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Morphology and biomass production of prairie cordgrass on marginal lands

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Abstract

Prairie cordgrass (*Spartina pectinata* Link.) is indigenous throughout most of the continental United States and Canada to 60°N latitude and is well suited to marginal land too wet for maize (*Zea mays* L.) and switchgrass (*Panicum virgatum* L.). Evaluations of prairie cordgrass in Europe and North America indicated it has high potential for biomass production, relative to switchgrass, in short-season areas. Our objective was to describe morphology and biomass production and partitioning in mature stands of 'Red River' prairie cordgrass and determine biomass production of natural populations on marginal land. This study was conducted from 2000 to 2008 in eastern South Dakota. Mean biomass production of mature stands of Red River was 12.7 Mg ha⁻¹. Leaves composed >88% of the biomass, and 60% of the tillers had no internodes. Belowground biomass to a depth of approximately 25 cm, not including roots, was 21 Mg ha⁻¹. Tiller density ranged from 683 tillers m⁻² for a 10-year-old stand to 1140 tillers m⁻² for a 4-year-old stand. The proaxis was composed of about eight phytomers, with rhizomes originating at proximal nodes and erect tillers at distal nodes. Vegetative propagation was achieved by both phalanx and guerilla growth. Differences among natural populations for biomass were expressed on gravelly marginal land. However, production, averaged across populations, was low (1.37 Mg ha⁻¹) and comparable to 'Cave-In-Rock' switchgrass (1.67 Mg ha⁻¹) over a 4-year period. The large carbon storage capacity of prairie cordgrass in proaxes and rhizomes makes it useful for carbon sequestration purposes. Prairie cordgrass should be compared with switchgrass and other C₄ perennial grasses along environmental gradients to determine optimum landscape positions for each and to maximize bioenergy production and minimize inputs.

Keywords: axillary bud, bioenergy, meristem, proaxis, rhizome, *Spartina pectinata*, tiller

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Introduction

Prairie cordgrass (*Spartina pectinata* Link.) is a tall, rhizomatous, perennial, warm-season species found predominantly in marshes, wet meadows, potholes, and drainage ways throughout Canada to 60°N latitude and throughout the continental United States, with the exceptions of Louisiana to South Carolina in the Southeast, and California, Nevada, and Arizona in the West (Hitchcock, 1950; Mobberley, 1956; Stubbendieck *et al.*, 1982). However, Mobberley (1956) frequently found prairie cordgrass in open dry prairie and on high ground along railroad rights-of-way in the Midwestern

United States. The genus *Spartina* has the most northerly distribution of any of the C₄ perennial grasses (Potter *et al.*, 1995).

Prairie cordgrass is recognized for tolerance to salinity and valued for wetland revegetation, streambank stabilization, wildlife habitat, and forage. It is adapted to soils that are too wet and not sufficiently aerated for big bluestem (*Andropogon gerardii* Vitman) and switchgrass (*Panicum virgatum* L.), grows more rapidly than other tall grass prairie dominants, and is conspicuously taller than big bluestem and switchgrass where their distributions overlap (Weaver, 1954). Weaver & Fitzpatrick (1932) noted that during the early 20th century the uplands and big bluestem lowlands of the tallgrass prairie were broken for growing maize (*Zea mays* L.); whereas, soils too wet for maize that were dominated

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by prairie cordgrass were left intact for hay production and control of soil erosion.

Weaver (1954) described a prairie cordgrass-dominated community that occurred over hundreds of hectares along the Mississippi and Missouri Rivers and their tributaries in the tallgrass prairie from northern Minnesota to Texas. He concluded that its dominance in dense pure stands was due to its height and extensive rhizome system. Weaver (1954) presented detailed line drawings of the rhizome systems of prairie cordgrass, big bluestem, switchgrass, and Indiangrass [*Sorghastrum nutans* (L.) Nash.], and Weaver & Fitzpatrick (1932) gave general descriptions of the morphology of the tillers and rhizomes of prairie cordgrass.

Although cultivars of smooth cordgrass (*Spartina alterniflora* Loisel.) and saltmeadow cordgrass [*Spartina patens* (Ait.) Muhl.] have been developed for coastal marsh revegetation (Alderson & Sharp, 1994), the development of improved populations of prairie cordgrass for inland wetland revegetation has been very limited. 'Red River Natural Germplasm' is a selected class release of prairie cordgrass from the USDA-NRCS Bismarck Plant Materials Center. The class of seed used for establishment of the stands sampled in this study is Generation 1, which is equivalent to foundation seed.

Red River was developed by interpopulation open pollination among vegetative propagules obtained from east central (Grant County) Minnesota, northeastern (Day County) South Dakota, and east central (Cass and Grand Forks Counties) North Dakota. This germplasm is morphologically diverse, containing both tall and coarse-leaved and short and fine-leaved plants. It is recommended for wetland restoration, streambank stabilization, filter strips, riparian buffers, prairie landscaping, wildlife habitat, and early-season forage in the northern Great Plains (<http://plant-materials.nrcs.usda.gov>). Seed and vegetative propagules of Red River are commercially available. 'Atkins Germplasm' is a selection from Washington County, Nebraska that was released by the Manhattan, Kansas Plant Materials Center. Only vegetative propagules are available (R. Wynia, personal communication, 2008).

