30   Gramas

STEVEN E. SMITH

University of Arizona
Tucson, Arizona

MARSHALL R. HAFERKAMP

USDA-ARS
Miles City, Montana

PAUL W. VOIGT

USDA-ARS
Beaver, West Virginia

No single genus may have a more significant role in the natural vegetation of the arid grasslands of central and southern North America than *Bouteloua* Lag.*,* the grama grasses. The genus consists of about 57 tufted annual and sod-forming or caespitose perennial species whose natural distribution is confined to the Western Hemisphere (Columbus, 1999a). *Bouteloua* is a member of the tribe Chlorideae, whose spikelets typically have multiple florets. However, in some Chlorideae genera, including *Bouteloua,* only a single floret develops fully in each spikelet. *Bouteloua* has a single basic chromosome number of $x = 10$, although aneuploidy and multiple levels of polyploidy are common (Gould, 1979).

The gramas are most common in rangelands of the western Great Plains of the USA and Canada and the desert grasslands of Mexico and the southwestern USA (Sims and Risser, 2000). They also are grown in sown pastures with a variety of management intensities (Berg, 1995; Biedenbender and Roundy, 1996; Bakker et al., 1997). Gramas provide substantial forage for domesticated and wild herbivores on rangelands (Peden et al., 1974; Smith et al., 1996; Hart and Ashby, 1998; Sims and Risser, 2000). They also may provide a habitat for wildlife (Clawson and Rotella, 1998), stabilize soil to help maintain watershed function (Wilson and Briske, 1979), play a major role in atmospheric carbon (C) sequestration (Epstein et al., 1998), represent a primary source of soil organic matter (Seastedt, 1995), serve as low-maintenance turfgrasses (Christians, 1998; Phillips, 1999), and comprise a key vegetation element associated with the visual appeal of many grassland landscapes (Rees, 1978).

This chapter focuses on three of the most widespread and economically important perennial gramas (Sims and Risser, 2000). Blue grama [*Bouteloua gracilis* (Kunth) Lag. *ex* Griffiths], which represents a dominant component of the short-

grass and mixed-grass prairies from central Mexico to the southwestern states of the USA and to central Canada. Sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] is one of the most widely distributed grasses in North America occurring commonly on mixed- and shortgrass sites from north central Mexico, Arizona, New Mexico and Texas, through the Central Plains to Ontario and Manitoba. Black grama [*Bouteloua eriopoda* (Torr.) Torr.] is most commonly found on desert grassland sites from northern Mexico and Arizona to Oklahoma and Texas north to Wyoming and Colorado.

The amount of scientific information available on these three species is roughly proportional to the size of their distributions and their dominance within plant communities they occupy. Thus, blue grama has been the focus of substantially more research than the other two species.

BLUE GRAMA

General Description

Morphology and Development

Blue grama plants usually are tufted bunchgrasses that produce numerous lateral tillers (Stubbendieck and Burzlaff, 1971) or short rhizomes (Gould, 1979). In more mesic (generally northerly) areas of its distribution, blue grama may form a dense sod (Sims et al., 1973). Successive cohorts of tillers produced over time by a single plant function as an integrated physiological individual with regard to N uptake (Derner and Briske, 1998). Its culms are erect 20- to 60-cm tall, with inflorescences of ine to four spicate branches (15–45-mm long) with each branch producing 40 to 90 crowded spikelets that are 4- to 7-mm long. Bluish green leaf blades are 3- to 5-mm wide and from 50- to 250-mm long. Seedings of this species typically involve use of mixtures of spikelets, florets and caryopses, and about 1.5 to 1.7×10^6 filled florets weigh 1 kg (McDonald and Copeland, 1997; Smith et al., 1997).

Stand establishment is often difficult in part because adventitious roots develop at or near the soil surface rather than where the caryopsis was planted (Hyder et al., 1971). Two periods of significant soil wetting are needed for successful establishment, one that germinates the seed and a second 2 to 8 wk later to allow adventitious roots to grow into the soil (Wilson and Briske, 1979). Plants may have to exist on their one seminal root for an extended period of time to establish (Van der Sluijs and Hyder, 1974; Wilson and Briske, 1979).

Blue grama roots begin to grow shortly before leaf growth is apparent (Ares, 1976). Functional roots may reach depths of 60 cm, but 85% of the root mass is typically in the upper 20 cm of soil (Ares, 1976; Lee and Lauenroth, 1994). Plants generally flower once in mid-summer and again following late-summer rains (Sims et al., 1973; White, 1977), although tillers may grow up to 3 yr before flowering. Dickinson and Dodd (1976) observed that limited soil water delayed and synchronized anthesis and accelerated caryopsis dispersal. They reported that plants exhibited four separate anthesis periods in a single year in response to multiple summer rainstorms that occurred at about 10-d intervals.

Distribution

Mature blue grama plants are well adapted to a scarce and highly variable water supply and to a precipitation pattern in which small rainfall events constitute a large portion of the annual precipitation (Sala et al., 1992). This species provides much of the native forage consumed by grazing livestock in an area of approximately 61 million hectares in the USA (Sims and Risser, 2000). It grows on clay and loam soils and as a subdominant on sandy soils. It is a minor component on saline-alkali soils. This species is associated with a wide variety of grasses, forbs, and shrubs in the dynamic and floristically complex mixed-grass prairies, which range from southern Manitoba and Saskatchewan southward through the Dakotas, and eastern Montana and Wyoming through west central Nebraska and Kansas to central Texas (Sims and Risser, 2000). Blue grama often dominates upland sites of these grasslands with buffalograss [*Buchloë dactyloides* (Nutt.) Engelm.; recently classified as *Bouteloua dactyloides* (Nutt.) J.T. Columbus](Columbus, 1999a), a species that may dominate following extended drought (Weaver and Albertson, 1956). Blue grama is most dominant within the more xeric shortgrass prairie in the region extending from western Nebraska and southeastern Wyoming through eastern Colorado to the high plains of Texas, Oklahoma, New Mexico, and Arizona (Weaver and Albertson, 1956). Annual precipitation in this region varies from about 200 to 600 mm with the majority occurring in June through August (Visher, 1954). Blue grama and buffalograss may constitute up to 90% of the standing herbaceous biomass in this vast region. The grass also occurs in a variety of desert shrub and forest communities in western North America.

Restoration of blue grama on once cultivated land in the Central Plains has been difficult (Sims and Risser, 2000). It represents a key vegetation component on the relatively undisturbed rangelands in this region. Given its extensive range, and adaptation to drought (Majerus, 1975) and tolerance of repeated defoliation (Sims et al., 1973; Hyder, 1974), it remains a primary forage resource for grazing on these sites. Blue grama is less important, but also may serve as an element of more intensively managed pastures throughout the Great Plains.

Genetic Variation and Breeding

Cytology, Reproductive Biology, and Evolution

Ploidy levels of blue grama range from diploid ($2n = 2x = 20$) through tetraploid ($2n = 4x = 40$) and hexaploid ($2n = 6x = 60$) (Snyder and Harlan, 1953). In this research, conducted with plants from Texas and New Mexico, diploids and hexaploids had the most limited distributions while tetraploids were the most widely distributed, being found to a limited degree throughout the area sampled. Snyder and Harlan (1953) also reported occasional aneuploids.

Meiotic chromosome pairing in diploid plants was highly regular with 10 bivalents; although, univalents were occasionally observed (Snyder and Harlan, 1953). In tetraploid plants, meiotic chromosome associations varied widely both within and among accessions. Aneuploids may be more prevalent than current information suggests. Hairy grama (*Bouteloua hirsuta* Lag.), with a distribution very similar to blue grama, has not only diploid, tetraploid, and hexaploid populations,

but also an extensive series of aneuploids between the three ploidy levels (Gould, 1979).

Intraspecific Variation

Following the drought and dust storms of the 1930s—which were especially severe in the shortgrass prairie region—the need for improved grass cultivars to revegetate abandoned and eroded farm lands resulted in the initiation of genetic research on several of the gramas. Considerable morphological and cytological variation is exhibited in populations of blue grama in western North America. Riegel (1940), working in Kansas, obtained seed from nine states ranging from Arizona, New Mexico, and Texas to Montana and North Dakota. Plants from the north were superior in growth during spring and early summer. Southern populations were taller, deeper rooted, and grew longer into autumn compared to northern ones. However, caryopses of the southern strains did not mature prior to frost. The northern strains usually flowered before the southern strains, but those from the Central Plains varied for time of anthesis. In North Dakota, winter survival decreased as the latitude of collection site decreased (Rogler, 1943). In common gardens in Nebraska, ecotypic variation within *Boutelouas* allowed transplants to adapt to a broad latitudinal range with widely varying lengths of season and temperatures (McMillan, 1959).

In Oklahoma, Harlan (1958) found that collections from higher elevations in New Mexico flowered the earliest while accessions from the Davis Mountains in west Texas were the last to flower and were among the least winter hardy. Germplasm collected east and north of the Pecos River was "rather similar for the most part and represented a broad, contiguous high plains type, highly variable, yet rather similar in growth habit and general aspect." In contrast, accessions from west of the Pecos River were unusually diverse. The Davis Mountains collections contained diploid and tetraploid plants that were similar phenotypically. Several collections were evaluated and wide differences in forage production and smaller differences in crude protein were documented between diploid and tetraploid accessions (Harlan, 1958).

Grazing resistance was studied by comparing genotypes from heavily grazed prairie dog (*Cynomys* spp.) colonies to those from a nearby uncolonized site (Jaramillo and Detling, 1988), a lightly-grazed site or from an exclosure built in 1938 (Painter et al., 1989). Both studies demonstrated genetic differences between heavily and lightly or nongrazed populations. In addition, the colony plants exhibited grazing avoidance by reducing biomass available for grazing through shorter vegetative shoots, shorter leaves, and greater leaf blade angles. They exhibited grazing tolerance by survival of higher percentages of defoliated shoots and smaller decreases in cumulative biomass (Painter et al., 1989).

When adventitious root growth of six ecotypes from the Central Plains were compared, Briske and Wilson (1977) found a north to south trend for total length and weight of adventitious roots and the longest adventitious root. Later they reported that although 'PMK-1482' (northern ecotypes) produced more roots per seedling, 'PMK-1483' (southern ecotypes) produced the longest roots and also had

the longest total root lengths, at least at high humidities (Briske and Wilson, 1978). Wilson and Sarles (1978) compared water use of plants whose growth was supported only by its seminal root. Water uptake of PMK-1482 and its component strains ranged from 3.0 to 3.5 g d^{-1} while that for PMK-1483 and its component strains ranged from 3.8 to 4.8 g d^{-1}. Wilson et al. (1981) grew plants of 'Lovington,' 'Hachita,' (Table 30–1), PMK-1482 and PMK-1483 near Los Lunas, NM. Mean forage production was 70 and 206 g plant^{-1} for PMK-1482 and Hachita, respectively. The southern ecotypes were usually highest for reproductive culms per plant, spikes per culm, spikelets per spike, and caryopsis weight. The Central Plains strains produced higher caryopsis yield per culm. They concluded selecting plants for both high caryopsis weight and high seed yields should be possible.

