Perenniality and Development of Shoots of 12 Forage Species in Montana

LARRY M. WHITE

A study was conducted to determine the perenniality and development of shoots of two sedges, four grass species of temperate origin, and six grass species of tropical origin. Floral shoots of sedges were at least 3 years old and had remained vegetative the first 2 years. Floral shoots of temperate-origin grasses varied between 2 and 3 years old, and those of tropical-origin, between 1 and 2 years old. By knowing the perenniality of floral shoots, it may be possible to develop management practices to change the ratio of floral to vegetative shoots.

Grazing management plans for native range in the northern Great Plains should include consideration of more than just the gross dynamics of the various plant communities or even individual plants. They need to include consideration of the perenniality and development of individual shoots. An established perennial grass or sedge consists of an uneven-aged stand of shoots, which emerge, grow, and die at rates dependent upon genetic and environmental factors (Langer 1958). Shoots arise from axillary buds of stem bases (crowns), rhizomes, or stolons, expand by vegetative growth, and eventually may reach reproductive status.

Shoots of many grasses live for more than one growing season before they flower. Flowering in perennial grasses involves three distinct phases: (1) juvenile, (2) induction, and (3) initiation of inflorescence (Calder 1966). Some grasses have an obligate vegetative (juvenile) stage, during which a shoot cannot be induced to flower even under the proper environmental conditions (Cooper and Calder 1964). A juvenile stage has been described in detail for only a few grasses, although a study by Cooper and Calder (1964) suggested that it is widespread in

temperate-origin grasses (generally these grasses have only the C3 photosynthetic pathway, Downton and Tregunna 1968). If shoots of many species of temperate-origin grasses or sedges do not complete the juvenile stage the first year, they can overwinter and continue growing the second year. Generally, shortened photo-periods or low temperatures (vernalization) or both are necessary for induction of many temperate-origin grasses (Evans 1964). Shoots that require vernalization are at least 2 years old when they flower. If a species requires both a juvenile stage and vernalization, it might be 3 years old when it flowers. Kirshin (1971) found that if shoots of meadow fescue (Festuca pratensis Huds.) and orchardgrass (Dactylis glomerata L.) did not develop to the 5th- and 6th-leaf stage the first year, they were not induced to flower until the fall of the second year and thus produced seed in the third year.

The age of shoots when they flower also depends upon environmental conditions. If adequate soil water and favorable temperatures are available long enough after floral induction, shoots of many species could flower that same year. However, in a temperate climate, if induction occurs in the fall from short days, temperatures are not favorable long enough for flowering that same year. If induction requires low temperatures, a shoot also cannot flower that same year.

Of the major grasses and sedges found in the northern Great Plains, little information was available on perenniality of floral shoots. In the central Great Plains, studies have only been conducted by Stubbendieck and Burzlaff (1971) and Sims et al. (1973) on blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.), and by Sims et al. (1973) on sideoats grama (*B. curtipendual* (Michx.) Torr.).

My objective in this study was to determine the age of floral shoots of two sedges—threadleaf (Carex filifolia Nutt.) and sun sedge (C. heliophila Mack.); four temperate-origin grasses -western wheatgrass (Agropyron smithii Rvdb.), prairie Junegrass (Koeleria cristata (L.) Pers.), needleandthread (Stipa comata Trin. and Rupr.), and green needlegrass (S. viridula Trin.); and six tropical-origin grasses—red threeawn (Aristida longiseta Steud.), sideoats grama, blue grama, prairie sandreed (Calamovilfa longifolia (Hook.) Scribn.), stoneyhills muhly (Muhlenbergia cuspidata (Torr.) Rydb.), and little bluestem (Schizachyrium scoparium Nash) (= Andropogon scoparius Michx.) in Montana.

