on the viability of reproductive and vegetative axillary buds of *Trifolium* repens L. Ann Bot 78:117–123

Heidemann GS, Van Riper GE (1967) Bud activity in the stem, crown, and rhizome tissue of switchgrass. J Range Manage 20:236–241

Hume DE (1991) Leaf and tiller production of prairie grass (*Bromus willdenowii* Kunth) and two ryegrass (*Lolium*) species. Ann Bot 67:111–121

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211

Kinucan RJ, Smeins FE (1992) Soil seed bank of a semiarid Texas grassland under three long-term (36-years) grazing regimes. Am Midl Nat 128:11–21

Langer RHM (1963) Tillering in herbage grasses. Herb Abstr 33:141–148

Langer RHM (1972) How grasses grow. Edward Arnold, London

Leakey RRB, Chancellor RJ, Vince-Prue D (1977) Regeneration from rhizome fragments of *Agropyron repens*. II. The breaking of "late spring dormancy" and the influence of chilling and node position on growth from single-node fragments. Ann Appl Biol 87:433–441

McIntyre GI (1970) Studies on bud development in the rhizome of *Agropyron repens*. I. The influence of temperature, light intensity, and bud position on the pattern of development. Can J Bot 40:1903–1909

McKendrick JD, Owensby CE, Hyde RM (1975) Big bluestem and indiangrass vegetative reproduction and annual reserve carbohydrate and nitrogen cycles. Agro-ecosystems 2:75–93

Mitchell KJ (1953) Influence of light and temperature on the growth of ryegrass (*Lolium* spp.). II. The control of lateral bud development. Physiol Plant 6:425–443

Mueller RJ, Richards JH (1986) Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum*. Ann Bot 58:911–921

Mullahey JJ, Waller SS, Moser LE (1991) Defoliation effects on yield and bud and tiller numbers of two Sandhills grasses. J Range Manage 44:241–245

Murphy JS, Briske DD (1992) Regulation of tillering by apical dominance: chronology, interpretive value, and current perspectives. J Range Manage 45:419–429

Newton PCD, Hay MJM (1996) Clonal growth of white clover: factors influencing the viability of axillary buds and the outgrowth of a viable bud to form a branch. Ann Bot 78:111–115.

Noble JC, Bell AD, Harper JL (1979) The population biology of plants with clonal growth: I The morphology and structural demography of *Carex arenaria*. J Ecol 67:983–1008

Novoplansky A (1996) Hierarchy establishment among potentially similar buds. Plant Cell Environ 19:781–786

Olson BE, Richards JH (1988) Tussock regrowth after grazing: intercalary meristem and axillary bud activity of tillers of *Agropyron desertorum*. Oikos 51:374–382

Pyke DA (1990) Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. Oecologia 82:537–543

Sharman BC (1945) Leaf and bud initiation in the Graminae. Bot Gaz 106:269–289

Silsbury JH (1964) Tiller dynamics, growth, and persistency of *Lolium perenne* L. and of *Lolium rigidum* Gaud. Aust J Agric Res 15:9–20

Smeins FE, Merrill LB (1988) Long-term change in a semiarid grassland. In: Amos BB, Gehlbach FR (eds) Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor University Press, Waco, Texas, pp 101–114

Smeins FE, Taylor TW, Merrill LB (1976). Vegetation of a 25-year exclosure on the Edwards Plateau, Texas. J Range Manage 29:24–29

Thompson K, Grime JP (1979) Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J Ecol 67:893–921

Tuomi J, Nilsson P, Åström M (1994) Plant compensatory responses: bud dormancy as an adaptation to herbivory. Ecology 75:1429–1436

Van Loo EN (1992) Tillering, leaf expansion and growth of plants of two cultivars of perennial ryegrass grown using hydroponics at two water potentials. Ann Bot 70:511–518

Vegis A (1964) Dormancy in higher plants. Annu Rev Plant Physiol 15:185–224

Villiers TA (1972) Seed dormancy. In: Kozlowski TT (ed) Seed biology. Academic Press, New York, pp 219–281

Vleeshouwers LM, Bouwmeester HJ, Karssen CM (1995) Redefining seed dormancy: an attempt to integrate physiology and ecology. J Ecol 83:1031–1037

Welker JM, Briske DD, Weaver RW (1987) Nitrogen-15 partitioning within a three generation tiller sequence of the bunchgrass *Schizachyrium scoparium*: response to selective defoliation. Oecologia 74:330–334

Welker JM, Briske DD, Weaver RW (1991) Intraclonal nitrogen allocation in the bunchgrass *Schizachyrium scoparium* Hubb.: an assessment of the physiological individual. Funct Ecol 5:433–440

White J (1980) Demographic factors in populations of plants. In: Solbrig OT (ed) Demography and evolution in plant populations. University of California Press, pp 21–40

Youngblood B, Cox AB (1922) An economic study of a typical ranching area on the Edwards Plateau of Texas. Texas Agric Exp Sta Bull 297