Evaluations of prairie cordgrass at 52°N latitude in Europe (Potter *et al.*, 1995), in southwestern Quebec (Madakadze *et al.*, 1998), and in eastern South Dakota (Boe & Lee, 2007) have indicated its high potential for biomass production, relative to switchgrass and other warm-season grasses, in short-season areas. Its high tolerance for soil salinity and early-season waterlogged soils has also been demonstrated (Montemayor *et al.*, 2008).

In the semiarid northern Great Plains, water is the major factor controlling the growth of perennial grasses (Willis *et al.*, 1983). The highest yields of biomass from

perennial grasses in the northern Great Plains would be expected from C₄ species that establish a photosynthetically active canopy early during the growing season in an environment where soil moisture is rarely deficient. Species in the genus *Spartina* develop photosynthetically active canopies earlier than most other warm-season grasses [United States Department of Energy (US DOE), 2006] and are well adapted to soils that are wet throughout the growing season (e.g., Land Capability Class V). On the other hand, the other native tallgrass prairie C₄ grasses are not well adapted to those types of soils (Weaver, 1954). Therefore, prairie cordgrass, as pointed out by Weaver (1954), should be superior to switchgrass and big bluestem for biomass production in low wet areas where it is a dominant component of the potential natural vegetation (USDA-SCS, 1981).

The feasibility of a billion-ton supply of biomass annually proposed by USDA/US DOE (2005) assumes a high-yield scenario of an average of 18 Mg DM ha⁻¹ for perennial grass crops. In the semiarid northern Great Plains, it is highly unlikely that level of biomass production can be reached on rain-fed, marginal uplands. However, such productivity might be attainable from high-yield potential grasses on poorly drained soils (i.e., Land Capability Class V). In South Dakota alone, there are >210 000 ha of Land Capability Class (Helm, 1992) V, which although too wet for conventional crop production, are generally regarded as the highest grass-producing soils in South Dakota (D. Malo, personal communication, 2009).

Below ground level at the base of the stem of tillers of many species of perennial grasses is a region of few to many, depending on the species, compressed nodes and internodes called a proaxis (Evans, 1958) or, more often, a crown (e.g., Hendrickson & Berdahl, 2002). For perennial warm-season grass bioenergy crops that are adapted to temperate areas with cold winters and are harvested for biomass once annually during autumn, nodes on the proaxis bear axillary buds that survive the winter and produce new tillers during the spring from the previous year's tiller.

Bunch grasses that reproduce vegetatively by intravaginal tillers have a caespitose habit referred to as a phalanx growth form. Sod-forming grasses that reproduce vegetatively through production of long rhizomes have a guerilla growth form. Intermediates, such as prairie cordgrass, that form a continuum between these two extreme growth forms are common (Harper, 1985).

Although prairie cordgrass: (1) occurs naturally throughout most of North America, (2) is well adapted for sustainable biomass production on marginal land too wet and or too saline (e.g., Land Capability Class V) for production of maize or switchgrass, (3) produced

higher biomass yields than switchgrass on a well-drained upland soil over a 4-year evaluation period in eastern South Dakota (Boe & Lee, 2007), (4) exhibited genetic variation among natural populations from eastern South Dakota for biomass production (Boe & Lee, 2007), and (5) can withstand three harvests for hay during a growing season (Weaver & Fitzpatrick, 1932), it has not received the attention that switchgrass and miscanthus (*Miscanthus × giganteus*) have for their potential as bioenergy crops. Consequently, because so little is known about its growth and development and potential for biomass production on marginal land, our objectives were to (1) acquire estimates of biomass production and describe the morphology and biomass partitioning of above- and belowground components of mature sods of Red River prairie cordgrass on poorly drained marginal land in eastern South Dakota, and (2) determine biomass production of seven natural populations of prairie cordgrass from eastern South Dakota on gravelly marginal land in central South Dakota.

Materials and methods

Biomass and morphology of seeded and transplanted stands of Red River prairie cordgrass

This study was conducted in three stands of 'Red River' prairie cordgrass ranging in age from 4 to 10 years. Two of these stands were established by seeding and the third by transplanting young seedlings. Ten- and 8-year-old seeded stands of about 8 ha each were located on land owned by Locken Farms near Aberdeen, SD. These stands were planted during June 1998 or 2000 with conventional farm equipment at a seeding rate of about 9 kg pure live seed per hectare and a row spacing of 91 cm. Inter-row cultivation was used for weed control and to maintain rows to stimulate seed production the first year after planting but was suspended thereafter as the vegetative spread by rhizomes formed a dense sod.

The stands were combine harvested for seed during October whenever a profitable seed crop was possible, which was about every other year. The stubble height was generally about 75 cm and all of the straw was left on the fields. For those years when seed production was sparse, no harvests were taken and the biomass was left standing in the field. Nitrogen fertilizer was applied about every other year at 75 kg N ha⁻¹. These two sites were taken out of annual crop production and sown to prairie cordgrass because of drainage issues that delayed or prohibited planting during most springs. The soil classifications are a Ludden silty clay [fine, montmorillonitic (calcareous), frigid, Vertic Haplaquolls] at Aberdeen Site 1, which is on the flood plain of the James

River, and a Beotia silt loam (fine-silty, mixed, Pachic Udic Haploborolls) at Aberdeen Site 2.