Materials and Methods

The study was conducted near Sidney, Mont., on a glaciated plains sandy range site in 1971 and 1973. The soil is a Williams loam, a fine-loamy mixed, typic Argiborolls (classification by Soil Conservation Service). Grass and grasslike forage on the site by weight when clipped in early July to ground level was composed of western wheatgrass (23%), blue grama (20%), threadleaf sedge (19%), prairie Junegrass (16%), and needleandthread (12%), while sun sedge, green needlegrass, red threeawn, sideoats grama, prairie sandreed, stoneyhills muhly, and little bluestem composed less than 1% of the vegetation. Annual rainfall averages 34.5 cm, of which 44% falls from April through June. Frostfree period averages 122 days; mean January and July temperatures average -13 and 20°C, respectively.

Author is range scientist, U.S. Department of Agricultural Research Service, Northern Plains Soil and Water Research Center, P.O. Box 1109, Sidney, Montana 59270.

The study is a contribution from the U.S. Dep. Agr., Agr. Res. Serv., in cooperation with the Montana Agricultural Experiment Station, Bozeman. Journal Series No. 653.

Manuscript received May 17, 1976.

Rainfall from April through June of 1971 was only 1 cm less than normal. It was dry from April until appreciable rains occurred the last of May. July and August were extremely dry with only 14% of normal rainfall. Fall growth started after rains in early September. Rainfall from April through June in 1973 was 7 cm above normal, but deficient soil water limited growth until heavy rains in late April. Rainfall was below normal in May, but nearly twice normal in June. Deficient soil water again limited growth from late July until rains in early September initiated fall growth.

Every 2 weeks in 1971 and 1973, from start of growth until summer dormancy, I collected 4 or 5 plants of each species that produced shoots by tillering and 20 to 30 shoots of each species that produced shoots from rhizomes. In 1971, plants were dried in a herbarium press. However, leaves of these plants were difficult to handle because they were brittle. Plants in 1973 were collected in plastic bags, frozen, and later examined in a moist condition. Shoots were detached intact and the leaf stage was determined by counting the number of fully expanded leaves and adding one-half for the last leaf; it was only partially expanded. A leaf is fully expanded when its collar emerges from the sheath of the last leaf (Sharman 1942). On a tiller, the prophyll (two keeled, membranous sheath that contains an axillary bud or shoot) was counted as the first leaf; on shoots produced from a rhizome, the first leaf was counted as the one with a blade longer than 2 mm. Leaves of new tillers from the parent shoot were not counted.

The criteria used to determine age of floral shoots were the number of different groups (shoots at about the same leaf stage were considered as being in the same group) of shoots present in the spring, and the number of leaves they developed until summer dormancy that year. For example, in the spring, threadleaf sedge would generally have shoots in the following groups: just starting growth, 51/2-, 81/2-, and 111/2-leaf stages. Shoots which had started growing in the spring generally reached only the 5½-leaf stage by summer dormancy and did not flower that year; those 5½ reached 81/2; those 81/2 would either flower that year in the 10th-leaf stage or remain vegetative reaching the 11½-leaf stage. Shoots in the 11½-leaf stage would generally flower that year in the 13th-leaf stage.

The only alternative to the above method of determining age of floral shoots was to tag individual shoots in the field and periodically examine them. Field observation is hard because it is difficult to count the leaves without injuring the shoot as the base of the first few leaves is below ground. Also, in the field, a shoot in the crown of a bunchgrass would often be a month old before it was visible.

Table 1. Average leaf stage reached by several species at the end of each growing season.