Breeding History

The relatively little selection that has been conducted within blue grama has been performed assuming the species is predominately cross-pollinated (Riegel, 1941; Nason et al., 1987; Phan and Smith, 2000). Recurrent best plant selection was used to develop broad-based populations from some of Harlan's collections (Harlan, 1958). The last of these were included in plot studies as 'WW-65' (P.W. Voigt and C.L. Dewald, unpublished data, 1990). WW-65 frequently out yielded Lovington and was more productive than three accessions from Texas; although, the latter were sometimes higher in crude protein concentration and in vitro dry matter disappearance rate. However, WW-65 was very similar in forage yield and appearance to Hachita (P.W. Voigt and C.L. Dewald, unpublished data, 1990); therefore, WW-65 was abandoned. No germplasm from the Harlan collection was released or preserved for future use.

Nason et al. (1987) selected for improved establishment using PMK-1482, PMK-1483, Lovington, and Hachita. Seedlings were selected for high water uptake and shoot weight from 42 to 49 d after planting. Nason et al. (1987) reported that average water uptake was 2.4 and 3.6 g d^{-1} for PMK-1482 and Hachita, respectively. None of the PMK-1482 plants were included in the first cycle of selection. By the second cycle, all plants derived from PMK-1483 as females had been eliminated, and the advanced cycles were based primarily on the germplasm from southern New Mexico. When evaluated using the same protocol, mean shoot weights for the first, second, and third cycles of selection were 0.50, 0.55, and 0.61 g seedling^{-1}, respectively. Progress was made in ability to transport water and support a larger shoot without the development of adventitious roots. This should result in an increased ability to survive prior to adventitious root formation in some environments. The third cycle population was released as 'Alma' (Table 30–1).

Barker et al. (1983) made extensive collections in western North and South Dakota. They found that although the collections varied in maturity and individuals with extreme vigor were noted, "We were unable to identify other meaningful characteristics because most plants were strikingly similar." This remark is similar to Harlan's (1958) comments about his collections from the high plains of Texas and New Mexico. Results from collections in very small areas have documented differences in plant spread, plant height, and anthesis date (McGinnies et al., 1988).

Table 30–1. Formally released cultivars or ecotypes of blue grama, sideoats grama and black grama.†

Species/variety‡	Accession name	Release type	Year of release	Other identifier§	Source (year of collection)	Notable characteristics reported by developer	Release agency (state)§
Blue grama	Lovington	Cultivar	1963	PI 476993	Lovington, Lea Co., NM, 1300 m (1944)	Excellent leafiness, vigor, and establishment; wide adaptation throughout southwestern USA	NRCS (NM); AES (NM)
Blue grama	Hachita	Cultivar	1980	PI 439880	S. of Hachita Mountain, NM; 2734 m (1957)	Drought tolerant in evaluation at Los Lunas, NM. Higher yield potential than Lovington	NRCS (NM); AES (NM)
Blue grama	Alma	Cultivar	1992	9044169 (NRCS)	Composite of 270 plants from Hachita, Lovington, and PMK-1483.	Robust with upright growth and good seedling vigor	ARS; NRCS (NM); AES (CO, NM)
Blue grama	Bad River	Selected	1996	PI 591814	Philip, Haakon Co., SD (1988)	Improved height, leafiness, stand establishment, crude protein and relative feed value	NRCS (ND); AES (SD); NDASCD§
Sideoats grama, unknown	Vaughn	Cultivar	1940	PI 476991	Vaughn, Guadalupe Co., NM (1935)	More drought tolerant than El Reno, Uvalde, and Tucson in eastern CO and NM; easily established, good seedling vigor; erect leaves	NRCS (NM); AES (NM)
Sideoats grama, curtip.	El Reno	Cultivar	1944	PI 421281	Canadian Co., OK	Outstanding leafiness, forage production and vigor in KS	NRCS (KS); AES (KS)
Sideoats grama, unknown	Uvalde	Cultivar	1950	PI 469219	Knippa, Uvalde, Co., TX	Leafy with high seed production; resistant to shattering; not resistant to winters at high elevations	AES (AZ); NRCS
Sideoats grama, caespi.	Coronado	Cultivar	1955	NSL 6765	Encinoso, NM (1946)	Large seeded, uniform, apomictic; higher forage yield than El Reno and more cold resistant than Tucson in OK and TX	ARS (OK); AES (OK)
Sideoats grama, curtip.	Trailway	Cultivar	1958	PI 477001	Holt Co., NE (1935)	Winter hardiness of northern strains and vegetative traits of southern strains; late maturity; resistant to rust; persistent	ARS (NE); NRCS (NE); AES (NE)
Sideoats grama, curtip.	Butte	Cultivar	1958	PI 477002	Holt and Platte Cos., NE	Composite of two high-yielding strains; excellent seed yield, seedling vigor, and winter hardiness in NE	ARS (NE); NRCS (NE); AES (NE)

Common name	Cultivar	Type	Year	PI number	Origin	Description	Maintained
Sideoats grama, *caespi*	Premier	Cultivar	1960	PI 469250	Between Cuauhtemoc and Chihuahua, Mexico (1 plant)(1953)	Superior to Coronado, Uvalde, and Vaughn in seed production; comparable forage production; rapid germination and seedling development	AES (TX); NRCS (TX); ARS (TX)
Sideoats grama, *curtip*	Pierre	Cultivar	1961	PI 476980	Pierre, Stanley Co., SD (1954)	Composite of seed from several vigorous plants at collection site; outstanding vigor, leafiness, freedom from disease	NRCS (ND)
Sideoats grama, *curtip*	Killdeer	Informal	late 1960s	PM-ND-89 (NRCS)	Bowman, Bowman Co. and Killdeer, Dunn, Co. ND (1956)	Composite from two populations; outstanding vigor and leafiness, fair seed production, and freedom from disease, persistence in cold, semi-arid environment	NRCS (ND)
Sideoats grama, *curtip*	Haskell	Cultivar	1983	PI 433946	Haskell Co., TX (1960)	Superior forage production in central and southern TX; drought tolerant with excellent regrowth; selected for better rhizome production and southern adaptation	NRCS (TX); ARS, AES (TX)
Sideoats grama *caespi*	Niner	Cultivar	1984	PI 478839	Socorro Co., NM, elev. 1500 m (1957)	Uniform with good seed production	NRCS (NM); AES (NM, CO)
Sideoats grama, *curtip.*	S. Iowa germplasm	Source identified	1995	9062280 (NRCS)	Collections from southern IA	Local adaptation	NRCS (MO)
Sideoats grama, *curtip.*	C. Iowa germplasm	Source identified	1995	9062279 (NRCS)	Black Hawk Co., IA	Local adaptation	NRCS (MO)
Sideoats grama, *curtip.*	N. Iowa germplasm	Source identified	1995	9062278 (NRCS)	Composite from northern IA	Local adaptation	NRCS (MO)
Black grama	Nogal	Cultivar	1971	PI 476992	Socorro Co., NM, 1450 m (1957)	Produced more forage than most strains; less erect than Sonora	NRCS (NM); AES (NM)
Black grama	Sonora	Cultivar	1965	PI 469220	58 accessions from AZ and NM, selected clones polycrossed	Outstanding leafiness, vigor, forage production, vegetative spread, and seed production	ARS (AZ); AES (AZ); NRCS (AZ)

† Englert et al. (2000), Alderson and Sharp (1994), and Hanson (1972).

‡ Variety of *Bouteloua curtipendula* (sideoats grama), "curtip." = *B. curtipendula* var. *curtipendula*, "caespi." = *B. curtipendula* var. *caespitosa*. For accessions other than Niner, variety is assumed based on locale of original collection sites.

§ Abbreviations: AES = Agricultural Experiment Station; NDASCD = North Dakota Association of Soil Conservation Districts; NSL = National Seed Storage Laboratory.

During the late 1990s, researchers in Canada began to develop blue grama populations that could be successfully seeded in the northern Great Plains (Phan and Smith, 2000). In this research, selection within a broad-based composite population using a combined index that included seed yield and its components was shown to improve overall seed production potential while maintaining genetic diversity (Phan, 2000).

Importance, Utilization, and Management

Ecophysiology

The optimum temperature for blue grama growth is near 30°C (Detling, 1979), and genetic variation exists in photosynthetic sensitivity to temperature (Bowman and Turner, 1993). An ecotype collected at 3050 m had lower photosynthetic rate than one from 1400 m. Photosynthetic rate of the high altitude ecotype also was less sensitive to brief periods of near freezing temperatures than was the ecotype collected at 1400 m.

Initiation of growth in the spring is controlled by temperature; whereas, the rate of spring regrowth is controlled primarily by water availability. Water (Sala et al., 1982) and temperature were proposed as the primary factors responsible for niche separation between blue grama and western wheatgrass [*Pascopyrum smithii* (Rydb.) Á. Löve], species that are often found growing together on shortgrass prairie sites (Monson et al., 1986).

Although water is considered the principal factor limiting primary production, blue grama plants are able to maintain net photosynthesis at about 20% of maximum when other environmental variables are optimum and soil water potential in the root zone is as low as −5 MPa (Detling, 1979). Predawn stomatal opening allows this species to maximize carbon (C) fixation during the early morning (Sala et al., 1982). Leaf conductance also is low before dawn and increases as quantum flux increases with maximum leaf conductance occurring at 1000 h, followed by decreasing conductance around 1200 h (Sala and Lauenroth, 1982).

The response of blue grama to elevated carbon dioxide (CO_2) may affect nutrient uptake and partitioning (Polley, 1997). This species also increased nitrogen (N) partitioning belowground with CO_2 enrichment. Read and Morgan (1996) reported tissue N was generally unaffected by CO_2 level. They suggested reduction in tissue N may result from a dilution effect due to CO_2-induced aboveground growth enhancement or increased N immobilization resulting from increased C translocation belowground. Hunt et al. (1991) used a simulation model to predict that N cycling rates could increase and partly offset the N limitation that resulted from greater production of blue grama biomass with increased CO_2.

Alternation of patches of bare ground with blue grama plants is characteristic of the arid grasslands that this species inhabits. Root systems of neighboring blue grama plants are highly intertwined but not interconnected (Lee and Lauenroth, 1994). Aguilera and Lauenroth (1993) found growth of blue grama plants apparently was affected by plant spacing suggesting competition for spatially distributed resources. Growth is significantly less when water is supplied to roots peripheral

to primary tillers than when water is supplied to more central roots (Hook and Lauen-
roth, 1994).

Stand Establishment

Natural regeneration of blue grama from seed on rangelands and complete
recovery after severe disturbance may require 50 or more years (Reichhardt, 1982;
Samuel and Hart, 1994; Coffin et al., 1996). Limited soil moisture (Lauenroth et
al., 1994) and seedling morphology (Hyder 1974) are clearly the primary factors
responsible for poor establishment although lack of a seed source (Coffin and
Lauenroth, 1989, 1992; Karl et al., 1999) and competition from established plants
(Aguilera and Lauenroth, 1995; Bakker et al., 1997; Fair et al., 1999) also affect
stand maintenance and regeneration.

Good seedbed preparation and seeding practices can reduce the effects of low
seed production, inadequate seed in the seed bank, and competition from nearest
neighbors when establishing blue grama in pastures. Soil water relations can be im-
proved via seed bed preparation and adjustment of seeding dates. Proposed sow-
ing dates are from April to mid-May in the central Great Plains, April or earlier in
the southern Great Plains, and from 15 June to 15 July in the Southwest (Wasser,
1982). Successful stands have been achieved from seedings made in November,
April, and May in central North Dakota (Ries and Hofmann, 1996). Fults (1944)
reported that planting grass seed in the Great Plains when moisture conditions were
favorable was more important than whether plantings were made in the spring or
autumn. Various methods of mechanical renovation involving tillage, brush con-
trol, seeding, or fertilization have increased forage production on rangelands sup-
porting a mixture of tall and short grasses including blue grama (Rauzi and Lang,
1956; Haferkamp et al., 1993).

