

Seasonal dynamics of prairie sandreed rhizome development

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Abstract

Multiple generations of rhizome-connected tillers stabilize soils and produce measurable amounts of herbage on sandy rangeland throughout the world. However, little is known about the dynamics of rhizome development in these clonal plant species. Seasonal relationships between foliar characteristics and rhizomes of prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] were examined on sands range sites at 30-day intervals from May through September 1989 and 1990 at the University of Nebraska, Panhandle Experimental Range near Scottsbluff. Quadrats were excavated each year from two, 5 x 5 Latin Square macroplots in each of 2 grazing histories, long-term rest or current-year deferment. Under dry conditions in 1989, a 65% reduction in the length of new rhizomes during July preceded a 64% reduction in live tillers in August. After which, rhizome length and live tiller density were unchanged and mean tiller weight increased during September. When average precipitation occurred in 1990, a 25% reduction in live tillers and concurrent increases in new rhizome length and mean tiller weight occurred during July. Rhizome bud densities increased throughout the growing season at different but predictable rates ($R^2 \geq 0.95$) for grazing histories, regardless of precipitation. Length of new rhizomes was highly correlated ($R^2 = 0.91$) with live herbage throughout the growing season. Measurable increases in total rhizome length did not occur until live herbage of prairie sandreed exceeded a threshold of about 50 g m⁻². Maximum increase in length of new rhizomes per unit of live herbage was about 10 cm g⁻¹ near 100 g m⁻². Given its dependence on vegetative reproduction and relatively high palatability to beef cattle, periodic or repeated years of full growing season deferment may be the only reliable method of obtaining measurable increases in prairie sandreed populations.

Key Words: *Calamovilfa longifolia*, warm-season grass, clonal growth, reproduction threshold, tiller dynamics

Resumen

Generaciones múltiples de hijuelos conectados por rizomas estabilizan los suelos y producen cantidades medibles de forraje en los pastizales arenosos del mundo. Sin embargo, poco se conoce respecto a las dinámicas de desarrollo de los rizomas en estas especies vegetales clonales. Se examinaron las relaciones estacionales entre las características foliares y los rizomas del zacate "Prairie sandreed" [*Calamovilfa longifolia* (Hook) Scribn.]; el estudio se llevó a cabo en la Estación Experimental de Pastizales Panhandle de la Universidad de Nebraska, cerca de Scottsbluff, y se realizó en sitios de pastizal arenosos en intervalos de 30 días de Mayo a Septiembre de 1989 a 1990. Cada año se excavaron cuadrantes en dos macro parcelas de un Cuadro Latino 5 x 5 situadas en dos áreas con diferente historial de manejo del apacentamiento, descanso a largo plazo y diferimiento del año actual. En 1989, bajo condiciones de sequía, una reducción del 65% de la longitud de los nuevos rizomas registrada en Julio precedió a una reducción del 64% de los hijuelos vivos registrada en Agosto. Después de la cual, la longitud de los rizomas y la densidad de los hijuelos vivos permanecieron sin cambio y la media de peso de los hijuelos se incrementó durante Septiembre. En 1990, año con precipitación promedio, en Julio se observó un 25% de reducción en los hijuelos vivos e incrementos concurrentes de la longitud de los rizomas nuevos y la media de peso de los hijuelos. Las densidades de yemas de hijuelos se incrementaron a través de la estación de crecimiento a diferentes tasas (pero predecibles) ($R^2 > 0.95$) para las historias de apacentamiento, sin importar la precipitación. A lo largo de la estación de crecimiento la longitud de los nuevos rizomas estuvo altamente correlacionada ($R^2 = 0.91$) con el forraje vivo. No ocurren incrementos medibles en la longitud total de los rizomas hasta que el forraje vivo del "Prairie sandreed" excedió un umbral de aproximadamente 50 g m⁻². El máximo incremento de la longitud de los rizomas nuevos por unidad de forraje vivo fue aproximadamente de 10 cm g⁻¹ casi 100 g m⁻². Dada su dependencia en la reproducción vegetativa y su gustocidad relativamente alta para el ganado para carne, el diferimiento periódico o repetido de la estación de crecimiento completa puede ser el único método confiable para obtener incrementos medibles en poblaciones de "Prairie Sandreed".

