RHIZOME AND TILLER DEVELOPMENT OF THREE NEBRASKA SANDHILLS WARM-SEASON GRASSES

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Abstract. Rhizome and tiller development of ungrazed switchgrass (*Panicum virgatum* L.), prairie sandreed [*Calamolvilfa longifolia* (Hook) Scribn.], and sand bluestem [*Andropogon gerardii* var. *paucipilus* (Nash) Fern.] were studied for two years in the Nebraska Sandhills. Rhizome growth of switchgrass began at the 4- to 5-leaf stage. Following tiller elongation, no new rhizomes developed but rhizome elongation continued. Many of the prairie sandreed tillers were biennial similar to those of indiangrass [*Sorghastrum nutans* (L.) Nash]. Spring tiller development on prairie sandreed came from both vertical and horizontal rhizomes and continuing growth of late emerging tillers from the previous year. New rhizomes began growth at the 4- to 5-leaf stage. Prairie sandreed was the only grass to have rhizomes deeper than 10 cm. In sand bluestem, buds on rhizomes that were underneath the previous year's tiller lived over winter. In the spring after a tiller emerged through the soil and reached the 4- to 5-leaf stage meristematic tissue below the shoot apex elongated forming a rhizome which pushed the shoot apex to the soil surface. The newly formed rhizome initiated buds which served as the site of the following year's tiller development. Normal tiller elongation and inflorescence formation occurred later in the season. Prairie sandreed and sand bluestem are adapted to sand burial while switchgrass requires a more stable soil.

Key Words. sand bluestem, *Andropogon gerardii* var. *paucipilus,* prairie sandreed, *Calamovilfa longifolia,* switchgrass, *Panicum virgatum,* rhizomes

INTRODUCTION

The Nebraska Sandhills cover approximately 52,000 km² in north-central Nebraska (Seevers *et al.* 1975). Soils are composed primarily of fine sand, and are very susceptible to wind erosion (Frolik and Shepherd 1940). Despite the highly erosive nature of the soil, vegetated dunes are stable. Soil stability is due largely to the rhizomatous grasses common to the Sandhills.

Rhizomes and tillers function in propagation and competition in many Sandhills grasses. Tolstead (1942) reported that seeds seldom formed in well developed communities of sand bluestem [*Andropogon gerardii* var *paucipilus* (Nash) Fern.] and that prairie sandreed [*Calamolvilfa longifolia* (Hook.) Scribn.] reproduced almost entirely by rhizomes. Axillary buds located on the rhizomes, crowns, and stems of grasses are meristematic areas for vegetative reproduction (Heidemann and Van Riper 1967). Rhizomes enabled grasses to spread into open spaces, and invade underground to initiate new tillers between or beneath other plants (Weaver 1963).

A direct relationship existed between rhizome length and the area occupied by plants within a given time (Evans and Ely 1935). Mueller (1941) reported that grasses which quickly produced numerous, long, well-branched rhizomes were most effective in exploiting new areas. Efficiency in exploiting new areas was influenced by time of initiation, duration of the period of elongation, amount of elongation, branching, number of buds developed annually, and rhizome life (Mueller 1941). If energy was expended for numerous short rhizomes rather than for elongation, a smaller area was more completely occupied (Mueller 1941). Frequent appearance of new rhizomes compensated for shorter rhizomes (Evans and Ely 1935).

Rhizomes were important for the endurance of and recovery from drought and overgrazing (Weaver 1930 and 1963, Booysen *et al.* 1963). Rhizomes help grass withstand heavy grazing and trampling by providing protected underground growing points (Rechenthin 1956). Rhizomes may remain viable in the soil for several years and may resume growth when decreased grazing or favorable weather conditions permit (Weaver 1930).