Environmental requirements for adventitious root development complicate
establishment of blue grama seedlings. Heavier seed classes emerged better from
sowing depths >3 cm (Carren et al., 1987b), and this was positively correlated with
greater shoot and adventitioius root biomass. With reduced soil water, relatively high
seed mass was required for emergence from a 2-cm depth (Carren et al., 1987a).
However, the correlation between caryopsis mass and percent emergence was $r = 0.73$, indicating genetic variation for emergence that is not associated with caryop-
sis mass must exist in this species as in other warm-season grasses (Voigt et al.,
1987).

Grazing Management

Blue grama is palatable to many wildlife species and to all classes of live-
stock (Hoffmann et al., 1995; Hart and Ashby, 1998). In Wyoming, crude protein
concentration of forage ranged from 154 g kg^{-1} in June to 53 g kg^{-1} by the end of
October (Rauzi et al., 1969). Crude protein concentration also varied considerably
during nine collection dates throughout the growing season because of new growth
following small precipitation events. The National Research Council (1971) has pro-
vided typical forage quality estimates for blue, sideoats and black grama.

Blue grama is well adapted to season-long grazing (Hyder, 1974). This is partially because of its propensity to produce a large number of culmless vegetative shoots and relatively few reproductive shoots (Sims et al., 1973). Sims et al. (1973) reported that prompt leaf regrowth from active shoot apices and abundant tillering from axillary buds provide tolerance to heavy grazing, even though close defoliation reduced productivity. This species appeared resistant to defoliation injury when plants were clipped to a 25-mm stubble height (Santos and Trlica, 1978). When clipped at 8-wk intervals, neither aboveground nor belowground production were severely reduced. However, multiple defoliations at more frequent intervals reduced forage production (Trlica et al., 1977). Its adaptation to defoliation has presumably evolved because of exposure to native grazing animals such as bison (*Bison bison*) and prairie dogs (Painter et al., 1993).

Bement (1969) recommended that managers should leave about 340 kg stubble ha^{-1} on shortgrass ranges at the end of the growing season in Colorado. Holechek and Galt (2000) reported that forage residue guides developed by Bement (1969) corresponded well with forage use levels, stubble heights, and qualitative assessments of grazing intensity in New Mexico. A minimum stubble height of 38 to 51 mm coincided well with moderate grazing (41–50% utilization) in a shortgrass prairie in New Mexico. Blue grama cover increased with heavy grazing on some sites (e.g., Schuman et al., 1999); however, these increases were not universal, and sometimes were quite small (Lauenroth et al., 1994; Milchunas et al., 1994; Biondini et al., 1998). A decline in forage production often occurs on mixed-grass prairie ranges as the shortgrass component (often blue grama) increases (Schuman et al., 1999).

Abiotic factors often have a greater impact on forage production on shortgrass and mixed grass ranges than grazing (Ellison and Woolfolk, 1937; Coupland, 1958; Hyder et al., 1975). Sensitivity analyses suggest a ranking of importance of weather > edaphic factors > biotic factors for forage production in shortgrass prairie of Colorado (Milchunas et al., 1994). During extended dry periods in the northern Great Plains, species composition shifts towards shortgrasses such as blue grama (Coupland, 1958; Newbauer et al., 1980), but when precipitation is above average, species composition moves toward midgrass dominance.

Invertebrate Herbivores

Blue grama is eaten by a variety of invertebrate herbivores most notably an assortment of grasshoppers {e.g., bigheaded [*Aulocara elliotti* (Thomas)], crenulatewinged [*Cordillacris crenulata* (Bruner)], and four-spotted [*Phlibostroma quadrimaculatum* (Thomas)] grasshoppers}. The bigheaded grasshopper is the most serious pest. Field tests in Montana and Wyoming show that populations of only 1.2 insects m^{-2} will consume 22.3 kg ha^{-1} of forage dry matter (Pfadt, 1994).

Nematodes can reduce blue grama growth (Barker et al., 1983; Stanton et al., 1984). White grubs (Scaribiidae) also attack this grass. Lauenroth and Milchunas (1991) reported that large areas of grassland denuded by white grubs can be recognized many years later by the absence of blue grama and the presence of red threeawn (*Aristida fasciculata* var. *nuttallii* Thurb. *ex* Beal), bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey], and other species.

Fertilization

Response to fertilization on sites containing blue grama varies with species composition, season and rate of application, availability of soil water, and grazing regime. Crowston and Goetz (1976) reported differential responses of blue grama accessions to N fertilizer when grown in a greenhouse. Annual and perennial C_3 plants, often growing in association with blue grama, initiate growth earlier in the spring and usually benefit more from spring and autumn N fertilization than blue grama. However, drastic changes in species composition usually occur when more than 170 kg N ha^{-1} are applied (Wight, 1976). Late spring or summer applications benefit C_4 species if adequate soil water is available. When there is carryover from high application rates or lack of spring and summer precipitation, C_3 species will benefit the following spring. Once a species shift occurs from high rates of N fertilization, the competitive advantage of C_3 species continues as long as no other compensating influence occurs, such as with early spring grazing in the northern Great Plains (Goetz et al., 1978). Many researchers report reductions in blue grama density or yield on ranges fertilized with N (Samuel and Hart, 1998). However, a few report increases in these variables for blue grama with N fertilization (Freeman and Humphrey, 1956; Lauenroth et al., 1978) or manure (Kipple and Retzer, 1959), but the largest increases in forage yield are associated with irrigation (Lauenroth et al., 1978). Hyder et al. (1976) found that N fertilization accentuated drought effects on blue grama. Generally fertilization is not recommended on blue grama ranges but is beneficial for seed production.

Fire

Ford (1999) reviewed the literature on blue grama response to fire. Positive effects of fire were associated with increased forage production, stand density, reproductive output, or basal cover. Of 34 studies evaluated, eight reported negative effects, 14 were neutral, and 12 described positive effects. Ford suggested that one must be cautious in interpreting fire effects on this species when considering the variety of fire types, seasons, weather conditions, and fuel conditions when the fire occurred. Following dry years, plants are seriously damaged by fire and sometimes require several years to recover. Generally the only benefit from burning shortgrass prairie in the southern Great Plains during wet years was to improve grazing distribution or remove a heavy litter cover.

Seed Production

In contrast to other gramas, agronomic and conditioning practices associated with successful blue grama seed production have been thoroughly described (Smith et al., 1997). Following these practices with irrigation in the northern Great Plains, seed yields of 110 to 340 kg ha^{-1} are expected while seed yields of 60 to 170 kg ha^{-1} are anticipated under dryland conditions. In the southern Great Plains, seed production is more difficult (Harlan et al., 1956). Low levels of N fertilization and irrigation are important, but delaying flowering until late summer is essential. With adequate insect control, yields of 340 to 450 kg ha^{-1} can be obtained in this region.

In 1999, applications were filed for certification of a total of 231 ha in the USA (ASOCA, 1999).

SIDEOATS GRAMA

General Description

Taxonomy, Morphology, and Development

Plants of sideoats grama usually take the form of clumpy bunchgrasses (Fig. 30–1), but some may also produce stolons or creeping rhizomes and an open sod. *Bouteloua curtipendula* (Michx.) Torr. var. *curtipendula* is recognized to have rhizomes and stiff, upright culms but no stolons (Gould, 1979). *Bouteloua curtipendula* (Michx.) Torr. var. *tenuis* Gould & Kapadia has stolons or slender decumbent culms and may have rhizomes. *Bouteloua curtipendula* (Michx.) Torr. var. *caespitosa* Gould & Kapadia is a prototypical bunchgrass that produces stiff culms from a "knotty" base but no stolons or rhizomes. All varieties produce slender culms 0.35- to 1.0-m tall and inflorescences with 30 to 80 pendulous spicate branches (10–40-mm long) along the rachis, with each branch producing 1 to 12 or more spikelets (7–12-mm long) (Fig. 30–1). These spikelets are often arranged flaglike, roughly in the same plane explaining the species common name. Leaf blades are generally bluish-green in color, 3- to 7-mm wide and from 50- to 160-mm long. Seedings of sideoats grama typically consists of mixtures of spikes, florets, and caryopses (about 1.59×10^6 pure caryopses would weigh 1 kg) (McDonald and Copeland, 1997). Canfield (1957) showed that individual plants of var. *caespitosa* in southern Arizona were able to survive for at least 7 yr.

Distribution

Sideoats grama occurs naturally in grasslands, shrublands, forests, and deserts and is one of the most widely distributed warm-season grass species in the Western Hemisphere (Gould, 1979). It is best adapted to fine-textured, calcareous, and moderately alkaline soils (Stubbendieck et al., 1992). The var. *curtipendula* commonly occurs from Ontario and Manitoba to eastern Montana and through the Central Plains to southern Utah and northern Arizona, New Mexico and Texas and the Mexican state of Coahuila. This taxon also may be found occasionally throughout most areas of the continental USA except for the extreme southeast and northwest. The distribution of var. *tenuis* is limited to the highlands of north central Mexico from the state of Chihuahua in the north to the states of Puebla and Veracruz in the south. The var. *caespitosa* is most prominent in Texas, New Mexico, Arizona, and northern Mexico where its distribution roughly parallels that of var. *tenuis*. Variety *caespitosa* also is found in adjoining states in the USA and in western South America from Venezuela south to Argentina and Paraguay (Gould, 1979). Populations within the Mexican states of Coahuila, Chihuahua, and Durango, where both var. *caespitosa* and *tenuis* exist, are especially variable morphologically (Gould, 1951), which may indicate intravarietal hybridization.