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The relative value of rhizomes in reproduction, resource acquisition, and interactions among rhizome-connected shoots has been reported for graminoid (Hartnett 1989, Jónsdóttir and Callaghan 1990, Jónsdóttir 1991, de Kroon et al. 1992, Wikberg et al. 1994, Makita 1996) and forb (Hartnett 1990, Hara and

Wakahara 1994, Schmid et al. 1995) species. However, most of this information is limited to end-of-season measurements. Field studies of grass rhizome dynamics during the growing season are rare (Brejda et al. 1989) and quantification of seasonal relationships between rhizome and shoot characteristics during the growing season has not been reported.

Networks of rhizome-connected tillers are highly effective in stabilizing sandy soils in the Nebraska Sandhills, the largest stabilized sand dune formation in the western hemisphere encompassing about 4.9 million ha. Prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] is a co-dominant, warm-season, rhizomatous grass in mid- to late seral plant communities on all upland sites in the Sandhills and on many sandy range sites in the northern Great Plains of USA and Canada (GPFA 1986). Prairie sandreed tillers develop almost exclusively from buds at the distal end of rhizomes which are unbranched and relatively long and deep compared to other plant species in the Sandhills (Brejda et al. 1989, Nixon 1993, Hendrickson et al. 1998).

Our primary objective was to quantify seasonal relationships between prairie sandreed shoot and rhizome characteristics in natural plant communities. Excavation macroplots were also blocked by grazing history and protected from defoliation to evaluate seasonal dynamics of rhizome development after more than 14 years of rest compared to a single year of full growing season deferment. Based on preliminary field evaluations, we hypothesized that length of new rhizomes within a given soil volume increases monotonically as live herbage of prairie sandreed increases within the sample area during the growing season. We further hypothesized that the rate of change in rhizome length per unit change in herbage is independent of grazing history.

Materials and Methods

The study was conducted during 1989 and 1990 at the University of Nebraska, Panhandle Experimental Range (PER, 42° 08' N, 103° 43' W), 19 km northwest of Scottsbluff, Nebraska. Soils are Valent fine sands (Mixed Mesic Ustic Torripsamment). About 73% of annual precipitation occurs during the growing season from May to September. Long-term average annual precipitation was 340 mm with 270 mm in 1989 and 350 mm in 1990. Rangelands in mid- to late seral

stages at this location are dominated by prairie sandreed. Other abundant species include needleandthread (*Stipa comata* Trin. & Rupr.), blue grama [*Bouteloua gracilis* (HBK) Lag. ex Griffiths], and sand dropseed [*Sporobolus cryptandrus* (Torr.) A. Gray]. Sand bluestem (*Andropogon halli* Hack.) is abundant in late seral stages (GPFA 1986).

Four macroplots with uniform distribution of prairie sandreed tillers were selected in a 5.0-ha enclosure constructed in 1974 and in the pasture where the enclosure was located. The pasture had been moderately stocked at 1.0 AUM ha⁻¹ and continuously grazed from May through September since 1978. Two macroplots within each grazing history were randomly selected for excavation in each year. Fences were constructed to exclude cattle from 2 previously grazed macroplots in the pasture in April each year. A 5 x 5 grid of 0.5-m² quadrats (0.71 x 0.71 m) with 0.71-m wide alleys was marked on selected macroplots in April 1989 and 1990. Excavation dates were assigned to quadrats within rows and columns according to randomization procedures for Latin Squares. Five quadrats were excavated to a depth of 30 cm from 2 macroplots in the long-term-rested area and 2 macroplots in the current-year-deferred areas at 30-day intervals from 30 May to 30 September in 1989 and 1990. Prairie sandreed plants were separated from soil and other plant material over wire screens at the excavation site, bagged, and transported on dry ice to freezers.

