Developmental Morphology of Blue Grama and Sand Bluestem

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Highlight: The purpose of this investigation was to study the normal growth and development of blue grama and sand bluestem. Blue grama and sand bluestem exhibited contrasting forms of growth, regrowth, and perenniality. Blue grama had culmless vegetative shoots and 12% reproductive shoots. Sand bluestem had culmed vegetative shoots and 36% of the shoots became reproductive. Regrowth of blue grama from active shoot apices proceeded rapidly after cutting when soil moisture was adequate. Good productivity, however, depended greatly on essentially free expansion of the leaf blades of phytomers 3 through 6. Good leaf growth and early drying of lowermost leaves when not utilized made sand bluestem suitable for grazing in June, when prompt regrowth of leaves from apical meristems occurred. Close harvesting in early July stopped all active shoot expansion. After grazing sand bluestem in June, a rest period in July should allow good plant development under dry land conditions. With favorable soil moisture conditions in July a close harvest near mid-July stopped first crop growth and promoted development of new tillers and high productivity of second-crop herbage of sand bluestem in late summer and fall.

Information about the developmental morphology of plants is needed to explain their responses to defoliation. Such information might define appropriate seasons or sequences of grazing, where an intensive control over land and livestock can be attained. This requirement of intensive control omits extensive situations of poorly distributed grazing where the rotation of deferred grazing and rest-rotation grazing prevents the destruction and sacrifice of critical sites such as drainage systems.

Grazing is not only a means of harvesting vegetation, but a treatment that affects subsequent herbage quantity and quality. At a given time and place, grazing might be conducted primarily to produce a strong tillering response, harvest a maximum quantity of nutrients per unit area, improve forage quality for subsequent grazing, manipulate botanical composition, protect and improve adjacent range, or create some other desirable effect. All desired responses or effects cannot be produced on rangeland at one time or in one way. Thus, information about the developmental morphology of plants can help define opportunities and alternatives for application in grazing management.

The subject of developmental morphology is new in the field of range management. Research methods and observational techniques need further development, but the primary objective is clear: how do plants grow? Growth can be measured grass unit (phytomer) by unit to help answer this question.

A phytometer consists of leaf blade, leaf sheath, culm internode (although the internode may not become visibly enlarged), and node with potential for axillary bud and adventitious roots (Evans and Grover, 1940; Hyder, 1969, 1971; Sims, et al., 1971). Vegetative shoots can produce an indeterminate number of phytomers: whereas, reproductive shoots are determinate (Sharman, 1947; Cook and Stoddart, 1953; Hyder and Sneva, 1963). The growth or regrowth of any shoot can be described phytomer by phytomer. However, the process of destructive sampling and differences in ages and types of shoots complicate the study. Therefore, any detailed study of developmental morphology can advance our knowledge of how to study plant morphology and growth.

Blue grama (Bouteloua gracilis (H.B.K.) Lag. ex Steud) is probably the most important native forage species on the Great Plains. This warm-season shortgrass is nutritious, widely adapted to many soil types, and palatable to all classes of livestock. Blue grama withstands heavy grazing and drought. Sand bluestem (Andropogon hallii Hack.), a native, warm-
season, rhizomatous, perennial tallgrass, is an important forage grass on sandhill rangeland in Colorado, Kansas, Nebraska, and Oklahoma. These important forage grasses justify intensive study and development.

The primary purpose of this investigation was to study the growth and development of Lovington blue grama and Elida sand bluestem. The study also included some measurements of regrowth after mowing closely at successive stages of development.

**Methods and Materials**

The study was conducted at the Eastern Colorado Range Station, located on the Central Great Plains near Akron in the sandhills of northeastern Colorado. The elevation is 1,203 m (4,275 ft) with the topography varying from nearly level to slightly rolling dunes. Study plots were located on a nearly level area of Davona loamy sand.

The climate is semiarid with cold, dry winter; moist, cool springs; hot, occasionally dry summers; and mild, usually dry autumns. Annual precipitation averages about 38 cm (15 inches), most of which falls as rain from April to September. During 1967, 38 cm of precipitation occurred, with one-half coming in May and June and two-thirds between May and August, inclusive. This was an exceptionally good growing season.