The 4-year-old stand was established by transplanting seedlings on 0.6 m centers during May 2004 at Brookings, SD. The area of this stand was about 70 m². Weed control was by hand for the first year after transplanting, but was not needed thereafter as vegetative spread formed a dense sod. The stand was harvested once only for biomass during November 2006, and no fertilizer was applied before or during this study. The stand was burned on May 2, 2008 to remove standing residue from 2007. The soil at this site is Vienna silt loam (fine-loamy, mixed, frigid Calcic Hapludoll).

Samples from the two seeded and the transplanted stands were obtained during early October 2008. For the two seeded 8 ha stands near Aberdeen, we identified areas in the fields that were visually representative of the stand. Within those areas, samples were taken at eight 10 m intervals along a transect. Although there was some lodged nondecomposed biomass from 2007 lying on the surface of the soil, we harvested only standing biomass that was produced during 2008. For the transplanted stand at Brookings, the area was divided into eight equal rectangular subareas and samples were taken near the center of each subarea. At each of the three sites, 0.2 m² plots were harvested by excising all tillers at the surface of the soil with a rice knife. Aboveground vegetation obtained from each sample was dried at 60 °C for 72 h to determine biomass yield.

After drying, the number of tillers was determined for each sample. From a subsample of 15 tillers selected at random from each sample, number of leaves tiller⁻¹ and weights of leaf blade, leaf sheath, and node + internode + inflorescence components for the subsample of tillers were determined. Each component was weighed on a laboratory balance with milligram accuracy to determine biomass partitioning to leaf and stem. Weight tiller⁻¹ was determined from plot biomass and tillers plot⁻¹. Leaf component was determined as the leaf (blade + sheath) fraction of the total weight of the 15-tiller subsample from each plot. Leaf blade-to-sheath ratio was determined as the ratio of the weight of all the blades to the weight of all the sheaths from the 15-tiller subsample. Simple linear correlation coefficients were calculated to determine the strengths of the associations between biomass production and the yield components tillers m⁻² and g tiller⁻¹.

To determine the morphology and biomass of the belowground tiller bases, buds, and rhizomes, a golf course cup cutter was used to extract two cylindrical cores 10 cm diameter × 25 cm height from each 0.2 m² plot. Soil was removed from the underground structures by washing over screens with warm water, and all

adventitious roots were removed by clipping with hand pruners. Underground structures with roots removed were dried at 60 °C for 72 h to determine biomass. Biomass data were collected for all three stands. Morphology data were collected for the Aberdeen Site 2 and Brookings stands.

For belowground structures, number of spent proaxes, number of active proaxes, number of activated meristems, and number of adventitious meristems were determined for each soil core. Spent proaxes were those produced during or before 2007. Active proaxes were those produced during 2008 that had a well-developed proaxis.

Activated meristems were meristems produced on proaxes of tillers produced during 2008. They broke dormancy during autumn 2008, had several well-developed scale-like leaves, and presumably had the potential to produce tillers during 2009. The tips of some of these activated meristems were emergent as 'spikes' about 5 cm above the soil surface at sampling during October 2008. Distribution of activated meristems on the proaxes was separated into distal (the upper three to four nodes) and proximal (lower three to four nodes) positions. Meristems at the base of the proximal section of the proaxis invariably produced relatively long (generally > 5 cm) rhizomes. Meristems on the distal section produced either short rhizomes (i.e., extravaginal tillers) or developed into intravaginal tillers.

Adventitious meristems that occurred in the core samples did not originate on proaxes within the core area; rather they were terminal meristems on rhizomes that originated outside and migrated into the sample area.

Biomass and above- and belowground morphology data from the two seeded stands near Aberdeen were analyzed as a completely randomized design with stand and within stand as sources of variation. No significant differences were found between the two seeded stands for any traits, therefore data were pooled across stands, and means and confidence intervals were determined. For the stand at Brookings established from transplants during 2004, means and confidence intervals were calculated for the same traits determined for the two seeded stands at Aberdeen. Because establishment method and age were different for the Aberdeen and Brookings stands, analysis of variance (ANOVA) was not conducted to determine if the Aberdeen stands differed from the Brookings stands for morphological traits.

In addition to the eight 0.2 m² plots harvested for morphological analysis during 2008, 1 m² plots were harvested by hand with a rice knife at a stubble height of 5 cm from each of the eight subdivisions within the Brookings stand for estimates of biomass production

during November 2006 and October 2008. After the biomass was removed from the sample areas, surrounding areas were also harvested to remove all standing biomass from the experimental area. Subsamples of wet biomass taken in the field were dried at 60 °C for 72 h to determine dry matter concentration. One-way ANOVA was used to determine the effect of temporal variation on biomass production at Brookings.

Biomass production of seven populations of prairie cordgrass on eroded marginal land

Seedlings from seven populations of prairie cordgrass from eastern South Dakota were transplanted in single-row plots on a gravelly upland near Wessington Springs, SD during spring 2000. The experiment was composed of 30 half-sib families from each of 'Summer' and 'Sunburst,' five natural populations of prairie cordgrass from southeastern South Dakota (42°56'N, 97°W), two natural populations of prairie cordgrass from east central South Dakota (44°23'N, 97°9'W), and 'Cave-In-Rock'. The design was two replicates of eight plant single-row plots of each of the Summer and Sunburst families and the seven populations of prairie cordgrass in a randomized complete block design. Cave-In-Rock was included as a 'check' with four single-row plots randomly located within each of the two replications. Inter-row spacing was 0.9 m and intrarow spacing was 0.35 m. The experiment was also conducted during the same time period in eastern South Dakota (Boe & Lee, 2007).