Plant material was separated into live shoots, crowns, rhizome buds, new rhizomes, and old rhizomes. Initially rhizomes grow horizontally from the point of origin followed by vertical growth which culminates in the development of a shoot if the rhizome is not aborted. Rhizomes originate from buds nears the base of vertical crowns. Rhizome buds were differentiated and visually discernable shoots less than 2-cm long. Buds elongating beyond 2 cm were classified as new rhizomes. New rhizomes had numerous, light tan, intact exterior scales. Rhizomes in this category formed connections between crowns of current-year and/or prior-year shoots or they originated from a shoot and had not emerged. Old rhizomes were dark tan to black with no scales or low densities of fractured scales. Length of rhizomes was measured by hand. Intact networks of old rhizomes often connected 6 to 8 crowns. Plant components were oven dried at 50°C to a constant weight. Mean tiller weights were calculated from total weight of live

herbage and density of live tillers within each excavated area.

The average laboratory time required to separate prairie sandreed from a single 0.5-m² quadrat into plant components in 1989 was 3.5 hours. During August and September 1989, the quarter of the quadrat with the density of live prairie sandreed tillers most similar to the average for the entire 0.5 m² quadrat was excavated separately. Variances and means for quarter and full quadrat data sets were similar based on F and t-tests at $P \leq 0.05$. In 1990, the area of excavated experimental units was reduced to 35 x 35 cm, the quarter with a tiller density most similar to the original 0.5 m² quadrat.

Data were analyzed as a Latin Square using old rhizome length as a linear covariate with the General Linear Models Procedure (SAS 1986). Experimental units were individual quadrats within Latin Square macroplots, blocked by grazing history. Season and season by year interaction effects with grazing history were tested. However, comparisons of means for grazing histories were not valid without replication which was precluded by labor constraints. The Least-Squares Means Procedure within SAS was used for mean separation among excavation dates (Searle et al. 1980). Treatment effects were reported as significant at $P \leq 0.10$. Values used to compute regression equations (SAS 1986) for seasonal changes in density of differentiated rhizome buds below crowns on long-term-rested and current-year-deferred macroplots were the means of 20 excavated quadrats. Values used to compute regression equations for the relationships between the length and weight of new prairie sandreed rhizomes and between live prairie sandreed herbage and the length of new rhizomes were the means of 10 excavated quadrats.

Results and Discussion

Dormant season precipitation from 1 October to 30 April was 42% of long-term average before the 1989 growing season compared to 129% before the 1990 growing season (Fig. 1). Peak standing herbage is highly correlated with the quantity of moisture in Valent soils in mid-April (Dahl 1963). Additionally, total herbage production per unit of spring soil moisture is about 58 and 167% greater than for soil moisture received during early and late summer, respectively (Dahl 1963). While precipitation during June was only 5% of the long-term average in 1989 and 23% in

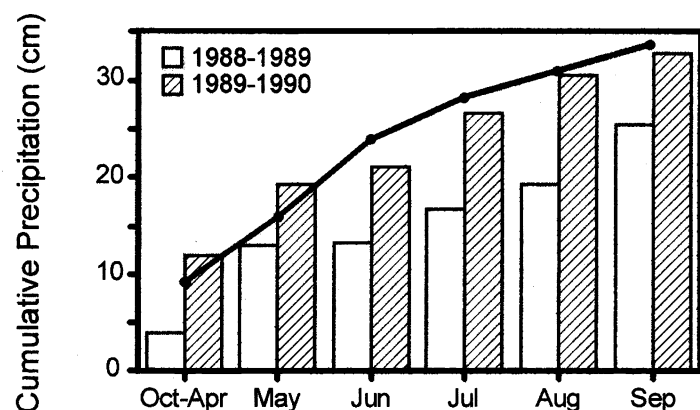


Fig. 1. Cumulative annual precipitation from 1 Oct. to 30 Sept. for the 1989 and 1990 growing seasons and the 30-year average (•—•) at the University of Nebraska, Panhandle Experimental Range near Scottsbluff, Nebr.