The importance of sand bluestem and prairie sandreed to the Sandhills vegetation was recognized during initial botanical surveys (Smith and Pound 1892, Rydberg 1895, Pound and Clements 1900, Pool 1914). More recently Burzlaff (1962) considered sand bluestem and prairie sandreed as co-dominants with prairie sandreed being the most uniformly distributed and abundant grass on all upland range sites. Because of its vigorous rhizomatous habit prairie sandreed spread rapidly in the dune sand and played a major role in stabilizing exposed dunes and blowouts and contributed over 40% of the upland dune production (Frolik and Shepherd 1940). Tolstead (1942) reported that prairie sandreed was the most characteristic grass of the Sandhills, growing in a wide range of habitats from coarse sand to very fine sandy loam. Switchgrass is distributed widely both within and outside the Sandhills.

A thorough understanding of rhizome and subsequent tiller formation is essential for understanding the ecological role in the Sandhills and evaluating the response of these grasses to grazing and environmental conditions. The objective of this study was to describe the time of bud development, period of rhizome and tiller development, and growth of sand bluestem, prairie sandreed, and switchgrass.

METHODS

This descriptive study of rhizome and tiller development was conducted during the summers of 1984 and 1985 at the University of Nebraska Gudmundsen Sandhills Laboratory (GSL) located in Grant County, 12 km northeast of Whitman, Nebraska. The GSL lies in an annual precipitation zone of 500-560 mm of which about 75% falls during the growing season (April-September). Precipitation in 1984 was 362 mm during April through August. June precipitation was much above normal, July precipitation was normal, and August precipitation was below normal. In 1985, 183 mm fell in the same time period, and precipitation for all months was below normal. May, June, and July were especially dry. The soil was a Valentine fine sand (fine, sandy, mixed, mesic Typic Ustipsamment).

A fall-grazed pasture was the study site (sands range site). Sampling was at weekly intervals from 4 July through 2 September 1984 and from 16 May through 22 August 1985. Phenological stage at each sampling date was recorded. Leaf stage was determined by counting the true leaves produced during the year of sampling. On each date, three sections of sod, 30 cm deep, containing only sand bluestem, prairie sandreed, or switchgrass were excavated. A section contained a minimum of 20 tillers with attached roots and rhizomes. The sod was washed free of soil under a gentle stream of water, air dried, and taken to the laboratory for characterization. Specimens were arranged in chronological order to identify patterns of rhizome and tiller development. Notes were taken and photographs of representative samples were made to illustrate the developmental process. Cross sections of rhizomes were made and the anatomy of vertical rhizomes were compared to horizontal rhizomes.

DESCRIPTION AND DISCUSSION

Switchgrass

Switchgrass produced new tillers in the spring from buds located on the below-ground stem bases of the previous year's tillers and on rhizomes. A study of 'Caddo' switchgrass on a sands range site in eastern Colorado showed that new tillers in the spring developed from axial buds on the proaxis (stem base), from rhizomes, and from continuation of growth of vegetative tillers that survived the winter (Sims *et al.* 1971). Regrowth of vegetative tillers that had grown the previous season was not observed in our study of switchgrass in the Sandhills.

Both extravaginal (exits through subtending leaf sheath) and intravaginal (exits within subtending leaf sheath) tillers developed. Intravaginal buds developed vertical (apogeotrophic) rhizomes (Figure 1) that remained closely associated with the parent axis. Vertical rhizomes were unbranched, determinate, and produced tillers which were located close to the previous year's tiller. Development of vertical rhizomes in switchgrass studied in the Sandhills was similar to descriptions of rhizomatous varieties common to the southeastern United States (Beaty *et al.* 1978).

Tillers developed from both vertically and horizontally oriented rhizomes (Figure 1) which is similar to that reported by Beaty *et al.* (1978). Rhizome cross sections indicated that the anatomy of horizontal and vertical rhizomes was identical. Horizontal rhizomes occasionally branched. The tiller that originated from the terminal bud was larger than tillers that originated from buds located along the length of the rhizome. However, if the terminal bud was damaged, multiple tillers of near equal size developed from buds located along the rhizome. If a shoot apex was removed new shoots originated from axial buds on the proaxis of the damaged tiller. Switchgrass rhizomes were not located as deep as those of prairie sandreed or sand bluestem nor were they as long as those of prairie sandreed.