On sites where sideoats grama occurs naturally it rarely forms extensive stands, but because of its drought resistance and leafiness, it can be an important

forage resource for grazing animals (Newell et al., 1962; Ruyle and Young, 1997). Within the Great Plains grasslands, sideoats grama (primarily var. *curtipendula*) represents a minor component of the tall and especially the mixed-grass prairies (Sims and Risser, 2000). Within mixed-grass communities, sideoats grama is often asso-
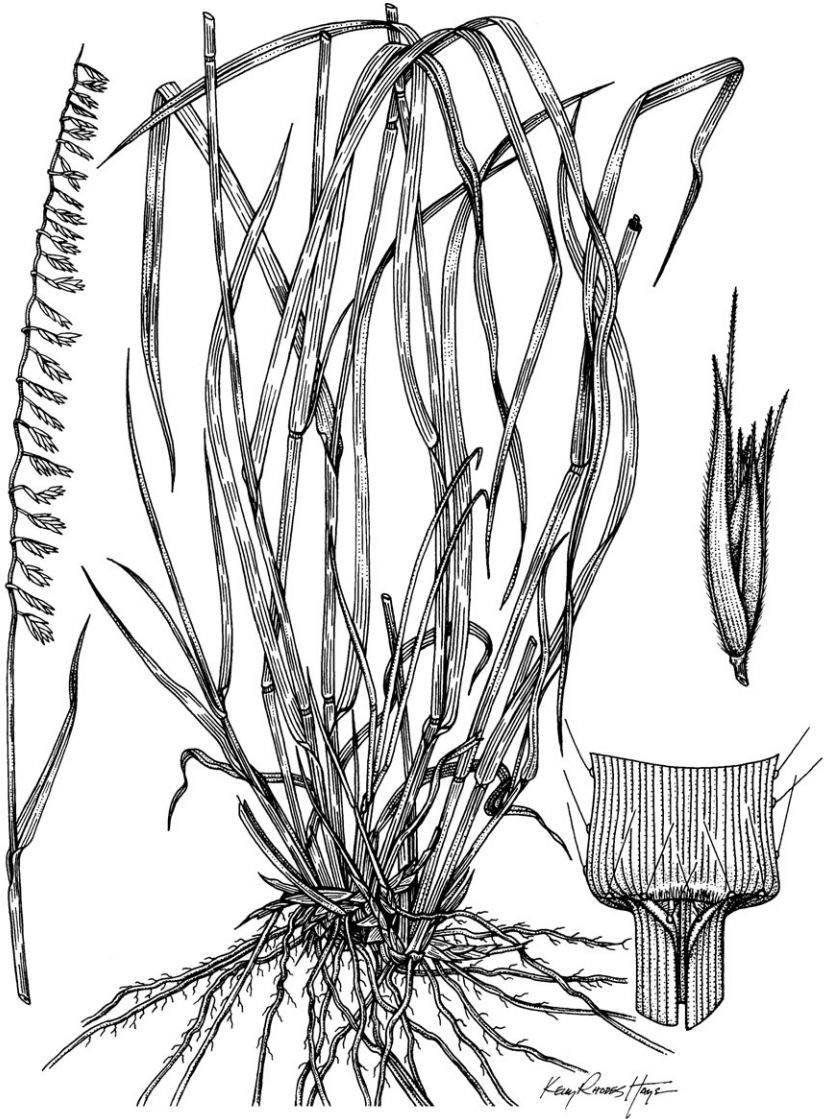

Fig. 30–1. Illustration of a side oats grama plant. (center; whole plant with erect culms 50–80-cm tall, leaf blades are flat to subinvolute and 3–4-mm wide), inflorescence (left; consists of numerous spicate branches, each branch has two to six spikelets attached to a flattened rachis, and the branches are twisted to one side of the central axis which is the basis for the species' common name), leaf collar (bottom right; showing short fringed ligule seldom more than 0.5-mm long), and individual spikelet (upper right; consisting of unequal glumes and short awns, spikelets are 6–10-mm long and typically have one fertile floret and one highly reduced sterile floret).

ciated with blue grama and buffalograss on more arid sites and with little bluestem [*Schizachyrium scoparium* (Michx.) Nash] and sand bluestem (*Andropogon hallii* Hack.) on more mesic sites. Considering its entire distribution, sideoats grama is most common and important in the central and southern mixed-grass regions (central Nebraska to south central Texas) (Voigt and MacLauchlan, 1985). Annual precipitation in this region varies from about 380 to 710 mm (Wright and Bailey, 1982) with the majority occurring in spring and summer. Within more arid desert grasslands and associated shrubland communities, sideoats grama (vars. *caespitosa* and *tenuis*) often occurs scattered on rocky slopes (Gould, 1979), explaining one of its alternative common names, "side-hill" grama (Flory and Marshall, 1942).

Cytology, Reproductive Biology, and Evolution

Ploidy levels of sideoats grama range from diploid (2n = 2x = 20) for var. *tenuis*, through tetraploid (2n = 4x = 40) for var. *tenuis* and *var. curtipendula*, to aneuploids and high polyploids in var. *caespitosa* with 2n = 58 to ca.103 (Gould, 1979). In central Texas, where the ranges of var. *curtipendula* and var. *caespitosa* overlap, an extensive series of rhizomatous aneuploids exist (2n = 41 through 64) (Gould and Kapadia, 1964). These authors hypothesized that the rhizomatous tetraploids evolved first while the caespitose aneuploids developed later and spread into central Texas. Rhizomatous aneuploids would have resulted from hybridization between the two varieties.

Chromosome pairing is regular in most var. *curtipendula* germplasm (Fretter and Brown, 1955). In the rhizomatous aneuploids with high chromosome numbers (Kapadia and Gould, 1964a), the first division of meiosis is "more or less irregular" with numerous univalents, multivalents, and laggards. However, at the first division nearly equal numbers of chromosomes segregated to the daughter cells. In the 'Tucson' ecotype of var. *caespitosa*, chromosome number ranged from 85 to 101 (Harlan, 1949). Chromosome pairing was low with essentially no pairing in some plants but up to a mean of 10 bivalents in others and highly unequal segregation of chromosomes resulted. The division at anaphase II was essentially regular and pollen was highly irregular in size.

Plants within var. *curtipendula* are generally considered to be cross-pollinated (Harlan, 1950). Given its ploidy level, var. *tenuis* appears to be largely cross-pollinated as well, although this has not been confirmed. Variety *caespitosa* is presumably apomictic via apospory (Gould, 1959; Mohamed and Gould, 1966). Progenies of the Tucson ecotype were very uniform in appearance (Harlan, 1949). Also, the high level of seed set observed in var. *caespitosa* was additional evidence for apomixis despite the highly irregular divisions during mega- and microsporogenesis.

The var. *curtipendula* is thought to have originated in northern Mexico and spread northward through the central USA and Canada (Gould and Kapadia, 1964) primarily through evolutionary changes in response to photoperiod (Olmstead, 1944, 1945) and temperature (Rogler, 1943). Variety *caespitosa* is not responsive to photoperiod and flowers as soon as temperature and moisture conditions allow (McMillan, 1961). This difference in flowering time means that var. *curtipendula* and var. *caespitosa* tend to flower at different times and raises questions concern-

ing the origin of proposed intermediates between the two and where hybridization might have occurred. Gould and Kapadia (1964) proposed that var. *caespitosa* probably arose through hybridization of many different combinations of diploid and tetraploid plants. Two candidate species considered closely related to *B. curtipendula* are Nealley or oneflower grama (*Bouteloua uniflora* Vasey) and Warnock's grama (*Bouteloua warnockii* Gould & Kapadia) (Gould and Kapadia, 1964).

Genetic Variation and Breeding

Intraspecific Variation

Hopkins (1941), working in Kansas, obtained seed of sideoats grama from nine states ranging from New Mexico and Texas to Montana and North Dakota. His findings essentially paralleled those observed for blue grama (Riegel, 1941). Southern sources were taller, had larger inflorescences, and produced more forage than northern materials. Rhizomes were generally better developed in the southern strains. Kapadia and Gould (1964b) studied variation in var. *caespitosa*. Although their evidence is difficult to evaluate, it is clear that variation does exist for a number of characteristics, for example, anther color, number of inflorescence branches, number of spikelets per branch, and terminal leaf width.

Smith (1998) studied two groups of var. *caespitosa* plants from near Mammoth, AZ. One group was collected from a site on top of a steep-walled butte that had never been grazed by livestock. The second group was collected from a site 5 km away that had been regularly grazed by cattle (*Bos taurus*) since before 1900. Then the plants were compared in a greenhouse study using three defoliation intervals. The cattle-free genotypes had greater mortality, with more frequent defoliation, than the cattle-impacted genotypes. The improved resistance of the cattle-impacted genotypes was associated with increased relative tiller numbers with a tendency to produce slightly smaller tillers. Another important difference was the lack of variation in leaf angle among the cattle-impacted genotypes while significant variation was detected among the cattle-free genotypes. Grazing had impacted these two populations of plants that can be presumed to be apomictic. Smith et al. (2000) also demonstrated that plants from the cattle-impacted population exhibited lower average seed production per spike indicating lower inherent floral fertility compared to the cattle-free population.

Sideoats grama can be established relatively easily in most environments to which it is adapted, due in part to its rapid seedling growth (Simanton and Jordan, 1986). In the more arid Southwest, sideoats grama can be more difficult to establish than species that germinate more slowly and have better survival during initial dry periods following emergence (Frasier et al., 1985). One way to address this problem is to identify genetic variability for seed dormancy. Major and Wright (1974) screened 148 accessions and found that genetic differences in seed dormancy do exist in this species. However, because many of these differences disappeared with germination in soil, their value for affecting establishment appears limited. It also seems unlikely that dormancy conditioned by caryopsis appendages would be useful for increasing seed survival following ingestion, a potential mechanism for seed dispersal (Barrow and Havstad, 1992). Differences in caryopsis size among sideoats

grama collections also have been reported (Kneebone, 1956; Major and Wright, 1974); although, the value of this variation for improving establishment may be environment specific.

Breeding History

Harlan (1950) selected for several plant types in spaced-plant nurseries of var. *curtipendula* germplasm originating from central Texas to Kansas. Two cycles of selection for traits such as increased leafiness and more upright growth habit were completed and progress was reported for at least some of the plant types. Kneebone (1956) selected vigorous seedlings from seeded rows of two ecotypes. One cycle of selection increased seedling vigor. A more detailed study with different germplasm and three cycles of selection was completed later (Voigt and Brown, 1969). These researchers found that selection resulted in an increase in seedling height over all cycles of selection. However, progenies resulting from open-pollination of the base population also showed increased seedling vigor, suggesting that some of the benefit of the artificial selection was obtained by natural selection during seed increase.

Sideoats grama cultivars are adapted to different latitudinal zones (Table 30–1). Most are increases of single ecotypes, although some ('Butte' and 'Killdeer') are more diverse in origin and one ('Trailway') resulted from more directed selection for late maturity and rust resistance (Hanson, 1972; Alderson and Sharp, 1994). Despite great promise (Harlan and Ahring, 1958), most cultivars of var. *caespitosa* have not been successful. Reasons for this are not completely understood; however, their area of adaptation was often limited by lack of adequate winter survival (Newell et al., 1962). Also, the high forage production of Tucson and 'Coronado' (Harlan and Ahring, 1958) was associated with high seed yields and many flowering culms. Because of this stemmy appearance, caespitose cultivars had a reputation of low palatability, although comparative studies with var. *curtipendula* have not been reported.

Initial releases of germplasm of var. *caespitosa* also failed because of poor animal acceptance and possibly because establishment was poorer than anticipated. Traditionally, rangeland seedings in the southern plains were made during mid- to late winter with the grasses expected to germinate and emerge with the warmer temperatures of spring. A uniform apomictic cultivar with a temperature requirement greater than that of other grasses would be at a disadvantage in those conditions.

Germplasm of var. *caespitosa* should be evaluated for important characteristics such as grazing tolerance, but not excessive grazing avoidance caused by steminess. Extensive genetic variation clearly exists within stands of this apomictic variety (Smith, 1998), but the mechanisms by which this variability was created and how it is maintained are not adequately understood. Mechanisms to manipulate apomixis in this species have not been developed and the possibility of using carefully selected bulks of multiple apomictic strains, rather than single apomictic genotypes, needs study. Although initial studies of variation for seed dormancy were not encouraging, additional collections specifically for this and other characters that might increase potential for successful establishment in the arid southwest should be initiated.