1990, cumulative precipitation beginning in October 1989 was similar to the 30-year average during most of the 1990 growing season because of above average precipitation during the preceding dormant season. Cumulative precipitation beginning in October 1988 was about 10 cm below the 30-year average from 1 June to 31 August 1989, the primary growing season for prairie sandreed (Fig. 1).

Tillers

Regardless of precipitation regime or grazing history, measurable declines in the density of live prairie sandreed tillers occurred during each growing season (Table 1). Densities of live tillers declined by about 64% on all macroplots during August 1989 and about 25% during July 1990 (Table 1). Similar changes in live tiller density for grazing histories in both

years indicated that mortality rates were density independent. Prairie sandreed tiller recruitment in western and central Nebraska is poorly correlated with concurrent 15 or 30 day precipitation totals (Hendrickson et al. 2000). However, in this and other studies of prairie sandreed, tiller recruitment and end-of-season tiller numbers increased as cumulative precipitation increased from the preceding October to the end of the current growing season (Cullan et al. 1999, Hendrickson et al. 2000). Epic events of tiller mortality are relatively common for rhizomatous graminoids in subarctic and temperate environments (Callaghan 1976, Kroon et al. 1992); however, they have not been observed in prairie sandreed populations 240 km east of the Panhandle Experimental Range (PER) at the University of Nebraska-Lincoln Gudmundsen Sandhills Laboratory (Cullan et al. 1999) where long-

term precipitation is 560 mm compared to 340 mm at the PER.

Mean tiller weights increased about 117% on current-year-deferred macroplots and about 175% on long-term-rested macroplots each year during the month in which measurable declines of live tiller densities occurred (Table 1). Tiller densities were unchanged and mean tiller weight continued to increase the remainder of the growing season in both years. Stable late-summer tiller densities are consistent with other studies which indicate about 80% of prairie sandreed tillers emerge by mid-June after which emergence generally remains low the remainder of the growing season (Hendrickson et al. 2000). End-of-season tiller densities increased 91% from 1989 to 1990 on current-year-deferred macroplots compared to 142% on long-term-rested macroplots (Table 1). Higher end-of-season densities and mean weights of live tillers on long-term-rested compared to current-year-deferred macroplots in 1990 are indicative of relatively high levels of plant vigor commonly observed in prairie sandreed in high seral plant communities in this area.

Rhizomes

Monthly rates of change in the density of differentiated buds that could produce rhizomes were similar for grazing histories except during July and August when bud density on long-term-rested macroplots increased by about 1.6 buds $m^{-2} day^{-1}$ compared to 0.3 buds $m^{-2} day^{-1}$ on current-year-deferred macroplots (Fig. 2). This pattern was consistent over years regardless of precipitation regime. Corresponding delays in differentiation of rhizome buds (Nixon 1993) and herbage production (Table 1) during May on long-term-rested compared to current-year-deferred macroplots indicated litter accumulation on rested sites may have reduced soil temperatures (Willms et al. 1993). Mean densities of buds for grazing histories in May 1990 were similar to densities in September 1989 indicating most of the rhizome buds in September survived into the subsequent year. End-of-season bud densities for grazing histories were similar in 1989, but 52% higher on long-term-rested than current-year-deferred macroplots in September 1990 when near average precipitation occurred (Nixon 1993).

The relationship between total weight and length of new rhizomes was highly predictable ($R^2 = 0.90$) regardless of the month or year of sampling (Fig. 3). Mean biomass ranged from 6.4 g m^{-1} with 52 cm

Table 1. Mean density and weight of live prairie sandreed tillers for grazing histories from May through September 1989 and 1990 at the University of Nebraska, Panhandle Experimental Range near Scottsbluff, Nebr.

Date	1989		1990	
	Current-year-deferred	Long-term-rested	Current-year-deferred	Long-term-rested
Tiller Density ¹ (no. m^{-2})				
May 30	169a	262a	139ab	240a
Jun 30	179a	200b	166a	258a
Jul 30	190a	248a	133b	181b
Aug 30	70b	87c	107b	186b
Sep 30	58b	69c	127b	200b
Mean Tiller Weight ² (mg)				
May 30	311cd	137d	162b	30d
Jun 30	399bc	300bc	291b	189c
Jul 30	237d	173cd	614a	527b
Aug 30	525b	467ab	492a	435b
Sep 30	681a	515a	505a	812a

¹Numbers within columns with the same letter are not significantly different, $P > 0.10$.