Both species were planted in May, 1965, and had developed into relatively closed communities at the time of sampling. Four randomly selected clumps of each grass species were collected on April 11 and May 1 and then weekly until August 25, 1967. The soil was excavated from around the clumps so as not to destroy the crowns, which are the stem bases having two or more closely spaced nodes. Each clump was washed, placed in a plastic bag, and frozen. Subsequently, the frozen plants were subdivided into individual shoots for observation and measurement. Beginning with the first (lowermost) phytomer, each blade, sheath, and internode of a shoot was measured separately. When a blade, sheath, and internode had been measured and recorded, the blade and sheath were removed to expose the next phytomer. This operation was continued until the smaller and more delicate blades and sheaths were measured. The exserted parts of the phytomer, however, were not measured separately. The internodes were measured individually when they were over 1 mm long or collectively when they were less than 1 mm long. The average lengths of phytomer parts define the growth curves for each phytomer, and total lengths among phytomers define the growth curve for a shoot. The shoots were observed to determine if they originated from rhizomes, axillary buds of the crown, or shoot apices of older vegetative shoots. In mid-October, when the heads of reproductive shoots had exserted, several clones were selected at random, excavated, and broken apart to count the numbers of reproductive and vegetative shoots.

To study the effects of mowing blue grama and sand bluestem at different growth stages, 11 plots, approximately 1 x 6 m, were staked out across a strip of each species. Beginning May 29, a new plot was mowed each week at a height of 3.5 cm with a rotary mower for 11 consecutive weeks. Comparative observations were made of mowed and unmowed plants. On August 16 and October 14, three clones from each plot were collected and the general pattern of the development of axillary buds of the crown and rhizomes was observed. Stems were also examined for any sign of increased axillary bud activity, changes in internodal elongation, increases or decreases in tillering, and the removal of growing points of inflorescences.

**Results**

**Lovington Blue Grama**

**Vegetative Growth**

Shoot apices, enclosed by three or four successive intercalary meristems of immature leaves and finally by the dead leaf sheaths of parent shoots, survived the winter in a quiescent state. Viable meristematic tissues resumed growth in the spring. Some green growth, topped by dead leaf tips, was evident on April 11. Subsequent growth by overwintering shoots was measured in detail. The vegetative shoots of blue grama produced 6 to 9 (average 7) phytomers during the
growing season (Fig. 1). Four leaves, one or two of which had
exserted the previous year as indicated by dead leaf tips,
resumed slow growth in April. The first one or two leaves
matured and dried by the end of June, and two additional
leaves dried before August 18. The fourth and fifth blades
were longer than others and together provided 42% of blade
length. Blades 3 through 6 provided 76% of blade length.
Good plant productivity must depend on essentially free
expansion of these major leaf blades. Thirty percent of blade
elongation occurred by May 29; whereas, 73% occurred by
June 30, and 96% by July 28.

Summations of phytometers provide mean growth curves of
leaf blades and leaf sheaths of vegetative shoots (Fig. 2).
About half of the blade elongation was essentially sigmoidal.
Blade growth decreased in early July and became insignificant
by mid July. Leaf sheaths of this warm season grass elongated
at a near linear rate from the first of June until measurements
were terminated on August 18.

The internodes of vegetative shoots failed to elongate at any
time. Therefore, this sequence of growth produced a small
central axis or “crown” of (by average) seven nodes, ranging
from 4 to 7 mm long, with its complement of adventitious
roots, axillary buds, and tillers. Headless or “blind” shoots
having elongated internodes were found. These were consid-
ered to be shoots. Small unidentified larvae were found on
some rudimentary inflorescences and shoot apices, but the
death of these structures might have been caused by other
factors as well.

Reproductive Growth

Twelve percent of the overwintering shoots of blue grama
became reproductive. Floral initiation was first observed on
June 30. Internode elongation began at the time of floral
initiation, but may not have followed closely after floral
initiation in an individual shoot. Elongation occurred in three
or four internodes, including the uppermost internode or
peduncle, leaving an average of seven nodes in the crown
section at the base. Since the total of 10 or 11 phytometers
exceeded the maximum found in vegetative shoots, it appears
that some reproductive shoots, by overwintering twice, re-
mained vegetative until June of their third growing season, or
attained competitive advantage over those that remained
vegetative. Since newly seeded stands can produce reproduc-
tive shoots the first year, wintering seems unnecessary for the
purpose of vernalization. The average lengths of elongated
culm internodes were as follows:

<table>
<thead>
<tr>
<th>Peduncle and inflorescence</th>
<th>13 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Internode 3</td>
<td>6 cm</td>
</tr>
<tr>
<td>Internode 2</td>
<td>7 cm</td>
</tr>
<tr>
<td>Internode 1</td>
<td>4 cm</td>
</tr>
<tr>
<td>Total</td>
<td>30 cm</td>
</tr>
</tbody>
</table>

Internode elongation was slow until July 21. Subsequently,
the rate of elongation increased greatly until anthesis. Heading
began July 18 and continued for about 30 days. Anthesis
began August 4 and continued about 2 weeks. Mature
caryopsis were found by September 15. Thereafter, the entire
shoot above the crown died.