Importance, Utilization, and Management

Especially within the natural range of vars. *caespitosa* and *tenuis*, and the margins of the range of var. *curtipendula*, sideoats grama is generally used by grazing animals as a minor component of diverse rangeland plant communities (e.g., Ruyle and Young, 1997; Lauver et al., 1999). This species is distinctive among the gramas because its value as a forage species in seeded permanent pastures now exceeds that of native rangeland stands. Efforts to revegetate disturbed sites in the Great Plains, beginning in the 1940s, often focused on sideoats grama because it was one of the few native grasses easily adaptable to farm cultivation for seed production because of its upright growth habit (Flory and Marshall, 1942). It also produces relatively high seed and forage yields (Newell et al., 1962), has good seedling vigor, reseeds well (Simaton and Jordan, 1986), and produces relatively palatable forage that cures well (Weaver and Albertson, 1956). Because of these desirable traits, this species became the focus of considerable plant breeding and agronomic research, primarily in the central and southern Great Plains. Sideoats grama has been seeded in pastures in this region, and more recently because of the USDA Conservation Reserve Program (Gillen and Berg, 1998). In 1999, applications were filed for certification of a total of 140 ha of sideoats grama in the USA (ASOCA, 1999).

A number of agronomic practices have been used in the establishment and management of pastures with sideoats grama as a primary component. Stands typically have been established by drilling in rows at a depth of about 20 mm or broadcasting at rates of 2.8 to 5.6 kg pure live seed (PLS) ha^{-1} (Newell et al., 1962). Seedings that include sideoats grama usually are mixtures and the species included vary widely over regions (Newell et al., 1962; Posler et al., 1993). Such seedings are generally recommended for late spring-early summer; although, this also depends on associated species, precipitation pattern, and latitude (Frasier et al., 1987; Ries and Hofmann, 1996).

The response of midgrass dominated pastures to fertilization has been investigated extensively (Wilkinson and Langdale, 1974; Berg, 1995). Sideoats grama generally is more responsive to N fertilization than shortgrasses such as blue grama and buffalograss that may be growing in association with it (Launchbaugh, 1962). Plants of var. *caespitosa* also can be more responsive to N fertilization than those of var. *curtipendula* (P.W. Voigt, unpublished data, 2000). As with blue grama, fertilization of sideoats may increase the competitiveness of cool-season grasses or weedy species that may be competing with it (Launchbaugh, 1962; Berg, 1995). Berg (1995) reported that overall N-use efficiency in a sown pasture in western Oklahoma containing sideoats grama was about 25 kg forage kg^{-1} N applied, which was similar to previous reports for comparable sites (e.g., Wilkinson and Langdale, 1974).

Many site and environment-specific grazing management systems are used on pastures or rangelands that contain sideoats grama (e.g., Taylor et al., 1997; Gillen and Berg, 1998). Compared to most grasses found in pastures it occupies, sideoats grama is highly palatable throughout the summer and autumn, and moderately palatable into the winter. Leaves are much more palatable than culms, which are usually not consumed (Weaver and Albertson, 1956). In Montana, its forage had average crude protein concentration of 103 g kg^{-1} and in vitro digestibility of 673 g

kg^{-1}, which was the highest among the species in the experiment (White, 1986). Newall and Moline (1978) reported higher digestibility in sideoats grama than big bluestem (*Andropogon gerardii* Vitman), sand bluestem, little bluestem, and switchgrass (*Panicum virgatum* L.) in Nebraska. In the southern Great Plains, pastures containing sideoats grama averaged between 77 and 86 g kg^{-1} crude protein and organic matter digestibility of 467 to 493 g kg^{-1} depending on stocking rate (Heitschmidt et al., 1989).

Sideoats grama is considered a late-seral species (Hendrickson and Briske, 1997) and its abundance typically decreases as grazing intensity increases (Taylor et al., 1997). The mechanisms of grazing resistance exploited by the species are at least partially understood. In a mixed-species grassland in Texas, Heitschmidt et al. (1990) showed that relatively tall tillers of sideoats grama were defoliated most frequently by cattle and that intensity of defoliation was positively associated to tiller height of individual plants. Hendrickson and Briske (1997) reported that while plants in west central Texas maintained large populations of axillary buds, and these buds were long lived, the growth of surviving buds was not sufficient to replace tillers that died or were removed by defoliation. This research compared communities that had not been grazed by domestic herbivores for more than 45 yr with those that had been grazed during this period. No evidence was found of compensatory growth of axillary buds following defoliation within either community. At the same location, Briske and Hendrickson (1998) demonstrated that selective defoliation (self only/self + neighbors/neighbors only) had little effect on the competitive interactions of individual sideoats grama plants. The grass is generally considered relatively intolerant of fire (Wright, 1974).

Sideoats grama seed yields are highest when it is cultivated as an irrigated row crop (Newell et al., 1962). Under these conditions, yields of 450 to 670 kg ha^{-1} (unconditioned) may be expected from either one or two harvests per year (McDonald and Copeland, 1997). Spicate branches bearing 1 to 12 sessile spikelets generally represent the "seed unit" although various floral appendages are present which explains the relatively low purity of seed lots (usually <40%). Seed set, which is typically low, is generally highest when flowering occurs in late summer when relative humidity is high. Not all spicate branches produce fertile spikelets (Harlan, 1950), and spicate branch filling <10% usually indicates the seed crop will be of exceedingly low quality (McDonald and Copeland, 1997). Sideoats grama is typically harvested by direct combining with low cylinder speeds and wind. Recombining or use of a scalper may be necessary to separate stems and leaves from branches containing filled caryopses. Debearders may be used to further condition lots and improve their purity and flowability.

BLACK GRAMA

General Description

Morphology and Development

Black grama plants are tufted, with a hard, basal crown and typically develop arching, wiry stolons that may produce a tangled sod (Gould, 1951), although in-

dividual plants are often scattered and behave as bunchgrasses. Importantly, the canopy produced by dense black grama stands may enhance infiltration of rainfall by absorbing much of the energy of falling raindrops (Bach et al., 1986). Culms of this species are generally 20- to 60-cm tall with three to eight branches (20–50-mm long) each of which has 8 to 10 nonpectinate spikelets (2–5-mm long) that persist after caryopses are shed. Leaf blades of black grama are <2-mm wide and are generally shorter than the internodes and leaf sheaths. Stolons and lower internodes of culms are pubescent and along with leaves are grayish green, curing to gray. Two consecutive favorable growing seasons are generally required for the establishment of rooted stolons as independent plants (Nelson, 1934). Stolons may remain green for two or more growing seasons providing an excellent cured feed in autumn, winter, and spring (Wright and Streetman, 1958). This species is considered highly drought tolerant both as a seedling and a mature plant (Wright and Streetman, 1958). As in blue and sideoats gramas, black grama seedlings develop adventitious roots near the soil surface that renders them particularly susceptible to dessication early in their development (Minnick and Coffin, 1999). Black grama is not particularly tolerant of fire (Cable, 1965; Gosz and Gosz, 1996). It should be noted that in many reports from the early 1900s the name "black grama" was applied to various species other than what is now recognized as *Bouteloua eriopoda*. This included tobosa (*Pleuraphis mutica* Buckl.) (Griffiths, 1901) and bush muhly *(Muhlenbergia porteri* Scribn. *ex* Beal) (Thornber, 1910).

The propensity of black grama to establish new plants from rooted stolons would suggest individual genets may persist for centuries. Individual plants (crowns) of black grama were shown to live up to 28 yr on rangeland in southern New Mexico (Wright and Van Dyne, 1976). Considering all seedlings that emerged during this study, average life span was about 2 yr. Because seedling establishment is a rare event (Valentine, 1970; Neilson, 1986; Minnick and Coffin, 1999), it may be more important to focus on the life span of plants that are able to live at least 1 yr. Wright and Van Dyne (1976) determined that the mean life span of black grama plants that survive for 1 yr is about 4 yr.

Distribution

Of the three most important gramas, black grama has the most restricted distribution. This species is regarded to be native primarily to relatively coarse-textured soils in the North American desert grassland (Schmutz et al., 1991). Within the USA, this grass occurs on scattered sites from western Texas and Oklahoma, to southern New Mexico, and central and southern Arizona. It occupies about 24 million hectares in these states, primarily on the gentle slopes of the broad basins associated with low hills or mountains on relatively shallow clay loam to sandy loam soils that are often underlain by gravel (Paulsen and Ares, 1962). The desert grassland extends from the southwestern USA through all or part of the Mexican states of Sonora, Chihuahua, Coahuila, Durango, Zacatecas, Nuevo Leon, San Luis Potosi, Jalisco, Guanajuato, Queretaro, Hidalgo, Puebla, and Mexico. While black grama may be found in all the subregions of the desert grassland, it is most closely associated with the Chihuahuan Desert grassland (Schmutz et al., 1991). In the mid-1990s, it was estimated that about 500 000 animal units of livestock and wildlife

used Chihuahuan Desert grasslands where black grama is most common (Holechek et al., 1994). This subregion is most pronounced in southern New Mexico and northern Chihuahua at elevations from 350 to 1400 m where annual precipitation ranges from 250 to 400 mm. Precipitation is divided between low-intensity winter (November–March) storms that cover broad areas and late-summer convective storms (July–September) (50–80% of annual total precipitation) that are isolated, intense, and short in duration. Summer temperatures regularly exceed 38°C and winter temperatures below −10°C are not infrequent (MacMahon and Wagner, 1985). The period of time when temperatures and soil water are favorable for black grama growth in southern New Mexico is typically <100 d each year (Canfield, 1939; Gibbens and Beck, 1988).

Cytology and Reproductive Biology

Streetman and Wright (1960) collected 35 accessions of black grama from Arizona and New Mexico and determined that the chromosome number of the species was $2n = 2x = 20$. Chromosome pairing in diploid plants was regular with 10 bivalents for most accessions. Meiosis in a highly sterile aneuploid accession ($2n = 28$) was more irregular. Florets are chasmogamous suggesting that the species is cross-pollinated (Columbus, 1999b).

Genetic Variation and Breeding

Little has been published characterizing the genetic variation in black grama. Problems in seed set and production (Wright and Streetman, 1958) are thought to have genetic (Hanson, 1972), climatic (Wright, 1964), and insect-related (Watts, 1965) causes. 'Sonora' (Table 30–1) produced 610% of the forage and 540% of the seed of the 'Flagstaff' ecotype (Wright, 1965), and was superior in vegetative spread at Tucson, AZ. However, the limited data available indicate that the two were similar in components of seed production (Wright, 1965). Increase in seed production appears related to greater plant spread or increased numbers of inflorescences area^{-1}.

Research that led to the development of Sonora is the only known breeding work with black grama. From the original nursery of 2067 plants used for cytogenetic investigations (Streetman and Wright, 1960), 79 were vegetatively propagated and reevaluated (Hanson, 1972). Polycross progenies of 19 of these were later evaluated for seed set and forage production and 12 of these became the base population for Sonora. Unfortunately, the origins of the clones were not reported, although the range in identification numbers suggests multiple sources. Sonora was never successfully commercialized although 'Nogal,' which is an unimproved New Mexico ecotype, has achieved limited commercial success (Table 30–1). In 1999, an application was filed for certification of 3.2 ha of foundation seed of Nogal (AOSCA, 1999).

Although black grama remains a species of major importance on arid rangelands and its increased resistance to drought and tolerance to grazing could be useful, there appears little justification for much genetic work with the species because of its poor seed production, difficulties in stand establishment, and limited commercial demand for its seed.

Importance, Utilization, and Management

Native stands of black grama were once extensive in southern New Mexico and Arizona and produced enough forage to be harvested for hay (Griffiths, 1904). Indeed, hay yields in excess of 1000 kg ha^{-1} were recorded on rangelands where black grama predominated in the early part of the 20th century (Wooten, 1916). However, since the early 1900s this species has been grazed almost exclusively on rangelands (Hennessy et al., 1983; Archer, 1994).