The experiment was located on a shoulder-upper backslope landscape position. The soil was primarily an Ethan (fine-loamy, mixed, superactive, mesic typic calciustolls) gravelly loam. The previous crop during 1999 was sorghum [*Sorghum bicolor* (L.) Moench]. No fertilizer was applied during the study. Weeds were controlled by mowing between the transplanted rows. The principal weed present across the experimental site during the study was Russian thistle (*Salsola iberica* Sennen & Pau.), a common annual weed that occurs most abundantly during dry years in drought stricken cultivated fields and pastures in the northern Great Plains (Van Bruggen, 1976).

Plots were harvested during October for each of the years 2001 through 2004. Plot wet weights were determined in the field. Grab samples of about 1 kg from each population were dried at 60 °C until constant weight to determine dry matter concentration. Biomass data were subjected to split-plot ANOVA for repeated measures with population whole plots and years subplots (Steel & Torrie, 1980; Analytical Software, 2003). Fisher's protected LSD ($P = 0.05$) was used to separate population and year means. The nearest

weather recording station was Wessington Springs, SD, about 25 km from the study site.

Results

Biomass and morphology of seeded and transplanted stands of Red River prairie cordgrass

In general, the three stands could be described as dense sods with high tiller density, leafy growth, and high levels of both above- and belowground biomass production (i.e., 11.7 Mg DM ha⁻¹ aboveground biomass for the seeded stands, 14.6 Mg DM ha⁻¹ aboveground biomass for the transplanted stand, and >20 Mg DM ha⁻¹ of belowground biomass). The biomass of belowground leaf, stem, bud, and rhizome structures to a depth of 25 cm was nearly twice that of the corresponding aboveground biomass (Table 1). The high level of aboveground biomass production was accomplished with little or no internode development (Table 1). In spite of low incidence of reproductive tillers, relatively high levels of biomass production for the northern Great Plains were obtained from mature stands composed predominantly of nonjointed vegetative tillers. Although the tillers averaged fewer than five phytomers, high tiller density and large leaf blades and sheaths contributed to biomass yields >11 Mg ha⁻¹.

Tiller morphology, as described by number of leaves tiller⁻¹ and biomass partitioning between leaves and stems and between blades and sheaths, was relatively consistent across stands. From a developmental standpoint, frequencies of vegetative, elongated, and reproductive tillers were also similar for the seeded and transplanted stands (data not shown). However, tiller density appeared to be higher for the younger transplanted stand (Table 1).

Table 1 Means and 95% confidence intervals for above- and belowground biomass and aboveground morphological traits of Red River prairie cordgrass in eastern South Dakota during October 2008

Trait	Stand type	
	Seeded	Transplanted
Aboveground (Mg DM ha ⁻¹)	11.7 (9.2, 14.2)	14.6 (11.0, 18.3)
Tillers m ⁻²	700 (562, 839)	1140 (944, 1336)
G tiller ⁻¹	1.81 (1.39, 2.24)	1.31 (0.99, 1.63)
Leaf fraction	0.96 (0.94, 0.99)	0.88 (0.84, 0.93)
Blade-to-sheath	1.46 (1.30, 1.62)	1.22 (1.04, 1.40)
Belowground (Mg DM ha ⁻¹)	20.6 (16.5, 24.8)	21.8 (19.1, 24.6)
Leaves tiller ⁻¹	4.8 (4.6, 5.0)	4.4 (4.1, 4.7)

The weights of blades exceeded the weights of sheaths (Table 1). Because most of the tillers were vegetative with one or two exposed collars, blade development was more advanced than sheath development. A significant positive correlation was found between biomass yield and tillers m⁻² ($r = 0.54^{**}$) but not between biomass yield and g tiller⁻¹ ($r = 0.28$) for data pooled across stands ($n = 24$). A significant negative correlation was found between tillers m⁻² and g tiller⁻¹ ($r = -0.56^{**}$).

The proaxis (Evans, 1958) of prairie cordgrass was especially well developed on tillers that arose from the terminal meristem of long (>2.5 cm) rhizomes. At its proximal end it was composed of a neck region similar to what has been described in bamboos (Poaceae: Bambusoideae) (McClure, 1993) of normally six to eight compressed internodes where the rhizome changed from horizontal to vertical growth. The internodes in the neck region were noticeably shorter than the internodes on either side (i.e., internodes of the rhizome that are proximal and the internodes of the proaxis that are distal) of it. The nodes in the neck region had no axillary buds and did not produce rhizomes or tillers (Fig. 1). However, this region had a high density of adventitious roots.