Species	Origin of shoots	Growth sequence							
		First		Second		Third		Fourth	
		Veg.	Floral	Veg.	Floral	Veg.	Floral	Veg.	Floral
Sedges						***************************************			
Threadleaf	Tiller	51/2		81/2		111/2	10	141/2	13
Sun	Tiller	71/2	_	111/2	_	151/2	13	181/2	16
Sun	Rhizome ¹	81/2	<u> </u>	111/2		171/2	15		_
Cool-season									
Western wheatgrass	Rhizome ¹	41/2		101/2	10			_	_
Western wheatgrass	Tiller	51/2		121/2	13		_		_
Junegrass	Tiller	71/2		111/2	9	151/2	14		
Needleandthread	Tiller	41/2	_	91/2	_	131/2	13		_
Green needlegrass	Tiller	41/2		91/2			13		_
Warm-season									
Red threeawn	Tiller	51/2	7	_	8		_	_	_
Red threeawn	Tiller	81/2	_		12	_		_	
Sideoats grama	Rhizome ¹	4 1/2	_	_	10		_		_
Blue grama	Tiller	71/2		_	13		_	_	_
Prairie sandreed	Rhizome ¹	71/2	10	_	-	-		_	
Prairie sandreed	Tiller	61/2	_	_				_	_
Stoneyhills muhly	Rhizome ¹		7	_			_		_
Little bluestem	Tiller	121/2	13	_			_		

¹Counted only leaves with blades longer than 2 mm.

Results and Discussion

Age of floral shoots varies among species (Table 1). The average leaf stage attained each growth period is listed in Table 1. Floral shoots of sedges were at least 3 years old and had remained vegetative in the first 2 years; floral shoots of temperate-origin grasses varied in age between 2 and 3 years; and floral shoots of tropical-origin grasses were between 1 and 2 years old.

Floral shoots of sedges were older than those of other species. Floral shoots of both sedges remained vegetative and flowered the fourth year. I found no information of the flowering requirements of these two sedges. If both species have juvenile and vernalization requirements, this could possibly explain why floral shoots were 3 years old, like some shoots of meadow fescue and orchardgrass (Kirshin 1971). Slow growth and competition may also have delayed flowering until the third and fourth years.

Some of the tillers of western wheatgrass that reached the 4½-leaf stage by fall flowered the next year and those that did not all remained vegetative the next year. Western wheatgrass shoots originating from rhizomes also could either flower the next year or remain vegetative. Generally, very few tillers or shoots of western wheatgrass flowered. However, Coupland and Abouguendia (1974), in Canada, found that most shoots of western and thickspike wheatgrass (Agropyron dasystachyum (Hook.) Scribn.) lived for 3 years (species were not separated).

Most shoots of prairie Junegrass were 3 years old before they flowered, although some shoots were 2 years old. Prairie Junegrass initiated the floral primordia in the fall (Johnston and MacDonald 1967). Therefore, shoots must be at least 2 years old when they flower, but in my study, most were 3 years old. If a shoot of prairie Junegrass started growth in the fall and induction of that shoot did not occur until the next fall, it would be 3 years old when it flowered.

Most floral shoots of both green needlegrass and needleandthread were 3 years old. Apparently, shoots of green needlegrass did not require vernalization because they flowered a second time after heavy rains in August of 1968. Green needlegrass apparently requires a certain day length to flower because plants of green needlegrass placed in a greenhouse in early October did not flower until late May the next year. Why shoots of green needlegrass took 3 years to flower in the field is not known. Applying N fertilizer to green needlegrass in late fall did not increase the number of floral tillers the next vear, but did increase the number of vegetative tillers (White et al. 1972) suggesting that shoots of green needlegrass took more than 1 year to flower. In the study by White et al. (1972), apparently shoots of green needlegrass that produced seed in early July had started growth 2 years earlier in the fall

(3 years old) and those that produced seed in late July had started growth a year before in the spring (2 years old).

Most floral shoots of red threeawn were 2 years old when they flowered. The leaf stage reached the first year affected the leaf stage reached the second year. Shoots that flowered the first year generally did not produce seed and were only two-thirds as tall as those that flowered the second year.

Sideoats grama required 2 years to fower at Sidney. Sims et al. (1971) reported that in eastern Colorado some shoots of El Reno sideoats grama fowered the first year, and others the next year. Apparently, environmental conditions and possibly competition within a plant can affect how old a shoot is when it flowers.