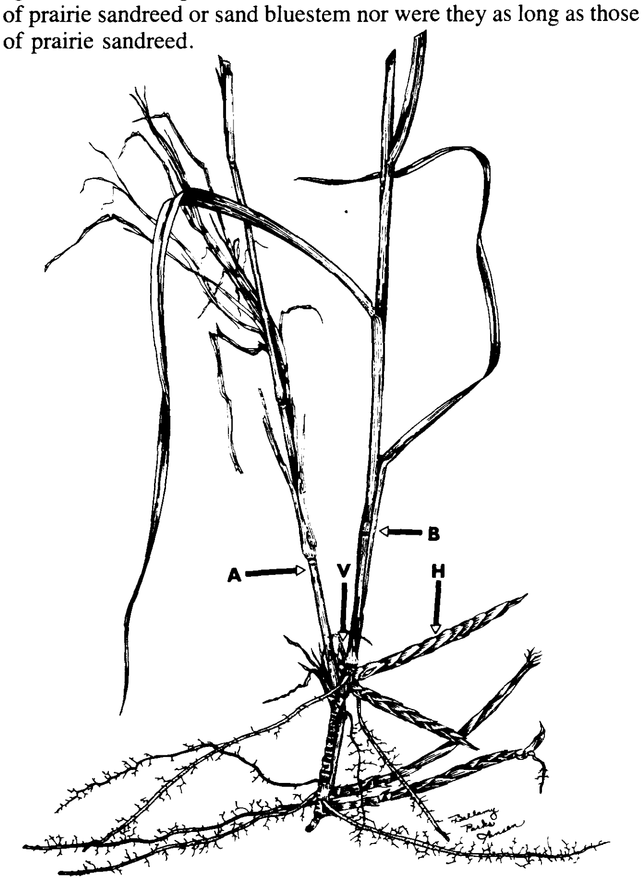

FIG. 1 Switchgrass plant showing previous year's tiller (A), current year's tiller (B), horizontally oriented rhizome (H), and a vertically oriented rhizome (V).

Switchgrass rhizomes initiated growth before early July in 1984 and in early to mid-June in 1985. During both years the rhizomes initiated growth when tillers were at the 4- and 5-leaf stage. Horizontal rhizomes initiated growth before vertical ones did. For six weeks, rhizomes elongated rapidly and new rhizomes were produced until the parent tillers began elongation. No new rhizomes were initiated thereafter but existing rhizomes continued to elongate.

Prairie Sandreed

New prairie sandreed tillers developed from rhizomes formed the previous year and from continuation of arrested vegetative growth of late emerging tillers from the previous year. Tillers originating from axial buds on the proaxis of last year's tiller were uncommon. Tillers that originated from axial buds emerged late, were smaller, and did not head (Figure 2). Many prairie sandreed tillers were biennial. Horizontal but more commonly, vertical rhizomes emerged late in the growing season in one year, overwintered, and then resumed growth from the same shoot apex (Figures 2 and 3). Growth of these tillers commenced early the second growing season and some developed culms and inflorescences. Biennial tiller development in prairie sandreed was similar to biennial tiller development for indiangrass [*Sorghastrum nutans* (L.) Nash] (McKendrick *et al.* 1975). However, prairie sandreed tillers in Montana did not live over winter but completed growth the same year they emerged (White 1977).