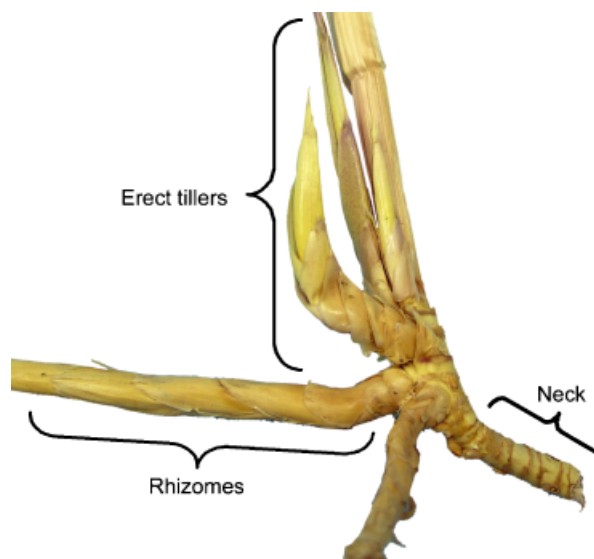


Fig. 1 Typical proaxis of prairie cordgrass at the end of the 2008 growing season. This proaxis has five activated meristems, the two most proximal are rhizomes; whereas the three most distal are erect tillers, the upper two being intravaginal. Leaf sheaths were removed to expose the intravaginal meristems. The intravaginal meristems provide the capacity for closely packed tillers (i.e., phalanx growth form); whereas the extravaginal meristems enable the plant to spread into previously unoccupied areas (i.e., guerilla growth form). The neck is an area of several compressed internodes at the base of the proaxis. No axillary buds occur in the neck region, but adventitious roots are prevalent.

Distal to the neck region was an area of the proaxis composed of six to eight more widely spaced nodes than occurred in the neck region. This region was the site of axillary buds that gave rise to rhizomes at the proximal three to four nodes and erect tillers at the distal three to four nodes (Fig. 1). Weaver & Fitzpatrick (1932) observed that stems of prairie cordgrass were most commonly singly spaced, but also occurred frequently in groups of three. The arrangement of activated meristems on the proximal and distal sections of the proaxis (Fig. 1) provided a morphological and developmental explanation for their observation. A detailed line drawing of the rhizomes of prairie cordgrass can be found in Weaver (1954).

Our observations indicated spent proaxes and rhizomes remained relatively intact for at least 3 years. Proaxes and rhizomes that we ascertained to be older than 3 years (Fig. 2), although faded to a grayish-black, were still firm and woody. The mean number of discernible spent proaxes, averaged across stands, was 1431 m^{-2} . Although mean number of active proaxes m^{-2} should logically estimate mean number of tillers m^{-2} , number of active proaxes m^{-2} was about 35% less than number of tillers m^{-2} (Tables 1 and 2). This difference is likely due to the fact that very small vegetative tillers that had no internodes and no appreciable proaxis development were still collected and counted in the aboveground samples. However, in the belowground samples, their bases would be inconspicuous and easily overlooked. Therefore, although those small tillers were produced during 2008, their proaxes were not considered to be active. About 10% of the plots had no spent proaxes indicating no recent tiller develop-

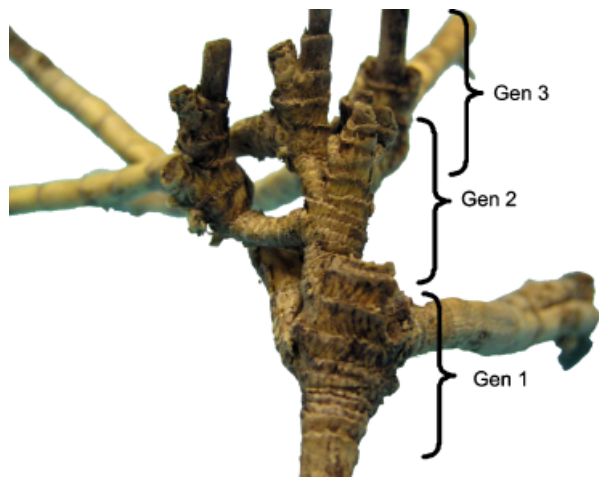


Fig. 2 Three generations (Gen) of spent proaxes of prairie cordgrass. The temporal sequence is most likely Gen 1, 2005; Gen 2, 2006; and Gen 3, 2007. Note that the three Gen 3 proaxes originated from axillary buds on a single Gen 2 proaxis.

Table 2 Means and 95% confidence intervals for belowground morphological traits of two stands of Red River prairie cordgrass in eastern South Dakota during October 2008

Trait	Stand	
	Aberdeen 2	Brookings
Spent proaxes m^{-2}	1096 (455, 1736)	1766 (1037, 2496)
Active proaxes m^{-2}	526 (356, 697)	705 (490, 920)
Meristems m^{-2}	1944 (1434, 2456)	1426 (1013, 1840)
Rhizomes/total meristems	0.33 (0.25, 0.42)	0.39 (0.33, 0.45)

ment in those regions. Less than 5% of the plots had no active proaxes.

The large bud bank, which arose from the six to eight nodes of the proaxis, produced two distinct types of axillary branches. The distal section of the proaxis generally produced intravaginal tillers or extravaginal tillers with short rhizomes (i.e., the phalanx situation for which tillers are closely packed together, as in tussock or bunch-type grasses). On the other hand, the proximal section of the proaxis invariably produced the contrasting guerilla growth form which increases spacing between tillers and allows for large areas to, at least initially, be loosely occupied. Activated meristem density, averaged across stands, was 1685 m^{-2} . Eighty-five percent of those meristems were indigenous to the sample area, and 15% were adventitious originating on the proximal halves of proaxes peripheral to the sample area. Thirty-six percent of the indigenous activated meristems were also the guerilla type, originating on the proximal three to four nodes of the proaxes (Table 2).