Floral tillers of blue grama were 2 years old. Stubbendieck and Burzlaff (1971) reported the same age for floral tillers of blue grama in Nebraska, except tillers there usually reached only the 5½-leaf stage the first year. Sims et al. (1973) reported that some tillers of blue grama overwintered twice before flowering.

Shoots of prairie sandreed, stoneyhills muhly, and little bluestem did not overwinter in Montana. Both tillers and shoots (those originating from rhizomes) of prairie sandreed completed growth the same year they were initiated, unlike those that overwintered in Colorado (B. E. Dahl, personal communication). Generally, all tillers of prairie sandreed remained vegetative while some of the shoots from rhizomes flowered. However, in 1969, following heavy rains in late June, shoots originating from tillers all flowered but were only half as tall as those originating from rhizomes. All shoots of stoneyhills mully flowered, while tillers of little bluestem either flowered or remained vegetative, but none overwintered for either species.

Many tropical-origin grasses produced few if any flower stalks at Sidney some years because of deficient soil water in July. Soil water is usually available through June, thus allowing temperate-origin species to complete their growth cycle and flower (unpublished data).

Length of individual leaves of needleandthread and red threeawn was affected by the time of year they initiated growth. The length of leaves from numbers 1 through 11 on a shoot of needleandthread in early July was 15, 20, 50, 60, 140, 220, 70, 55, 65, 130, and 200 mm, respectively. Leaves number 5 and 6, which had started growth in the spring of the second growing season, were longer than those of the previous season. Leaves number 7 and 8 were short because they had completed growth in the late summer when lack of soil water limited growth. The first leaf produced the third season (leaf number 9) was short, but leaves number 10 and 11, produced during more favorable conditions, were long.

The perenniality and development of the 12 forage species apply only to the conditions that prevailed during the 2 years of this study. Under different environmental conditions, the growth sequence and age of floral shoots could be different. The perenniality and development of blue grama was the same in Montana as in the central Great Plains, but not for sideoats grama or prairie sandreed. If a species requires vernalization or develops its floral primordia in the fall, floral shoots are at least 2 years old. Usually, with fall rains, shoots produced only a few additional leaves, but did not flower because of vernalization or photoperiod requirements.

If adequate soil water and temperatures are available for a long enough time, species which normally take two or more years to flower can flower during the same year that the shoots were initiated if there is no vernalization or special photo-period requirement for floral induction. Species such as green needlegrass and blue grama have been observed to flower a second time the same year following heavy rains in August. These two species plus needleandthread and red threeawn have been observed to flower a second time (late August) during the same year when grown in a greenhouse with adequate water. The time required for a species to flower in the field can be different from what occurs under ideal conditions. Temperature or availability of soil water often limits the growth period in the field and thus extends the time required for an individual shoot to flower.

It is possible that management practices could be developed to change the ratio of floral to vegetative shoots by understanding the perenniality and development of shoots. Increasing the ratio of floral shoots could increase forage and seed production but decrease forage quality. A high ratio of

floral shoots would be valuable for seed, and possibly, hay production. Lawrence and Ashford (1964) found that Russian wildrye (Elymus junceus Fisch.) initiated floral shoots in September. If the floral primordia was allowed to elevate aboveground in the fall, low winter temperatures destroyed many of the floral primordia. Grazing or cutting this grass in the fall prevented elevation of floral primordia and increased winter survival and seed production the next year. Johnston and MacDonald (1967), in Canada, and Hodgson (1966), in Alaska, found that many temperate-origin grasses initiated floral primordia in the fall, the year before the shoots produced seed.