Tillering and Perenniality of Shoots

The first new tillers appeared during the week of June 5 to
12. They originated from the first and second axillary buds of
parent shoots. Reproductive shoots gave rise to more tillers
than did vegetative shoots. Among the vegetative shoots, the
larger ones, found primarily at the edges of clumps, generally
produced tillers. New tillers continued to arise until July 28.
By October 14, the new tillers had exserted one to four leaf
blades ranging up to 12 cm in length, but the longest blades
average 4 to 5 cm. Shoot apices remained below the soil
surface because there was no internode elongation or differ-
tentiation to reproductive status by new tillers.

Mowing in late June and early July stimulated additional
tillering, mostly from reproductive shoots that had elevated
above the height of cut. Earlier mowing depressed tillering.
Mowing in late July and early August also stimulated tillering,
but insufficient growing season remained for complete devel-
opment of these late tillers. Tiller populations were not
counted to determine survival rates and obtain exact compari-
sions among cutting treatments.

In late summer and early fall, the exserted leaves of new
tillers died back leaving basal green material, leaf intercalary
meristems, and shoot apices enclosed and protected by the
dead leaf sheaths of parent shoots. The next spring, these new
tillers would be prepared to resume leaf growth, pushing up
the dead tips of previously exserted leaves and initiating
additional leaves from leaf primordia of the shoot apex. Older
vegetative shoots appear to survive the winter in the same way,
and attain sufficient status to become reproductive. However,
we do not have a complete account of the perenniality and
longevity of individual shoot apices. The main point is that an
individual tiller is not an annual structure that initiates in the
spring and dies in the fall. Perenniality derives from overwin-
tering shoot apices of culmless vegetative shoots, overwintering
intercalary meristems of immature leaves, and axillary buds of
the crowns.

Elida Sand Bluestem

Vegetative Growth

The shoots of sand bluestem originated primarily from
axillary buds and apical meristems of short, terminal rhizomes,
which turned upward in late summer or fall to initiate negative
geotropic growth. A crown section was formed where the
rhizomes turned upward and the internodes failed to elongate.
Each node of the crown attained capacity for adventitious
tillers and axillary buds, which could produce either rhizomes
or shoots.

To maintain consistency in numbering the phytometers of a
shoot, the last scale leaf was counted as leaf number 1, and the
first leaf with a blade was counted as number 2. Some such
arbitrary procedure was necessary for shoots arising from
apical meristems of terminal rhizomes because the point of
origin of that apical meristem was the axillary bud of the
parent crown or rhizome. Transformation from horizontal or
diageotropic to negative geotropic growth by a rhizome began
with the upward thrust. Then a sequence of phytometers
established the lower part of the crown before growth
appeared aboveground.

The vegetative shoots produced as many as 9 phytometers
(Fig. 3). Five leaves were evident on April 11, but only the
third one had green growth exserted from surrounding sheaths.
Throughout the season, the shoots contained two or three
leaves that were beginning growth but still completely
enclosed by the sheaths of older leaves. Four to six leaves
showed green growth by July 7. Leaf blades 5 and 6 attained
greatest lengths, and together accounted for 41% of total blade
length. Blades 4 to 7, inclusive, accounted for 74% of the total
blade length and maintained active growth until late July.
Over all phytomers of vegetative shoots, blade elongation was essentially sigmoidal (Fig. 4). Only 26% of blade growth occurred by May 29, but 81% occurred by June 30 and 99% by July 28. The growth rate of sheaths was nearly linear. Portions of nine leaves remained green when measurements were terminated on August 18. The first leaf dried early in the season, and two or three more dried by mid-July. Most leaves were dry by September 5, and all exposed parts were dry by October 14.

The internodes of both vegetative and reproductive shoots began elongation between June 21 and June 30, and attained sufficient total length (7cm) to elevate shoot apices to heights which made them removable by grazing by July 7. At that time, leaf blade elongation amounted to 84% of the total attained during the season. There was great variability in internode elongation among vegetative shoots. Average lengths among shoots indicated that six internodes made substantial elongation (Fig. 3), but most shoots (modal tendency) had only four (range from two to seven) internodes elongated. Internodes of phytomers 5, 6, and 7 attained greatest lengths, and together accounted for about 80% of total vegetative culm length.