Under good growing conditions, tillers of prairie cordgrass emerge as 'spikes' during autumn. These needle-like structures (Fig. 3) are overlapping bladeless scale-like leaves composed of stiff pointed sheaths that elevate to a height of about 5 cm above the soil surface before freeze up during autumn in the northern Great Plains. However, the growing point does not elevate and remains well below the soil surface until growth resumes during the following spring.

Tillers of prairie cordgrass that emerge as spikes during autumn resume growth about 3 weeks before switchgrass tillers begin to emerge during spring at Brookings, SD. Therefore, tillers of prairie cordgrass have two to three normal leaves and reach a height of about 25 cm before switchgrass tillers emerge from the soil. From September through December 2005, precipitation at Brookings was 2.5 times the long-term average. This promoted tiller development during autumn and provided abundant moisture for resumption of



Fig. 3 Activated adventitious meristems on long rhizomes. These meristems were collected from the core samples, but their origins were axillary buds on an active proaxis peripheral to the area of the core sample. Note the overlapping, stiff, scale-like leaves that form a spike that emerges above the soil surface during autumn.

vigorous growth during spring, thus resulting in abundant biomass production by the end of the growing season. On the other hand, autumn precipitation during 2007 and spring precipitation during 2008 were slightly lower than the long-term average.

A significant difference (ANOVA not shown) was found between 2006 and 2008 for biomass production at Brookings. Mean biomass production in 2006 was 13.2 Mg ha^{-1} compared with 10.5 Mg ha^{-1} in 2008. The higher estimate of 2008 yield obtained from smaller plots from this same stand in the aforementioned morphology study is plausibly due to the 0.2 m^2 plots having been harvested at the soil surface and the 1 m^2 plots having been harvested to leave a 5-cm-tall stubble.

Also, the stand was heavily infested with *Ischnodemus falicus* (Say) (Hemiptera: Lygaeidae), and morphological symptoms of feeding by this insect were evident during 2008. This piercing-sucking insect reduced biomass production of natural stands of prairie cordgrass by 40% in Kansas (Johnson & Knapp, 1996).

Biomass production of seven populations of prairie cordgrass on gravelly marginal land

Significant differences were found among years and among populations for biomass production on gravelly marginal upland near Wessington Springs, SD (Table 3). Biomass production during 2003 (1.96 Mg ha^{-1}) and 2004 (2.01 Mg ha^{-1}) were greater than in 2001 (1.24 Mg ha^{-1}) and 2002 (0.63 Mg ha^{-1}). However, even during

Table 3 Mean squares for sources of variation for biomass production of seven natural populations of prairie cordgrass and Cave-In-Rock, Summer, and Sunburst switchgrass on gravelly marginal upland near Wessington Springs, SD during 2001 through 2004

Source of variation	df	Mean squares
Population (P)	9	794 740*
P × replication	9	236 029
Year (Y)	3	9 187 468**
P × Y	27	244 062
Error	30	156 795

***Significant at the 0.05 and 0.01 levels, respectively.

Table 4 Mean biomass yields for seven natural populations of prairie cordgrass and three switchgrass cultivars averaged across 4 years on eroded marginal land near Wessington Springs, SD

Population	Biomass yield (Mg ha^{-1})
Sunburst	1.84
PCG 4	1.83
Cave-In-Rock	1.67
Summer	1.67
PCG 3	1.55
PCG 5	1.48
PCG 2	1.43
PCG 6	1.26
PCG 7	1.22
PCG 1	0.81
LSD (0.05)	0.55

above normal precipitation periods (e.g., 2003 and 2004), biomass yields were extremely low.

Biomass production was similar for the three switchgrass cultivars and four of the prairie cordgrass populations. Sunburst and PCG 4 produced more biomass than the three lowest-yielding prairie cordgrass populations. Mean biomass for Cave-In-Rock and Summer (1.67 Mg ha^{-1}) were only greater than the mean biomass production of the lowest yielding prairie cordgrass population (Table 4).

The range in prairie cordgrass population means was from 0.81 to 1.83 Mg ha^{-1} (Table 4). The three lowest yielding populations of prairie cordgrass were the same in this study as in a sister study in a much higher yielding environment on prime land in eastern South Dakota (Boe & Lee, 2007). In that sister experiment conducted during the same 4-year period on prime land at Aurora, SD, the range in prairie cordgrass population means was from 4.97 to 7.87 Mg ha^{-1} (Boe & Lee, 2007). Although the number of populations of

prairie cordgrass evaluated in this and the previous study was small, distinct differences among populations for biomass production occurred in both marginal and favorable environments.

Total precipitation at Wessington Springs, SD between transplanting during June 2000 and biomass harvest during September 2001 was 930 mm. In comparison, total precipitation between October 2001 and September 2002 was only 459 mm, with 314 mm falling during the growing season (i.e., April–September 2002). Moisture conditions were more favorable for biomass production during 2003 and 2004 than during 2002, with 557 mm falling between October 2002 and September 2003 and 724 mm between October 2003 and September 2004. Low precipitation certainly was a limiting factor to biomass production during 2002, as indicated by twofold increases in biomass production during 2003 and 2004. However, the relatively low biomass production during 2003 and 2004, when precipitation was seemingly adequate for much higher yields, indicated that presumably soil characteristics of the gravelly site prohibited major increases in biomass in response to increased precipitation.