²The month by grazing history by year interaction for mean tiller weight was significant at $p = 0.021$.

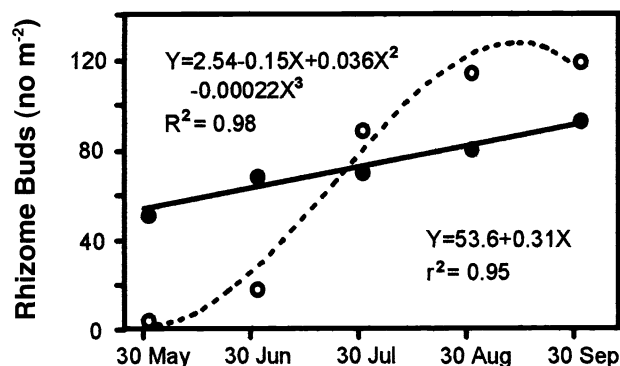


Fig. 2. Seasonal patterns in the density of differentiated buds on vertical rhizomes below crowns of prairie sandreed that could produce new rhizomes (x = days after 30 May) from May through September on long-term-rested (\circ) and current-year-deferred (\bullet) macroplots at the University of Nebraska, Panhandle Experimental Range.

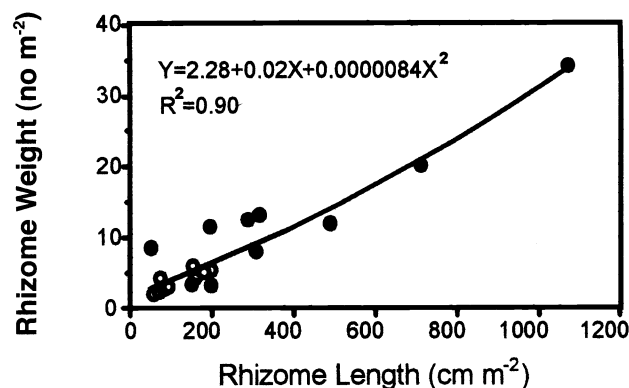


Fig. 3. The relationship between total weight and total length of new prairie sandreed rhizomes from May through Sept. 1989 (\circ) and 1990 (\bullet) at the University of Nebraska, Panhandle Experimental Range.

m^{-2} to $3.1 g m^{-2}$ with $1073 cm m^{-2}$ (Fig. 3). About 94% of the reduction in mean biomass per unit length occurred within the first 20% of the observed range in total length. Mean biomass was about $3.3 g m^{-2}$ when length of new rhizomes reached $200 cm m^{-2}$. After soil moisture deficits induced reductions in total length of new rhizomes during July 1989 (Fig. 4), mean biomass per unit length was 82% greater on current-year-deferred macroplots and 49% greater on long-term-rested macroplots (Fig. 3) indicating low-weight rhizomes may have senesced more frequently than heavy rhizomes. Additionally, remaining intact rhizomes may have received proportionately greater amounts of carbohydrates from shoots (Welch 1968) or carbohydrates may have been translocated from senescing rhizomes into intact rhizomes (Jónsdóttir and Callaghan 1990). Carbohydrate concentrations in prairie sandreed rhizomes generally increase rapidly during late summer (Welch 1968). However, little change occurred in mean biomass per unit length when rapid rhizome growth occurred during August and September 1990 (Fig. 3 and 4).