Reproductive Growth

Thirty-six percent of the shoots of sand bluestem became reproductive. Floral initiation was first observed on July 14, which was 2 to 3 weeks after the initiation of internode elongation. Growth proceeded as for vegetative shoots until July 28. Thereafter the growth of reproductive shoots accelerated. Heading (head exsertion) was first observed on August 15, anthesis on September 5, and ripe seeds on October 14. Ten internodes attained substantial elongation, with average length as follows:

<table>
<thead>
<tr>
<th>Internode</th>
<th>Length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peduncle plus inflorescence</td>
<td>14</td>
</tr>
<tr>
<td>Internode 9</td>
<td>8</td>
</tr>
<tr>
<td>Internode 8</td>
<td>11</td>
</tr>
<tr>
<td>Internode 7</td>
<td>14</td>
</tr>
<tr>
<td>Internode 6</td>
<td>17</td>
</tr>
<tr>
<td>Internode 5</td>
<td>18</td>
</tr>
<tr>
<td>Internode 4</td>
<td>16</td>
</tr>
<tr>
<td>Internode 2</td>
<td>9</td>
</tr>
<tr>
<td>Internode 1</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>127</td>
</tr>
</tbody>
</table>

The uppermost 4 phytomers generally produced lateral inflorescences from the axillary buds, but these lateral inflorescences developed later than terminal inflorescences.

Rhizome Growth, Tillering, and Perennality

Tillering was scarce in the absence of mowing, but rhizomes began growing from axillary buds of the crowns in late June and continued into July. The primary tendency was for diaeotropic (rhizome) growth from axillary buds in June and July and for geotropic (tiller) growth in August. Rapid elongation of reproductive stems occurred after the most active period of rhizome growth. The short rhizomes turned upward in late summer and were then prepared for shoot growth the following year.

After mowing in June, regrowth occurred promptly from, as yet, nonelevated shoot apices. A few shoot apices were elevated to cutting height by July 1 and nearly all of them by July 7. Thereafter, regrowth after mowing was much delayed because growth was dependent on the initiation of new tillers. Tillering proceeded in two ways: (1) tillers grew from axillary buds at the base (crown) of the shoots which had their elongation stopped by mowing, and (2) the rhizomes turned upward to begin negative geotropic growth. Mowing after July 1 eliminated the first set of shoots, both vegetative and reproductive, but some new tillers attained reproductive status. Most late inflorescences did not develop beyond the boot stage because soil moisture was insufficient to sustain prolific growth in late summer. Thus, by September, there was a great distinction between plots mowed before and after July 1. Regrowth by new tillers was very short, but with adequate moisture could probably have provided a highly productive second crop.

All shoots were annual structures, dying back to the base at
Discussion

Blue grama and sand bluestem provided contrasts in form of growth, regrowth, and perenniality. Blue grama had culmless vegetative shoots and a small proportion (12%) of shoots becoming reproductive. This percentage is about the same as the 13% reported for blue grama by Branson (1953). Regrowth from active shoot apices proceeded quickly after cutting when growing conditions were favorable. Nevertheless, good productivity depended greatly on essentially free expansion of the leaf blades of phytomers 3 through 6. This grass is well adapted to continuous grazing, but the prompt regrowth of leaves from active shoot apices and abundant tillering from axillary buds of small, compact crowns provide tolerance of heavy grazing, even though close harvest reduces productivity.

Sand bluestem had culmed vegetative shoots with an intermediate proportion (36%) of shoots becoming reproductive. That percentage is about the same as the 32% reported for sideoats grama (Bouteloua curtipendula), less than the 76% reported for little bluestem (Andropogon scoparius), and greater than the 26% reported for big bluestem (A. gerardi) (Branson, 1953). Good leaf growth and early drying of lowermost leaves when not utilized made sand bluestem suitable for grazing in June, when regrowth of leaves from active apical meristems was prompt. However, close harvest in early July stopped all active shoots and drastically reduced growth. Thus, after grazing in June, a rest period for 2 or 3 weeks in July should allow good plant development under native sandhill-range conditions. With adequate soil water provided by precipitation or irrigation in July, and perhaps nitrogen fertilization as well, a close harvest about July 10 would stop first-crop growth and promote good development of new tillers and high productivity of second-crop herbage for late summer and fall.

Literature Cited