Discussion

Biomass and morphology of seeded and transplanted stands of Red River prairie cordgrass

The highly similar aboveground morphologies of the three stands of Red River in this study suggested a common constraint to internode elongation, stem development, and frequency of reproductive tillers in stands that ranged from 4 to 10 years of age, as was previously described by Jensen (2006) and Haas & Holzworth (n.d.). In contrast, stands of switchgrass harvested during October in South Dakota were >50% stem (Boe & Casler, 2005).

Historically, seed production from the stands at Aberdeen was highest for years when water stood on the stands for several weeks during the spring. During spring 2008, the stands were not inundated (R. Locken, personal communication, 2008), and the October 2007 through June 2008 precipitation was 238 mm, which is 72% of the long-term average (<http://climate.sdstate.edu/coop/monthly.asp>). In Nebraska, production of reproductive tillers on prairie cordgrass clumps transplanted from a marsh to upland occurred only in wet years (Weaver & Fitzpatrick, 1932).

Another factor that may have reduced internode development and frequency of reproductive tillers was high infestation by *I. falcus* in all three stands. High infestations (80–120 insects m⁻²) of natural stands of prairie cordgrass in Kansas by *I. falcus* caused

yellowing of leaves, necrosis of tips of leaf blades, and reduced height. It also reduced photosynthetic rates and biomass production by 40% (Johnson & Knapp, 1996). We observed similar morphological symptoms in all three stands. We did not determine insect densities, however it was not unusual to find >20 individuals of *I. falcus* on individual tillers. In Kansas, population densities of this insect fluctuated widely between 2 years and no long-term effects on biomass production were found (Johnson & Knapp, 1996). Insecticide trials are needed to determine the impact of *I. falcus* on biomass production of prairie cordgrass in the northern Great Plains.

Maximizing biomass production in prairie cordgrass will require development of populations with the capacity to produce a high frequency of reproductive tillers across a range of environments. Mature reproductive tillers of a synthetic cultivar developed by one cycle of selection among and within seven populations from eastern South Dakota (Boe & Lee, 2007) can exceed 2.8 m in height and weigh >30 g at Brookings, SD. Preliminary results (unpublished data, 2008) from a biomass trial at Brookings indicated this improved population can produce 18 Mg ha⁻¹. The national goal set by US DOE (2006) for energy crops is at least 22 Mg ha⁻¹. A stand of well-developed reproductive tillers with a mean individual weight of 30 g would meet that desired goal with a density of only 75 tillers m⁻². Weaver & Fitzpatrick (1932) reported reproductive culms of prairie cordgrass exceeded 3 m in height and 10 mm in diameter in wet areas in the tallgrass prairie. At this time, little is known about the abiotic and biotic factors that influence biomass production in prairie cordgrass. However, age of stand (Jensen, 2006) and high density of a piercing-sucking bug (Johnson & Knapp, 1996) were determined to be important factors in determining seed and biomass yields, respectively.

Boe (2007) and Boe & Beck (2008) reported significant positive linear correlations between tillers m⁻² and biomass yield and between mass tiller⁻¹ and biomass yield during stem elongation through seed maturity in unfertilized stands of switchgrass in eastern South Dakota. Negative correlations between tiller density and tiller mass in grasses are common (e.g., Nelson *et al.*, 1977). Boe & Lee (2007) found weights of blades on reproductive culms of prairie cordgrass decreased about fourfold acropetally across phytomers; whereas, sheath weights were more constant. The general pattern was blade weight to exceed sheath weight for basal phytomers and vice versa for apical phytomers.

Few estimates exist for biomass production of prairie cordgrass in cultivated or natural stands. Natural stands of prairie cordgrass on the Konza prairie in northeastern Kansas produced >15 Mg ha⁻¹ (Johnson

& Knapp, 1996) and natural stands recovering from long periods of drought produced $>9 \text{ Mg ha}^{-1}$ in eastern Nebraska (Weaver & Albertson, 1944). In addition to their future potential for biomass production, these multifunctional stands have (1) produced several highly valuable seed crops, (2) stabilized problem areas that were unsuitable for annual crops due to wet soil conditions that delayed planting during the spring, and (3) provided habitat for wildlife (R. Locken, personal communication, 2008).

Weaver (1954) noted that natural stands of prairie cordgrass were not damaged from harvesting for hay three times during a growing season, and Boe & Lee (2007) found no detrimental effects from a single harvest at the end of the growing season for transplanted stands over a 4-year period in eastern South Dakota. Therefore, we do not expect negative impacts on mature stands from an annual single harvest during autumn for biomass production. However, studies are needed to determine the effects of multiple harvests during a growing season and nitrogen and phosphorus fertilizer on: (1) reproductive tiller frequency and development, (2) biomass production, and (3) persistence of mature stands of prairie cordgrass.

Results from our study of belowground structures revealed morphological characteristics of prairie cordgrass that undoubtedly: (1) contribute to its competitiveness and widespread natural occurrence in pure stands (Weaver & Fitzpatrick, 1932), and (2) provide it with the potential to respond quickly by vegetative reproduction to fluctuations in abiotic environmental conditions (Benson *et al.*, 2004; Dalgeish *et al.*, 2008). The solid, woody, and persistent rhizomes occupied an extensive amount of the volume of the soil in the upper 25 cm of the profile. Similar belowground morphology has been described for switchgrass (Beaty *et al.*, 1978; Brejda *et al.*, 1989). Both intravaginal and extravaginal meristems give rise to tillers in switchgrass, but the proaxis of switchgrass, compared with prairie cordgrass, has fewer nodes and buds from which rhizomes develop (Beaty *et al.*, 1978; Boe & Bortnem, 2003).