Length of old rhizomes within excavated sample volumes was a significant linear covariate in the analysis of tiller density, herbage, and density of buds that could produce rhizomes. Water and/or nutrients may be translocated from old non-assimilating tillers to connected tillers with live shoots (Jónsdóttir and Callaghan 1988). In contrast, length and weight of new rhizomes were not affected by length of old rhizomes. This contrasts with highly sig-

nificant linear relationships between preceding and current-year rhizome biomass for herbaceous species in temperate environments (de Kroon et al. 1992). However, based on the number of interconnected crowns and assuming 1 crown per year, old rhizomes may have been as much as 7 years old in our study. While crowns may produce more than 1 rhizome in a single year, only 1 crown has developed at the distal end of rhizomes per year in our preliminary field studies of plants grown in containers. Additionally, a percentage of preceding-year rhizomes may have been included in the new rhizome category if color and scale condition criteria were met. Growth of new prairie san-

dreed rhizomes after buds differentiated appeared to be primarily dependent upon resources from assimilating tillers.

The limiting effects of soil moisture deficits on length of new rhizomes in 1989 were uniformly profound regardless of grazing history (Fig. 4). Tiller weights increased from July to September (Table 1) with no change in length of new rhizomes and no difference in rhizome length between grazing histories (Fig. 4) in September. However, when average precipitation occurred in 1990, length of new rhizomes at the end of the growing season was 3.4 times greater for long-term-rested than current-year-deferred macroplots (Fig. 4). Density and mean weight of live

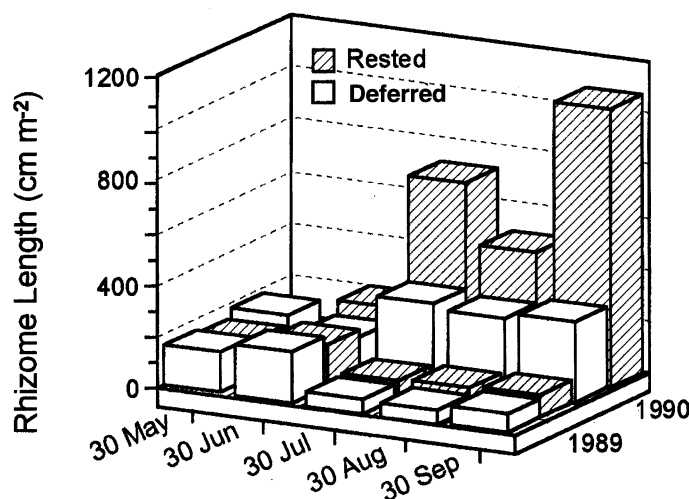


Fig. 4. Mean total length of new prairie sandreed rhizomes at 30-day intervals during the growing season on long-term-rested and current-year-deferred macroplots at the University of Nebraska, Panhandle Experimental Range.

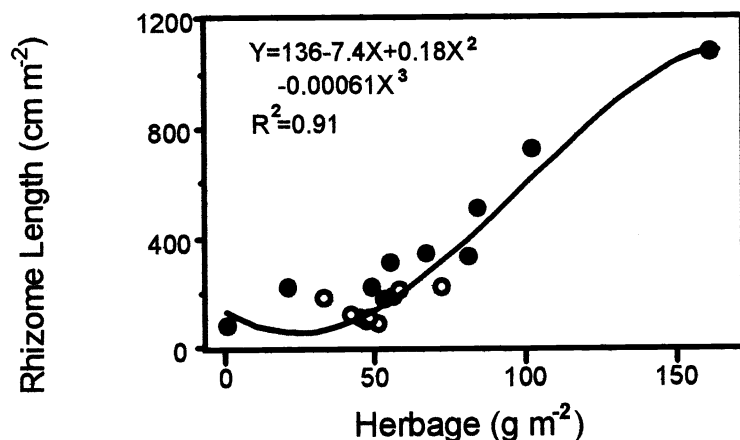


Fig. 5. The relationship between total length of new rhizomes and total live herbage of prairie sandreed from May through Sept. 1989 (○) and 1990 (●) at the University of Nebraska, Panhandle Experimental Range.

tillers in late September were both about 60% higher on rested than on deferred macroplots in 1990 (Table 1) resulting in a mean of 10.7 in of new rhizomes per 1.0 m².