Black grama is not highly grazing resistant and its response to defoliation is dependent on precipitation. With relatively conservative utilization (<40% of available forage removed), production of black grama forage in southern New Mexico was most closely associated with precipitation over the preceding 15-mo period (Gibbens and Beck, 1988). Gibbens and Beck (1988) also showed that basal area of black grama plants may be affected by precipitation over more extended periods of time, up to 4 yr in some cases. During extended droughts, the basal area of this species was reduced to the same amount regardless of the extent of defoliation (Paulsen and Ares, 1962). Extending earlier work, Stephens and Whitford (1993) showed that productivity in black grama also is more closely linked with rainfall than with N availability in southern New Mexico.

Watkins (1943) reported that crude protein concentration of black grama forage averaged 82 g kg^{-1} during the growing season in southern New Mexico. During the November to June dormant season, average crude protein of black grama was 49 g kg^{-1}, which is below the values recommended for most livestock (National Research Council, 1996). Because it may retain green tissue year-round, dormant season grazing of black grama has been common (Paulsen and Ares, 1962). However, continuous grazing of the grass may reduce its persistence on desert grassland sites (Nelson, 1934; Miller and Donart, 1979). Overall, utilization near 35% resulted in increased vigor and persistence compared to higher utilization or the complete lack of grazing (Valentine, 1970). Higher utilization reduced the number of stolons produced and would be expected to reduce vegetative spread through rooted stolons, either due to defoliation directly or to trampling damage (Paulsen and Ares, 1962). Importantly, Paulsen and Ares (1962) showed that from 1916 until 1953, research pastures in southern New Mexico that were conservatively grazed (35% utilization) maintained higher cover of black grama than those where livestock were excluded. Bock and Bock (1993) also showed that cover of black grama plants was greater on sites in southern Arizona that were grazed by cattle compared to sites nearby where livestock had been excluded for 22 yr. Defoliation only during the growing season produced more forage in the following year than did year-long grazing or grazing during dormant periods (Miller and Donart, 1979).

REFERENCES

Aguilera, M.O., and W.K. Lauenroth. 1993. Neighborhood interactions in a natural population of the perennial bunchgrass *Bouteloua gracilis*. Oecologia 94:595–602.

Aguilera, M.O., and W.K. Lauenroth. 1995. Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. J. Ecol. 83:87–97.

Alderson, J.S., and W.C. Sharp. 1994. Grass varieties of the United States. Agric. Handb. 170. USDA-SCS, Washington, DC.

Association of Official Seed Certifying Agencies. 1999. Acres applied for certification in 1999. Publ. 53. AOSCA, Meridian, ID.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: Rates, patterns and proximate causes. p. 13–68. *In* M. Vavra et al. (ed.) Ecological implications of livestock herbivory in the west. Soc. Range Manage., Denver, CO.

Ares, J. 1976. Dynamics of the root system of blue grama. J. Range Manage. 29:208–213.

Bach, L.B., P.J. Wierenga, and T J. Ward. 1986. Estimation of the Philip infiltration parameters from rainfall simulation data. Soil Sci. Soc. Am. J. 50:1319–1323.

Bakker, J.D., J. Christian, S.D. Wilson, and J. Waddington. 1997. Seeding blue grama in old crested wheatgrass fields in southwestern Saskatchewan. J. Range Manage. 50:156–159.

Barker, R.E., J.D. Berdahl, J.M. Krupinsky, and E.T. Jacobson. 1983. Collections of western wheatgrass and blue grama and associated nematode genera in the western Dakotas. p. 237–240. *In* J.A. Smith and V.W. Hays (ed.) Proc. Int. Grassl. Congr., 14th, Lexington, KY. 12–24 June 1981. Westview Press, Boulder, CO.

Barrow, J.R., and K.M. Havstad. 1992. Recovery and germination of gelatin-encapsulated seeds fed to cattle. J. Arid Environ. 22:395–399.

Bement, R.E. 1969. A stocking-rate guide for beef production on blue-grama range. J. Range Manage. 22:83–86.

Berg, W.A. 1995. Response of a mixed native warm-season grass planting to nitrogen fertilization. J. Range Manage. 48:64–67.

Biedenbender, S.H., and B.A. Roundy. 1996. Establishment of native semidesert grasses into existing stands of *Eragrostis lehmanniana* in southeastern Arizona. Restoration Ecol. 4:155–162.

Biondini, M.E., B.D. Patton, and P.E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecol. Applic. 8:469–479.

Bock, C.E., and J.H. Bock. 1993. Cover of perennial grasses in southeastern Arizona in relation to livestock grazing. Conserv. Biol. 7:371–377.

Bowman, W.D., and L. Turner. 1993. Photosynthetic sensitivity to temperature in populations of two C_4 *Bouteloua* (Poaceae) species native to different altitudes. Am. J. Bot. 80:369–374.

Briske, D.D., and J.R. Hendrickson. 1998. Does selective defoliation mediate competitive interactions in a semiarid savanna? A demographic evaluation. J. Veg. Sci. 9:611–622.

Briske, D.D., and A.M. Wilson. 1977. Temperature effects on adventitious root development in blue grama seedlings. J. Range Manage. 30:276–280.

Briske, D.D., and A.M. Wilson. 1978. Moisture and temperature requirements for adventitious root development in blue grama seedlings. J. Range Manage. 31:174–178.

Cable, D.R. 1965. Damage to mesquite, Lehmann lovegrass, and black grama by a hot June fire. J. Range Manage. 18:326–329.

Canfield, R.H. 1939. Maintaining the balance between summer and winter forage on black grama ranges under year-long grazing use. Note 82. USDA-FS Southwestern Forest and Range Exp. Stn. Res., Santa Rita Exp. Range, Tucson, AZ.

Canfield, R.H. 1957. Reproduction and life span of some perennial grasses of southern Arizona. J. Range Manage. 10:199–203.

Carren, C.J., A.M. Wilson, and R L. Cuany. 1987a. Caryopsis weight and planting depth of blue grama. II. Emergence in marginal soil moisture. J. Range Manage. 40:212–216.

Carren, C.J., A.M. Wilson, R.L. Cuany, and G.L. Thor. 1987b. Caryopsis weight and planting depth of blue grama. I. Morphology, emergence and seedling growth. J. Range Manage. 40:212–216.

Christians, N. 1998. Fundamentals of turfgrass management. Ann Arbor Press, Chelsea, MI.

Clawson, M.R., and J.J. Rotella. 1998. Success of artificial nests in CRP fields, native vegetation and field borders in southwestern Montana. J. Field Ornith. 69:180–191.

Coffin, D.P., and W.K. Lauenroth. 1989. Spatial and temporal variation in the seedbank of a semiarid grassland. Am. J. Bot. 76:53–58.

Coffin, D.P., and W.K. Lauenroth. 1992. Spatial variability in seed production of the perennial bunchgrass *Bouteloua gracilis* (Gramineae). Am. J. Bot. 79:347–353.

Coffin, D.P., W.K. Lauenroth, and I.C. Burke. 1996. Recovery of vegetation in a semiarid grassland 53 years after disturbance. Ecol. Applic. 6:538–555.

Columbus, J.T. 1999a. An expanded circumscription of Bouteloua (Gramineae: Chloridoideae): New combinations and names. Aliso 18:61–65.

Columbus, J.T. 1999b. Morphology and leaf blade anatomy suggest a close relationship between *Bouteloua aristidoides* and *B*. (Chondrosium) *eriopoda* (Gramineae: Chloridoideae). Syst. Bot. 23:467–478.

Coupland, R.T. 1958. The effects of fluctuations in weather upon the grasslands of the great plains. Bot. Rev. 24:273–317.

Crowston, W.A., and H. Goetz. 1976. Fertilizer and clipping effects on ecotypes of western wheatgrass and blue grama. Bull. 502. N. Dak. Agric. Exp. Stn., Fargo.

Derner, J.D., and D.D. Briske. 1998. An isotopic (N-15) assessment of intraclonal regulation in C-4 perennial grasses: ramet interdependence, interdependence or both? J. Ecol. 86:305–314.

Detling, J.K. 1979. Processes controlling blue grama production in the shortgrass prairie, p. 25–42. *In* N.R. French (ed.) Perspectives in grassland ecology, results and applications of the US/IBP grassland biome study. Springer-Verlag. New York.

Dickinson, C.E., and J.L. Dodd. 1976. Phenological pattern in the shortgrass prairie. Am. Midl. Nat. 96:367–378.

Ellison, L., and E.J. Woolfolk. 1937. Effects of drought on vegetation near Miles City, Montana. Ecology 18:329–336.

Englert, J.M., J.G. Scheetz, and R.S. White. 2000. Improved plant materials released by NRCS and cooperators through September 1999. USDA, NRCS Natl. Plant Materials Ctr., Beltsville, MD.

Epstein, H.E., W.K. Lauenroth, I.C. Burke, and D.P. Coffin. 1998. Regional productivities of plant species in the Great Plains of the United States. Plant Ecol. 134:173–195.

Fair, J., W.K. Lauenroth, and D.P. Coffin. 1999. Demography of *Bouteloua gracilis* in a mixed prairie: Analysis of genets and individuals. J. Ecol. 87:233–243.

Flory, E.L., and C.G. Marshall. 1942. Regrassing for soil protection in the Southwest. USDA Farmer's Bull. 1913.

Ford, P.L. 1999. Response of buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*) to fire. Great Plains Res. 9:261–276.

Frasier, G.W., J.R. Cox, and D.A. Woolhiser. 1985. Seedling survival response of seven grasses to initial wet-dry sequences. J. Range Manage. 38:372–377.

Frasier, G.W., J.R. Cox, and D.A. Woolhiser. 1987. Wet-dry cycle effects on warm-season grass seedling establishment. J. Range Manage. 40:2–6.

Freeman, B.N., and R.R. Humphrey. 1956. The effects of nitrates and phosphates upon forage production of a southern Arizona desert grassland. J. Range Manage. 9:176–180.

Fretter, L.E., and W.V. Brown. 1955. A cytotaxonomic study of *Bouteloua curtipendula* and *B. uniflora*. Bull. Torrey Bot. Club 82:121–130.

Fults, J.L. 1944. Some factors affecting the establishment of perennial grass for erosion control in eastern Colorado. J. Am. Soc. Agron. 36:615–625.

Gibbens, R.P., and R.F. Beck. 1988. Changes in grass basal area and forb densities over a 64–year period on grassland types of the Jornada Experimental Range. J. Range Manage. 41:186–192.

Gillen, R.L., and W.A. Berg. 1998. Nitrogen fertilization of a native grass planting in western Oklahoma. J. Range Manage. 51:436–441.

Goetz, H., P.E. Nyren, and D.E. Williams. 1978. Implications of fertilizers in plant community dynamics of Northern Great Plains rangelands. p. 671–674. *In* D.N. Hyder (ed.) Proc. Int. Rangeland Congr., 1st, Denver, CO. 14–18 Aug. 1978. Soc. Range Manage., Denver, CO.

Gosz, R.J., and J.R. Gosz. 1996. Species interactions on the biome transition zone in New Mexico: Response of blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eripoda*) to fire and herbivory. J. Arid Environ. 34:101–114.