Estimates of meristem density have been made for tallgrass prairie in Kansas (Benson *et al.*, 2004); however, we know of no previous estimates for prairie cordgrass communities. In the Kansas study, bud bank densities ranged from 600 to 1800 meristems m^{-2} (this included grasses plus forbs) and was twofold greater in burned vs. unburned prairie. Benson *et al.* (2004) counted all living meristems (grass and forb). In contrast, we counted only activated meristems. Buds that showed no growth, even though they may have been bright in color and firm, were not counted.

The high levels of meristem density quantified for mature stands in this study indicated a large capacity to

reproduce in phalanx and guerilla forms in response to environmental cues. This inherent diversity in underground morphology is obviously why this species has been used so successfully for restoration, stabilization, filterstrip, buffer, cover, and habitat purposes (Jensen, 2006). The guerilla growth form enables expansion out of resource depleted zones (Harper, 1985). Weaver & Albertson (1944) observed that rhizomes of prairie cordgrass went dormant for several years during severe drought periods, but responded vigorously and competitively to increases in precipitation by rapid production of new tillers.

The magnitude of biomass contained in spent and active proaxes and rhizomes of prairie cordgrass on poorly drained marginal (Aberdeen) and prime (Brookings) land revealed the potential of this grass for sequestering atmospheric carbon and increasing soil organic matter. Most of the rhizomes of prairie cordgrass are concentrated in a layer between 15 and 25 cm below the soil surface; whereas the rhizomes of switchgrass and big bluestem are concentrated in the upper 10 cm of the soil (Weaver, 1954). Rice *et al.* (1998) estimated total belowground biomass (roots + rhizomes) in Konza Prairie to a depth of 60 cm to be 1914 g m^{-2} , with a root:shoot ratio of 3.2. In that study, rhizomes made up 25% of the total belowground biomass of the tallgrass prairie. They also found increases in belowground biomass in response to fire and nitrogen fertilizer. For the prairie cordgrass monocultures in this study, the ratio of belowground rhizome + proaxis biomass to aboveground biomass was about 1.6. Because roots were not included in these belowground biomass estimates, it appears that prairie cordgrass has great potential to play a role in regional carbon storage efforts and carbon credit programs.

The ability to accumulate and store large amounts of belowground biomass has been documented in the genus *Spartina*. Gross *et al.* (1991) found dead and live belowground biomass of smooth cordgrass (*S. alterniflora* Loisel.), the dominant grass in salt marshes along the Atlantic and Gulf Coasts of United States, were concentrated in the upper 10–15 cm and collectively exceeded 80 Mg DM ha^{-1} in Delaware. Live belowground biomass was highest during autumn and lowest during early summer. Our results indicated that monocultural stands of prairie cordgrass, relative to native tall grass prairie, can sequester high amounts of carbon in underground stem (i.e., proaxes and rhizomes) and leaf components. We did not determine root biomass in these stands, but Weaver (1954) and Weaver & Fitzpatrick (1932) described a coarse and extensive root system for prairie cordgrass greater in depth and size than that of switchgrass.

Biomass production of seven populations of prairie cordgrass on gravelly marginal land

Biomass production of seven populations of prairie cordgrass on marginal upland in this study was less than one-third of the production on prime land. This reduction in biomass production was slightly greater than the reduction that occurred for Sunburst switchgrass (Boe & Lee, 2007). Although Mobberley (1956) considered open dry prairie and gravelly railroad embankments as primary habitats for prairie cordgrass in the Midwestern United States, as opposed to marshes, sloughs, and floodplains in the eastern United States and Canada, biomass production potential of prairie cordgrass, as well as that of switchgrass, was severely depressed in this study on a gravelly soil in east central South Dakota.

Much of the marginal farmland in the semiarid northern Great Plains that has limitations for crop production related to soil characteristics is undulating with soil conditions on shoulders and back slopes similar to those in this study. At this study site, 8 years after transplanting the prairie cordgrass populations have spread >2 m by rhizomes and have formed a sod. On the other hand, the rows of switchgrass are still easily discernible, and appreciable within-row mortality has occurred. For soil stabilization and erosion control on the gravelly site in this study, prairie cordgrass was superior to switchgrass.

We recognize that the optimum environments for long-term production of prairie cordgrass for biomass production are poorly drained soils (e.g., Land Capability Class V) and that the upland site used for this study was obviously unsuitable for perennial grass biomass production *per se*. However, our results are useful in that they (1) revealed genetic differences among populations of prairie cordgrass for biomass production in an inhospitable environment, and (2) suggested that comparisons between prairie cordgrass and switchgrass, and perhaps big bluestem, miscanthus, and other stress-tolerant grasses along environmental gradients are needed to determine amplitudes of adaptation and optimum landscape positions for species that have potential for use in an integrated multispecies approach to the establishment and maintenance of multifunctional (i.e., biomass production, carbon sequestration, soil conservation, and wildlife habitat) plant communities.

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