Lack of correlation between length of new prairie sandreed rhizomes and tiller density was similar to *Carex bigelowii* (Wikberg et al. 1994) which also exhibits epic events of tiller mortality. In contrast, live herbage of prairie sandreed accounted for 91% of the variation in new rhizome length regardless of grazing history or the year or month of sampling (Fig. 5). The relationship between total length of new rhizomes and mean tiller weight was similar to, but less predictable ($R^2 = 0.76$) compared to total live herbage (Nixon 1993). Therefore, we accept our hypothesis that the relationship between rhizome length and live herbage is not affected by grazing history. The lack of grazing history effects is consistent with studies of *Carex bigelowii* on subarctic rangeland (Jónsdóttir 1991). Strong relationships between total live herbage and length of new rhizomes have also been reported for forbs *Aster lanceolatus* and *Solidago canadensis* (Schmid et al. 1995) and *Paris tetraphylla* (Hara and Wakahara 1994).

During both years, measurable increases in total length of new rhizomes did not occur until herbage exceeded a threshold of about 50 g m⁻² (Fig. 5) which may correspond to the 4 to 5 leaf stage after which Brejda et al. (1989) reported initiation of new rhizome growth. Beyond this threshold, increases in rhizome length per unit of herbage were highest, about 10 cm g⁻¹, near 100 g m⁻² (Fig. 5). Increases in rhizome length per unit of live herbage were about 40% lower when live herbage was near 50 and 150 g m⁻¹ (Fig. 3 and 5).

Therefore we reject our hypothesis that length of new prairie sandreed rhizomes increases at a constant rate as the mass of live herbage increases.

Precipitation regime by grazing history interaction effects on herbage production were pronounced; however, the relationship between live herbage and length of new prairie sandreed rhizomes was independent of precipitation, grazing history, or excavation date indicating a wide population of inference for the results of this study. Measurable increases in rhizome length in a given year may increase the potential for herbage production if the percentage of tillers originating from relatively long rhizomes increases (White 1977 Brejda et al. 1989) and/or access to limited soil nutrients increases. Interaction between grazing history and precipitation in this study indicates availability of soil moisture will control the extent to which potential herbage production is expressed in semiarid environments.

Prairie sandreed is a mid- and late seral species capable of producing relatively large amounts of herbage critical for ecosystem functions and livestock production. Reproduction of this species is almost exclusively vegetative from crowns formed at the distal end of rhizomes (Brejda et al. 1989, Cullan et al. 1999). Clonal growth into surrounding areas without prairie sandreed and its ability to survive burial on disturbed sites are important processes in secondary succession (Weaver 1965, Maun and Perumal 1999). Consequently, the occurrence of a live-herbage threshold for rapid growth of rhizomes should be considered when developing grazing management strategies designed to increase the composition of

this species. Heavy defoliation during the growing season before threshold levels of herbage have been produced would preclude measurable increases in the composition of prairie sandreed in most years, regardless of grazing systems. The likelihood of producing enough herbage for rapid rhizome development after heavy defoliation in summer-grazed pastures, declines as the growing season progresses and/or precipitation declines (Reece et al. 1999).

Deferring grazing until seedheads have emerged in August would improve the potential for increasing the composition of prairie sandreed (Reece et al. 1996). Tillers that develop from the longest prairie sandreed rhizomes are generally the largest and most likely to produce seedheads (White 1977). Nutritive value and palatability of reproductive tillers to beef cattle decline when seedheads emerge (Reece et al. 1999). These relatively large and generally ungrazed tillers may be critically important for grazing resistance in prairie sandreed by translocating nutrients to connected vegetative tillers (Jónsdóttir and Callaghan 1990, Cullan et al. 1999) that continue to be highly palatable through the summer grazing season (Northup 1993). Given the relatively high preference by cattle for prairie sandreed (Northup 1993, Cullan et al. 1999), periodic or repeated full growing season deferment may be the only reliable method of obtaining measurable increases in prairie sandreed populations. On sites where cool-season graminoids produce 20 to 50% of the herbage, heavy grazing of cool-season species in April, before prairie sandreed tillers emerge, may enhance this species response to full growing-season deferment (Reece et al. 1999).

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