Gould, F.W. 1951. Grasses of the southwestern United States. Univ. of Arizona Press, Tucson.

Gould, F.W. 1959. Notes on apomixis in sideoats grama. J. Range Manage. 12:25–28.

Gould, F.W. 1979. The genus *Bouteloua* (Poaceae). Ann. Mo. Bot. Garden 66:348–416.

Gould, F.W., and Z.J. Kapadia. 1964. Biosystematic studies in the *Bouteloua curtipendula* complex. II. Taxonomy. Brittonia 16:182–207.

Griffiths, D.A. 1901. Range improvement in Arizona. Bull. 4. USDA, Bureau of Plant Industry, Washington, DC.

Griffiths, D.A. 1904. Range investigations in Arizona. Bull. 6. USDA, Bureau of Plant Industry, Washington, DC.

Haferkamp, M.R., J.D. Volesky, M.M. Borman, R.K. Heitschmidt, and P.O. Currie. 1993. Effects of mechanical treatments and climatic factors on the productivity of Northern Great Plains rangelands. J. Range Manage. 46:346–350.

Hanson, A.A. 1972. Grass varieties in the United States. USDA-ARS Agric. Handb. 170. U.S. Gov. Print. Office, Washington, DC.

Harlan, J.R. 1949. Apomixis in side-oats grama. Am. J. Bot. 36:495–499.

Harlan, J.R. 1950. The breeding behavior of side-oats grama in partially isolated populations. Agron. J. 42:20–24.

Harlan, J.R. 1958. Blue grama types from West Texas and Eastern New Mexico. J. Range Manage. 11:84–87.

Harlan, J.R., and R.M. Ahring. 1958. Coronado side-oats grama. Bull. B-515. Okla. Agric. Exp. Stn., Stillwater.

Harlan, J.R., R.M. Ahring, and W.R. Kneebone. 1956. Grass seed production under irrigation in Oklahoma. Bull. B-481. Okla. Agric. Exp. Stn., Stillwater.

Hart, R.M., and M.M Ashby. 1998. Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. J. Range Manage. 51:392–398.

Hendrickson, J.R., and D.D. Briske. 1997. Axillary bud banks of two semiarid perennial grasses: Occurrence, longevity, and contribution to population persistence. Oecologia 110:584–591.

Heitschmidt, R.K., D.D. Briske, and D.L. Price. 1990. Pattern of interspecific tiller defoliation in a mixed–grass prairie grazed by cattle. Grass Forage Sci. 45:215–222.

Heitschmidt, R.K., S.L Dowhower, W.E. Pinchak, and S.K. Canon. 1989. Effects of stocking rate on quantity and quality of available forage in a southern mixed grass prairie. J. Range Manage. 42:468–473.

Hennessy, J.T., R.P. Gibbens, J.M. Tromble, and M. Cardenas. 1983. Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. J. Range Manage. 36:370–374.

Hoffmann, L.A., E.F. Redente, and L.C. McEwen. 1995. Effects of selective seed predation by rodents on shortgrass establishment. Ecol. Applic. 5:200–208.

Holechek, J.L., and D. Galt. 2000. Grazing intensity guidelines. Rangelands 22:11–14. Bull. 367.

Holechek, J.L., A. Tembo, A. Daniel, M.J. Fusco, and M. Cardenas. 1994. Long-term grazing influences on Chihuahuan Desert rangeland. Southwest. Nat. 39:342–349.

Hook, P.B., and W.K. Lauenroth. 1994. Root-system response of a perennial bunchgrass to neighborhood-scale soil-water heterogeneity. Func. Ecol. 8:738–745.

Hopkins, H. 1941. Variations in the growth of side-oats grama grass at Hays, Kansas, from seed produced in various parts of the Great Plains region. Trans. Kans. Acad. Sci. 44:86–95.

Hunt, H.W., M.J. Trlica, E.F. Rendente, J.C. Moore, J.K. Detling, T.G.F. Kittel, D.E. Walter, M.C. Fowler, D.A. Klein, and E.T. Elliott. 1991. Simulation model for the effects of climate change on temperate grassland ecosystems. Ecol. Modell. 53:205–246.

Hyder, D.N. 1974. Morphogenesis and management of perennial grasses in the United States. p. 89–98. *In* K.W. Kreitlow and R.H. Hart (ed.) Plant morphogenesis as the basis for scientific management of range resources. Proc. Workshop United States-Australia Rangelands Panel. Misc. Publ. 1271. USDA, Washington, DC.

Hyder, D.N., R.E. Bement, E.E. Remmenga, and D.F. Hervey. 1975. Ecological responses of native plants and guidelines for management of shortgrass range. USDA-ARS, Washington, DC.

Hyder, D.N., A.C. Everson, and R.E. Bement. 1971. Seedling morphology and seeding failures with blue grama. J. Range Manage. 24:287–292.

Hyder, D.N., W.R. Houston, and J.B. Burwell. 1976. Drought resistance of blue grama as affected by atrazine and N fertilizer. J. Range Manage. 29:214–216.

Jaramillo, V.J., and J.K. Detling. 1988. Grazing history, defoliation, and competition: Effects on shortgrass production and nitrogen accumulation. Ecology 69:1599–1608.

Kapadia, Z.J., and F.W. Gould. 1964a. Biosystematic studies in the *Bouteloua curtipendula* complex. III. Pollen size as related to chromosome number. Am. J. Bot. 51:166–172.

Kapadia, Z.J., and F.W. Gould. 1964b. Biosystematic studies in the *Bouteloua curtipendula* complex. IV. Dynamics of variation in *B. curtipentula* var. *caespitosa*. Bull. Torrey Bot. Club 91:465–478.

Karl, M.G., R.K. Heitschmidt, and M.R. Haferkamp. 1999. Vegetation biomass dynamics and patterns of sexual reproduction in a northern mixed-grass prairie. Am. Midl. Nat. 141:227–237.

Kipple, G.E., and J.L. Retzer. 1959. Response of native vegetation of Central Great Plains to application of corral manure and commercial fertilizer. J. Range Manage. 12:239–243.

Kneebone, W.R. 1956. Breeding for seedling vigor in sand bluestem (*Andropogon hallii* Hack) and other native grasses. Agron. J. 48:37–40.

Lauenroth, W.K., J.L. Dodd, and P.L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in semiarid grassland. Oecologia 36:211–222.

Lauenroth, W.K., and D.G. Milchunas. 1991. Short-grass steppe. p. 183–226. *In* R.T. Coupland (ed.) Natural grasslands: Introduction and western hemisphere. Ecosystems of the World, 8A. Elsevier, New York.

Lauenroth, W.K., O.E. Salz, D.P. Coffin, and T.B. Kirchner. 1994. The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. Ecol. Appl. 4:741–749.

Launchbaugh, J.L. 1962. Soil fertility investigations and effects of commercial fertilizers on reseeded vegetation in west-central Kansas. J. Range Manage. 15:27–34.

Lauver, C.L., K. Kindscher, D. Faber-Langendoen, and R. Schneider. 1999. A classification of the natural vegetation of Kansas. Southwest. Nat. 44:421–443.

Lee, C.A., and W.K. Lauenroth. 1994. Spatial distributions of grass and shrub root systems in the shortgrass steppe. Am. Midl. Nat. 132:117–123.

Majerus, M. 1975. Response of root and shoot growth of three grass species to decreases in soil water potential. J. Range Manage. 28:473–476.

MacMahon, J.A., and F.H. Wagner. 1985. The Mojave, Sonoran and Chihuahuan Deserts of North America. p. 105–202. *In* M. Evenari et al. (ed.) Ecosystems of the world 12A. Hot deserts and arid shrublands. Elsevier, Amsterdam.

Major, R.L., and L.N. Wright. 1974. Seed dormancy characteristics of sideoats gramagrass. Crop Sci. 14:37–40.

McDonald, M.B., and L.O. Copeland. 1997. Seed production. Principles and practices. Chapman and Hall, New York.

McGinnies, W.J., W.A. Laycock, T. Tsuchiya, C.M. Yonker, and D.A. Edmonds. 1988. Variability within a native stand of blue grama. J. Range Manage. 41:391–395.

McMillan, C. 1959. The role of ecotypic variation in the distribution of the central grassland of North America. Ecol. Monogr. 29:285–308.

McMillan, C. 1961. Nature of the plant community. VI. Texas grassland communities under transplanted conditions. Am. J. Bot. 48:778–785.

Milchunas, D.G., J.R. Forward, and W.K. Lauenroth. 1994. Productivity of long-term grazing treatments in response to seasonal precipitation. J. Range Manage. 47:133–139.

Miller, R.F., and G.B. Donart. 1979. Response of *Bouteloua eriopoda* (Torr.) Torr. and *Sporobolus flexuosus* (Thurb.) Rybd. to season of defoliation. J. Range Manage. 32:63–67.

Minnick, T.J., and D.P. Coffin. 1999. Geographical patterns of simulated establishment of two *Bouteloua* species: Implications for distributions of dominants and ecotones. J. Veg. Sci. 10:343–356.

Mohamed, A.H., and F.W. Gould. 1966. Biosystematic studies in the *Bouteloua curtipendula* complex. V. Megasporogenesis and embryo sac development. Am. J. Bot. 53:166–169.

Monson, R.K., M.R. Sackschewsky, and G.J. Williams. 1986. Field measurements of photosynthesis, water-use efficiency, and growth in *Agropyron smithii* (C_3) and *Bouteloua gracilis* (C_4) in the Colorado shortgrass steppe. Oecologia 68:400–409.

Nason, D.A., R.L. Cuany, and A.M. Wilson. 1987. Recurrent selection in blue grama. I. Seedling water uptake and shoot weight. Crop Sci. 27:847–851.

National Research Council. 1971. Atlas of nutritional data on United States and Canadian feeds. Natl. Academy Press, Washington, DC.

National Research Council. 1996. Nutrient requirements of beef cattle. 7th ed. Natl. Academy Press, Washington, DC.

Neilson, R.P. 1986. High-resolution climatic analysis and Southwest biogeography. Science (Washington, DC) 232:27–34.

Nelson, E.W. 1934. The influence of precipitation and grazing on black grama range. Tech. Bull. 409. USDA, Washington, DC.

Newbauer, J.J., L.M. White, R.M. Moy, and D.A. Perry. 1980. Effects of increased rainfall on native forage production in eastern Montana. J. Range Manage. 33:246–250.

Newell, L.C., and W.J. Moline. 1978. Forage quality evaluations of twelve grasses in relation to season of grazing. Res. Bull. 283. Nebr. Agric. Exp. Stn., Lincoln.

Newell, L.C., R.D. Staten, E.B. Jackson, and E.C. Conard. 1962. Side-oats grama in the central great plains. Res. Bull. 207. Nebr. Agric. Exp. Stn., Lincoln.

Olmstead, C.E. 1944. Growth and development in range grasses. IV. Photoperiodic responses in twelve geographic strains of side-oats grama. Bot. Gaz. 106:46–74.

Olmstead, C.E. 1945. Growth and development in range grasses. V. Photoperiodic responses of clonal divisions of three latitudinal strains of side-oats grama. Bot. Gaz. 106:382–401.

Painter, E.L., J.K. Detling, and D.A. Steingraeber. 1989. Grazing history, defoliation, and frequency-dependent competition: Effect on two North American grasses. Am. J. Bot. 76:1368–1379.

Painter, E.L., J.K. Detling, and D.A. Steingraeber. 1993. Plant morphology and grazing history: Relationships between native grasses and herbivores. Vegetatio 37:62.