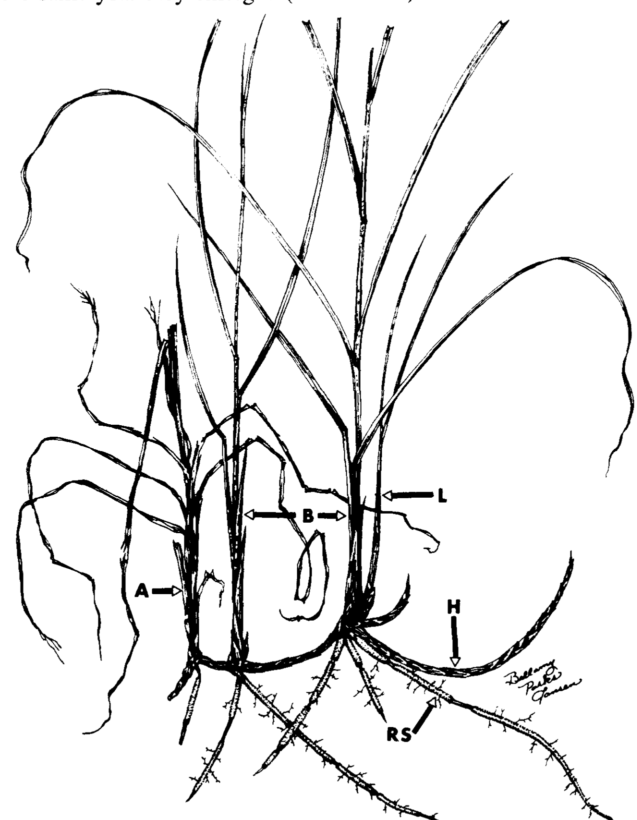

FIG. 2 Prairie sandreed plant showing previous year's tiller (A), current year's spring tillers (B), a late emerging current year's tiller from a vertically oriented rhizome (L), a horizontally oriented rhizome showing upward curvature in late summer (H), and the rhizosheath on the roots (RS).

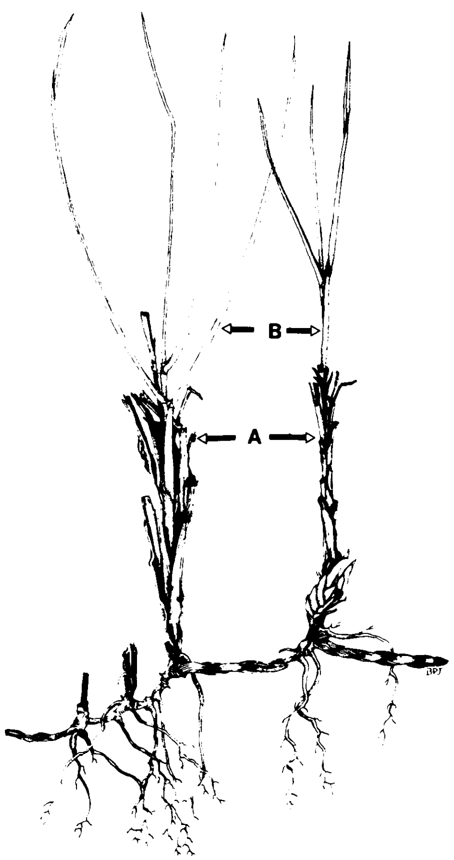

FIG. 3 Biennial tillers of prairie sandreed. Remains of previous year's tiller growth (A) and new spring growth from the same shoot apex (B).

In prairie sandreed extravaginal branching produced both horizontal and vertical rhizomes (Figure 2), which were identical anatomically. Rhizomes were strongly determinate with tillers produced only from rhizome tips. Tillers originating along the rhizome were not observed at any time. Rhizomes were unbranched even when the terminal bud was damaged. New rhizomes had begun growth by the time observations started in 1984. In 1985 rhizomes were just starting growth at the mid-May 1985 sampling date. Parent tillers were at the 4- to 5-leaf stage when rhizomes began growth so both tillers and rhizomes developed early in the growing season. During May and early June horizontal rhizomes elongated and a little later when parent tillers were generally at the 6-leaf stage vertical rhizomes began growth. Rhizomes continued elongation into August and many reached lengths of over 15 cm. Mueller (1941) reported a maximum length of 33 cm for prairie sandreed tillers and an average length of 15 cm.