A lower ratio of floral to vegetative shoots would generally be more valuable if the forage was harvested by grazing unless grazing was done during a specific season and specific intensity of use. Floral shoots die after seed production and their nutritional value then rapidly decreases well below that of vegetative shoots (unpublished data). Vegetative shoots often continue to live, but old age and lack of soil water can eventually kill the shoot. Death of the leaf starts at the tip and gradually progresses toward the base. However, the degree of difference in both forage production and quality depends upon whether the vegetative shoots are culmed or culmless. Defoliants, like paraquat (1,1'-dimethyl-4,4'-bipyridinium), have been used to dessicate grass herbage and prevent quality deterioration in late stages of maturation herbage and prevent quality deterioration in late stages of maturation (Sneva 1967). Hyder and Sneva (1963) proposed a two-crop management plan for crested wheatgrass (Agropyron desertorum (Fisch.) Schult.) using heavy livestock grazing when the shoots were in the boot stage to remove floral primordia. Many more management practices could be developed to change the ratio of floral to vegetative shoots by understanding the perenniality and development of shoots.

Literature Cited

Calder, D. M. 1966. Inflorescence induction and initiation in the *Gramineae*, p. 59-73. *In:* F. L. Milthorpe and J. D. Ivins (ed.) The Growth of Cereals and Grasses. Butterworths, London.

Cooper, J. P., and D. M. Calder. 1964. The inductive requirements for flowering of some temperate grasses. J. Brit. Grassland Soc. 19:6-14.

Coupland, R. T., and Z. Abouguendia. 1974. Producers: V. Dynamics of shoot development

Project. Univ. of Saskatchewan, No. 51. 110 p. Downton, W. J. S., and E. B. Tregunna. 1968. Carbon dioxide compensation—its relation to photosynthetic carboxylation reactions, systematics of the Gramineae, and leaf anatomy. Can. J. Botany 46:207-215. Evans, L. T. 1964. Reproduction, p. 126-153. In: C. Barnard (ed.) Grasses and Grasslands. St. Martin's Press, New York. Hodgson, H. J. 1966. Floral initiation in Alaskan Gramineae, Bot. Gaz. 127:64-70. Hyder, D. N., and Forrest A. Sneva. 1963. Morphological and physiological factors affecting the grazing management of crested wheatgrass. Crop Sci. 3:267-271.

Johnston, A., and M. D. MacDonald. 1967.

in grasses and sedges. Tech. Rep. Matador

scabrella Torr, Can. J. Plant Sci. 47:577-583. Kirshin, I. K. 1971. The time of completing the autumn induction of flowering in winter perennial grasses. Botanicheskii Zhurnal 56(11): 1625-1631. (Ru, en) from Herb. Abst. 42: 1921 Langer, R. H. M. 1958. Changes in the tiller population of grass swards. Nature, London 182:1817-1818. Lawrence, T., and R. Ashford, 1964, Seed yield and morphological development of Russian wild ryegrass as influenced by grazing. Can. J. Plant Sci. 44:311-317. Sharman, B. C. 1942. Developmental anatomy of the shoot of Zea mays L. Ann. Bot. NS 6:245-282

Sims, Phillip L., Lucas J. Ayuko, and D. N.

Floral initiation and seed production in Festuca

Manage. 24:357-360.
Sims, Phillip L., Robert K. Lang'at, and D. N. Hyder. 1973. Developmental morphology of blue grama and sand bluestem. J. Range Manage. 26:340-344.
Sneva. Forrest A. 1967. Chemical curing of

Hyder. 1971. Developmental morphology of

switchgrass and sideoats grama. J. Range

range grasses with paraquat. J. Range Manage. 20:389-394.

Stubbendieck, J., and D. F. Burzlaff. 1971.

Nature of phytomer growth in blue grama.

J. Range Manage. 24:154-156.

White, Larry M., Clee S. Cooper, and Jarvis

H. Brown. 1972. Nitrogen fertilization and clipping effects on green needlegrass (Stipa

and quality. Agron. J. 64:328-331.

viridula Trin.): I. Development, growth, yield,