Paulsen, H.A., and F.N. Ares. 1962. Grazing management of black grama and tobosa grasslands and associated shrub ranges of the southwest. Tech Bull. 1270. USDA, Washington, DC.

Peden, D.G., G.M. Van Dyne, R.W. Rice, and R.M. Hansen. 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. J. Appl. Ecol. 11:489–497.

Pfadt, R.E. 1994. Field guide to common western grasshoppers. Bull. 912. 2nd ed. Wyo. Agric. Exp. Stn., Laramie.

Phan, A.T. 2000. Genetic diversity of blue grama (*Bouteloua gracilis*) and little bluestem (*Schizachyrium scoparium*) as affected by selection. Ph.D. diss. Univ. of Manitoba, Winnipeg.

Phan, A.T., and S.R. Smith. 2000. Seed yield variation in blue grama and little bluestem plant collections in Manitoba, Canada.. Crop Sci. 40:555–561.

Phillips, J. 1999. Native grasses for high desert landscapes. Easy lawns. Low maintenance native grasses for gardeners everywhere. Brooklyn Botanic Garden, Brooklyn, NY.

Polley, H.W. 1997. Invited synthesis paper: Implications of rising atmospheric carbon dioxide concentration for rangelands. J. Range Manage. 50:561–577.

Posler, G.L., A.W. Lenssen, and G.L. Fine. 1993. Forage yield, quality, compatibility, and persistence of warm-season grass legume mixtures. Agron. J. 85:554–560.

Rauzi, F., and R.L. Lang. 1956. Improving shortgrass range by pitting. Bull. 344. Wyo. Agric. Exp. Stn., Laramie.

Rauzi, F., L.I. Painter, and A.K. Dobrenz. 1969. Mineral and protein contents of blue grama and western wheatgrass. J. Range Manage. 22:47–49.

Read, J.J., and J.A. Morgan. 1996. Growth and partitioning in *Pascopyrum smithii* (C_3) and *Bouteloua gracilis* (C_4) as influenced by carbon dioxide and temperature. Ann. Bot. 77:487–496.

Rees, R. 1978. Direct perception and pictorial perception of the prairie. Can. Geographer 22:343–345.

Reichhardt, K.L. 1982. Succession of abandoned fields on the shortgrass prairie, northeastern Colorado. Southwest. Nat. 27:299–304.

Riegel, A. 1940. A study in the variations in the growth of blue grama grass from seed produced in various sections of the Great Plains region. Trans. Kans. Acad. Sci. 43:155–171.

Riegel, A. 1941. Life history and habits of blue grama. Trans. Kans. Acad. Sci. 44:76–83.

Ries, R.E., and L. Hofmann. 1996. Perennial grass establishment in relationship to seeds dates in the Northern Great Plains. J. Range Manage. 49:504–508.

Rogler, G.A. 1943. Response of geographical strains of grasses to low temperatures. J. Am. Soc. Agron. 35:547–559.

Ruyle, G.B., and D.J. Young. 1997. Arizona range grasses. Their description, forage value, and grazing management. Ext. Publ. 197005. Ariz. Coop. Ext., Univ. of Ariz., Tucson.

Sala, O.E., and W.K Lauenroth. 1982. Small rainfall events: An ecological role in semiarid regions. Oecologia 53:301–304.

Sala, O.E., W.K. Lauenroth, and W.J. Parton. 1992. Long-term soil water dynamics in the shortgrass steppe. Ecology 73:1175–1181.

Sala, O.E., W.K. Lauenroth, and C.P.P. Reid. 1982. Water relations: A new dimension for niche separation between *Bouteloua gracilis* and *Agropyron smithii* in North American semi-arid grasslands. J. Appl. Ecol. 19:647–657.

Samuel, M.J., and R.H. Hart. 1994. Sixty-one years of secondary succession on rangelands of Wyoming. J. Range Manage. 47:184–191.

Samuel, M.J., and R.H. Hart. 1998. Nitrogen fertilization, botanical composition and biomass production on mixed-grass rangeland. J. Range Manage. 51:408–416.

Santos, G.L., and M.J. Trlica. 1978. Clipping effects on production and carbohydrate reserves of blue grama and western wheatgrass. Crop Sci. 17:384–386.

Schmutz, E.M., E.L. Smith, P.R. Ogden, M.L. Cox, J.J. Klemmedson, J.J. Norris, and L.C. Fierro. 1991. Desert grassland. p. 337–362. *In* R.T. Coupland (ed.) Natural grasslands: Introduction and western hemisphere. Elsevier, New York.

Schuman, G.E., J.D. Reeder, J.T. Manley, R.H. Hart, and W.A. Manley. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecol. Applic. 9:65–71.

Seastedt, T.R. 1995. Soil systems and nutrient cycles of the North American prairie. p. 157–174. *In* A. Joern and K.H. Keeler (ed.) The changing prairie. North American grasslands. Oxford Univ. Press, New York.

Simanton, J.R., and G.L. Jordan. 1986. Early root and shoot elongation of selected warm-season perennial grasses. J. Range. Manage. 39:63–67.

Sims, P.L, R.K. Lang'at, and D.N. Hyder. 1973. Developmental morphology of blue grama and sand bluestem. J. Range Manage. 26:340–344.

Sims, P.L., and P.G. Risser. 2000. Grasslands p. 323–356. *In* M.G. Barbour and W.D. Billings (ed.) North American terrestrial vegetation. 2nd ed. Cambridge Univ. Press, Cambridge.

Smith, G., J.L. Holechek, and M. Cardenas. 1996. Wildlife numbers on excellent and good condition Chihuahuan Desert rangelands: An observation. J. Range Manage. 49:489–493.

Smith, S.E. 1998. Variation in response to defoliation between populations of *Bouteloua curtipendula* var. *caespitosa* (Poaceae) with different livestock grazing histories. Am. J. Bot. 85:1266–1272.

Smith, S.E., R. Mosher, and D. Fendenheim. 2000. Seed production in sideoats grama populations with different grazing histories. J. Range Manage. 53:550–555.

Smith, S.R., D. Cattani, D. Feindel, R. Haas, D. Tober, L. Holzworth, M. Majerus, D. Hall, and K. Borcher. 1997. Native grass seed production manual. S.R. Smith and S. Smith (ed.) USDA-NRCS, Ducks Unlimited Canada, Manitoba Forage Seed Assoc., and Univ. of Manitoba, Abborg, MB.

Snyder, L.A., and J.R. Harlan. 1953. A cytological study of *Bouteloua gracilis* from western Texas and eastern New Mexico. Am. J. Bot. 40:702–707.

Stanton, N.L., D. Morrison, and W.A. Laycock. 1984. The effect of phytophagous nematode grazing on blue grama die-off. J. Range Manage. 37:447–450.

Stephens, G., and W.G. Whitford. 1993. Responses of *Bouteloua eriopoda* to irrigation and nitrogen fertilization in a Chihuahuan Desert grassland. J. Arid Environ. 24:415–421.

Streetman, L.J., and N. Wright. 1960. A cytological study of black gramagrass, *Bouteloua eriopoda*. Am. J. Bot. 47:786–793.

Stubbendieck, J., and D.F. Burzlaff. 1971. Nature of phytomer growth of blue grama. J. Range Manage. 24:154–156.

Stubbendieck J., S.L. Hatch, and C.H. Butterfield. 1992. North American range plants. 4th ed. Univ. of Nebraska Press, Lincoln.

Taylor, C.A., M.H. Ralphs, and M.M. Kothmann. 1997. Vegetation response to increasing stocking rate under rotational stocking. J. Range Manage. 50:439–442.

Thornber, J.J. 1910. The grazing ranges of Arizona. Bull. 65. Ariz. Agric. Exp. Stn., Tucson.

Trlica, M.J., M. Buwai, and J.W. Menke. 1977. Effects of rest following defoliations on recovery of several range species. J. Range Manage. 30:21–27.

Valentine, K.A. 1970. Influence of grazing intensity on improvement of deteriorated black grama range. Bull. 553. New Mexico Agric. Exp. Stn., Las Cruces.

Van der Sl uijs, D.H., and D.N. Hyder. 1974. Growth and longevity of blue grama seedlings restricted to seminal roots. J. Range Manage. 27:117–119.

Visher, S.S. 1954. Climatic Atlas of the United States. Harvard Univ. Press, Cambridge, MA.

Voigt, P.W., and H.W. Brown. 1969. Phenotypic recurrent selection for seedling vigor in side-oats grama, *Bouteloua curtipendula* (Michx.) Torr. Crop Sci. 9:664–666.

Voigt, P.W., and R.S. MacLauchlan. 1985. Native and other western grasses. p. 177–187. *In* M.E. Heath et al. (ed.) Forages. The science of grassland agriculture. 4th ed. Iowa State Univ. Press, Ames.

Voigt, P.W., C.R. Tischler, and B.A. Young. 1987. Selection for improved establishment in warm-season grasses. p. 177–187. *In* G.W. Frasier and R.A. Evans (ed.). Seed and seedbed ecology of rangeland plants. USDA-ARS, Springfield, VA.

Wasser, C.A. 1982. Ecology and culture of selected species useful in revegetating disturbed lands in the West. FWS/OBS-82/56. USDI-FWS, Washington, DC.

Watkins, W.E. 1943. Composition of range grasses and browse at varying stages of maturity. Bull. 311. N. Mex. Agric. Exp. Stn., Las Cruces.

Watts, J.G. 1965. *Chirothrips falsus* on black grama grass. Bull. 499. N. Mexico Agric. Exp. Stn., Las Cruces.

Weaver, J.E., and F.W. Albertson. 1956. Grasslands of the Great Plains. Johnsen Publ. Co., Lincoln, NE.

White, L.M. 1977. Perenniality and development of shoots of 12 forage species in Montana. J. Range Manage. 30:107–110.

White, L.M. 1986. Forage yield and quality of warm-and cool-season grasses. J. Range Manage. 39:264–268.

Wight, J.R. 1976. Range fertilization in the Northern Great Plains. J. Range Manage. 29:180–185.

Wilkinson, S.R., and G.W. Langdale. 1974. Fertility needs of the warm-season grasses. p. 119–145. *In* D.A. Mays (ed.) Forage fertilization. ASA, Madison, WI.

Wilson, A.M., and D.D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the Central Plains. J. Range Manage. 32:209–213.

Wilson, A.M., R.L. Cuany, J.G. Frazer, and W.R. Oaks. 1981. Relationships among components of seed yield in blue grama. Agron. J. 73:1058–1062.

Wilson, A.M., and J.A. Sarles. 1978. Quantification of growth drought tolerance and avoidance of blue grama seedlings. Agron. J. 70:231–237.

Wooten, E.O. 1916. Carrying capacity of grazing ranges in southern Arizona. Bull. 367. USDA, Washington, DC.

Wright, G.R, and G.M. VanDyne. 1976. Environmental factors influencing semidesert grassland perennial grass demography. Southwest. Nat. 21:259–274.

Wright, H.A. 1974. Effect of fire on southern mixed grass prairie grasses. J. Range Manage. 27:417–419.

Wright, H.A., and A.W. Bailey. 1982. Fire ecology. John Wiley & Sons, New York.

Wright, N., and L.J. Streetman. 1958. Past performance and future potential of black grama for southwestern ranges. J. Range Manage. 11:207–214.