In addition to producing the longest rhizomes of the three grasses studied prairie sandreed's rhizomes grew deep in the soil (below 10 cm). Mueller (1941) reported a depth range of 3.8-20.3 cm for prairie sandreed rhizomes. The production of long rhizomes with the ability to emerge from considerable depths allow prairie sandreed to be a early perennial colonizer in bare areas such as blowouts. Also prairie sandreed rhizomes can emerge through 15 cm of deposited sand (Mueller 1941). Weaver (1958) indicated that where prairie sandreed was subjected to blowing sand and shifting soil levels roots and rhizomes were intermixed in a dense mat to a depth of 0.6-1.0 m. Very few prairie sandreed tillers completed seed production and most tillers remained vegetative. Tillers that became reproductive often had their shoot apices removed by grasshoppers during stem elongation. Since prairie sandreed is less palatable than many other sandhills grasses it is not often grazed as closely as others. This gives it a competitive advantage in producing rhizomes. Selective grazing together with late emerging tillers can make it quite competitive in pasture situations.

Roots often had a surrounding sand sheath (Figure 2). Sheathed roots were young and actively growing and the sand sheath covered the upper 75% of the sampled roots. Rhizosheaths have been observed on both temperate and tropical grasses (Wullstein and Pratt 1981, Vermeer and McCully 1982, Duell and Peacock 1985). The significance of the rhizosheaths on prairie sandreed roots is not evident. Rhizosheaths were not present in switchgrass and poorly developed in sand bluestem.

Sand Bluestem

Buds on rhizomes beneath the previous year's tillers were the site of new growth in the spring (Figure 4). Buds near the soil surface generally did not develop into tillers. Early tillers originated from buds deeper in the soil, emerging through as much as 15 cm of sand before reaching the soil surface. When spring tiller growth initiated beneath the soil surface, the shoot apex was at the point of attachment to the rhizome of the previous year's tiller (Figure 5). When tillers emerged and reached the 4- to 5-leaf stage, elongation below the shoot apex occurred forming a rhizome that pushed the shoot apex to the soil surface (Figure 6). Examinations of cross-sections of above and below ground portions of stem and rhizome indicated that they were anatomically identical except the underground portion had larger vacuoles in the cells. Despite being anatomically similar, the aboveground portion died at the end of the season while the below ground portion remained alive giving rise to new tillers the following spring from buds along the rhizome (Figure 4). Tillers originating from buds near the soil surface often did not have rhizomes formed beneath them.

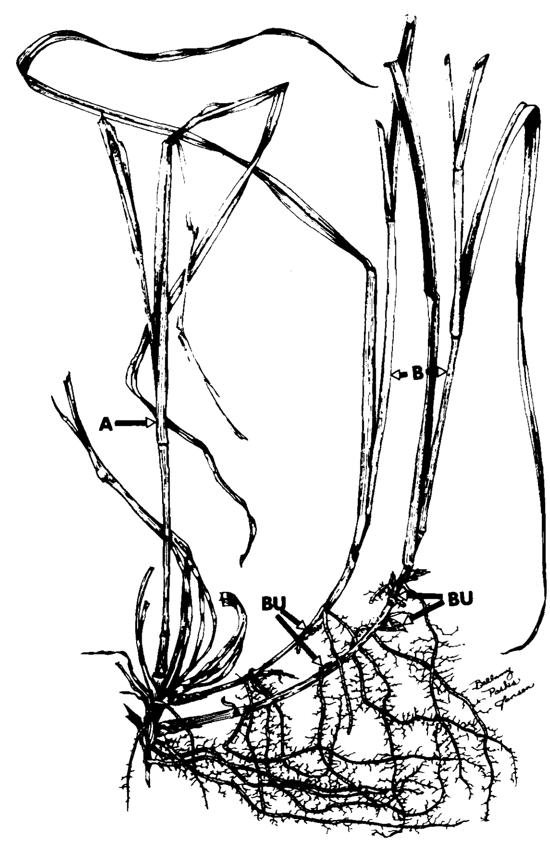

FIG. 4 Sand bluestem plant in midsummer showing bud formation on rhizomes. Previous year's tiller (A), current year's tillers (B), and buds (BU), formed on spring rhizomes.

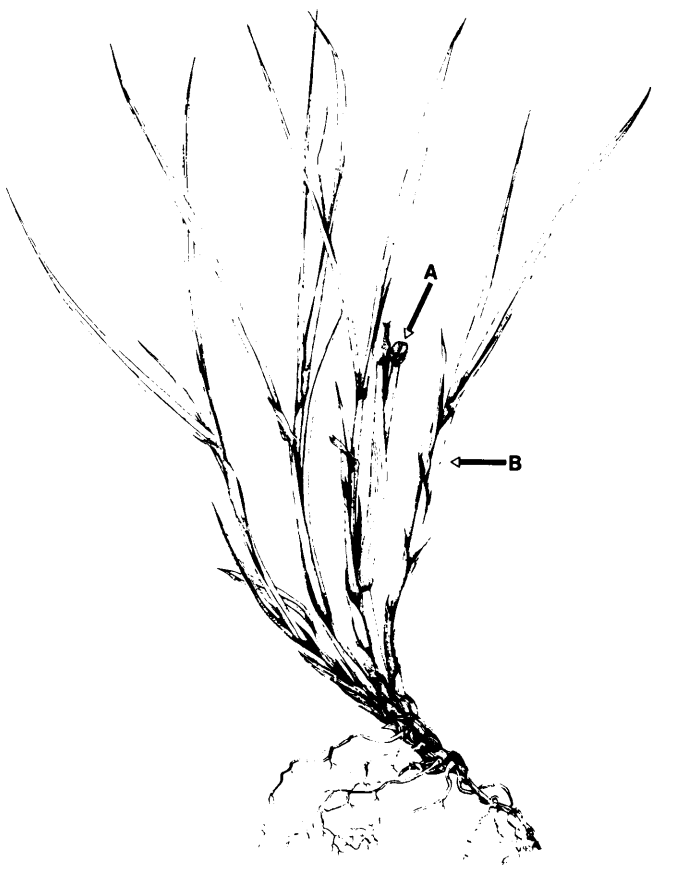

FIG. 5 Sand bluestem plant prior to rhizome formation in the spring. Previous year's tiller (A) and current year's tiller (B).

FIG. 6 Sand bluestem after rhizome elongation. Previous year's tiller (A), one of three current year's tillers (B), and a rhizome (R), that developed under a current year's rhizome forcing the shoot apex to the soil surface.

Bud formation occurred in late June when tillers were at about the 6-leaf stage. Buds increased in size and number in July and occasionally some elongated up to 1 cm during the current season but did not develop into tillers. However, Sims *et al.* (1973) reported that new tillers of 'Elida' sand bluestem originated from axial buds and apical meristems of short terminal rhizomes which turned upward in late summer or fall. Sand bluestem rhizome and tiller development in this study fit the description for big bluestem (*Andropogon gerardii* Vitman) in Kansas more closely (McKendrick *et al.* 1975). Generally, rhizomes of sand bluestem in this study were associated with tillers and there was limited rhizome development elongation from buds located on these rhizomes (Figure 6).

If the shoot apex of the parent tiller was removed, new tillers did not develop from buds located on the rhizome underneath the damaged tiller, but arose from axial buds located in leaf axes at the soil surface. Some vegetative tillers became reproductive and elongated, forming an inflorescence.

Sand bluestem is a common pioneer plant in blowouts. It maintained an open stand in mature communities but formed a dense sod in blowouts (Tolstead 1942). Sand bluestem appears to be adapted to shifting soil levels of blowouts and tillers commonly emerged through 10 cm of sand. Following soil removal, tiller buds further down on a rhizome would produce tillers and following sand deposition tillers closer to the original soil surface could develop. The elongation below the soil surface in the spring formed a rhizome and a source of new buds near the new soil surface for the following year. Sand bluestem may be adversely affected by heavy early spring grazing at a time when subterranean elongation occurs since the supply of carbohydrates would be reduced.

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