January 2004

FORAGE & GRAZING LANDS: Morphological Characteristics of Big Bluestem and Switchgrass Plants Divergently Selected for Seedling Tiller Number

Alexander J. Smart
South Dakota State Univ., Brookings, SD

Lowell E. Moser
University of Nebraska - Lincoln, lmoser1@unl.edu

Kenneth P. Vogel
University of Nebraska - Lincoln, Ken.Vogel@ars.usda.gov

FORAGE & GRAZING LANDS

Morphological Characteristics of Big Bluestem and Switchgrass Plants Divergently Selected for Seedling Tiller Number

Alexander J. Smart,* Lowell E. Moser, and Kenneth P. Vogel

ABSTRACT

Selection at the seedling stage in grass breeding would be useful if seedling traits were correlated to desired agronomic traits of mature plants. Objectives of this study were to determine if seedlings from big bluestem (*Andropogon gerardii* Vitman) and switchgrass (*Panicum virgatum* L.) populations that differ genetically in seedling tiller number differ in mature plant (i) morphological characteristics, (ii) forage yield managed by a three-cut harvest system or a single end-of-season harvest, and (iii) leaf elongation rate. Field experiments were conducted on a Kennebec silt loam soil (fine-silty, mixed, superactive, mesic Cumulic Hapludolls). In addition, greenhouse studies were conducted in 1999 through 2001. Seedlings from big bluestem and switchgrass populations that differed for seedling tiller numbers were transplanted into spaced-planted field nurseries and greenhouse pots for study. Leaf width, leaf length, plant height, number of tillers per plant, yield, and leaf elongation rate were measured. Mature plant morphological characteristics differed between multiple-tiller and single-tiller plant types for both big bluestem and switchgrass. There were no differences in forage yield for big bluestem plant types. Switchgrass single-tiller plant types yielded 200 g plant^{-1} more than multiple-tiller types when harvested only once. Leaf elongation rate was 22 and 28% greater for single-tiller types vs. multiple-tiller types for big bluestem and switchgrass, respectively. Selection at the seedling level for tiller number appears to be an effective method to develop genotypes differing in yield per tiller, which has been shown to affect herbage yield when grown in swards.

Selection at the seedling stage in grass breeding would be extremely useful if seedling traits were correlated to desired agronomic traits of mature plants. Selection for large leaf size in perennial ryegrass (*Lolium perenne* L.) and Italian ryegrass (*Lolium multiflorum* Lam.) resulted in decreased tillering and increased weight per tiller, but the opposite occurred when selection was made for high leaf appearance rate (Edwards and Cooper, 1963). In tall fescue (*Festuca arundinacea* Schreb.), seedling populations that were selected for high leaf extension rate produced higher yield per tiller and fewer tillers than seedling populations that were selected for low leaf extension rate (Skinner and Nelson, 1994). In reed canarygrass (*Phalaris arundinacea* L.), tillering was negatively correlated to specific leaf weight (dry weight per unit leaf area) (Topark-Ngram et al., 1977). The authors speculated that plants with low specific leaf weight used less photosynthate in leaves and more for tiller production than plants with high specific leaf weight that also tillered less.

Switchgrass and big bluestem populations that differ genetically for seedling tiller number at 6 to 8 wk after planting were developed by divergent selection for seedling tiller number in two cycles (generations) of breeding using stratified mass selection for seedling shoot number and shoot weight followed by mating the selected plants in isolated polycross nurseries (Smart et al., 2003a). This produced four populations [big bluestem high seedling weight, multiple tiller (BMT); big bluestem high seedling weight, single tiller (BST); switchgrass high seedling weight, multiple tiller (SMT); and switchgrass high seedling weight, single tiller (SST)]. In greenhouse evaluation studies, big bluestem and switchgrass populations that differed in seedling tiller number also differed for seedling shoot weight (Smart et al., 2003a, 2003b). Single-tiller Cycle 2 seedling populations had greater shoot weight than multiple tiller Cycle 2 seedling populations or base populations for both species (Smart et al., 2003a). In field evaluation trials, populations selected for different seedling tiller traits of these two species did not differ in establishment capability primarily because selection did not alter seedling root morphology or development (Smart et al., 2003b).

Previous work with cool-season grasses has shown that selection at the seedling level was successful in developing populations that differed in forage yield under different management systems (Nelson et al., 1977; Jones et al., 1979; Zarrough and Nelson, 1980; Zarrough et al., 1983). The relationship between seedling tiller number and mature plant traits and herbage yield for the populations that we have developed has not been reported.

Objectives of this study were to test the hypotheses that seedlings from big bluestem and switchgrass populations that differ genetically in seedling tiller number at 6 to 8 wk of age differ in (i) mature plant morphological characteristics, (ii) mature plant forage yield managed by a three-cut harvest system or a single end-of-season harvest, and (iii) mature plant leaf elongation rate.

A.J. Smart, South Dakota State Univ., Dep. of Animal and Range Sci., Box 2170, Brookings, SD, 57007-0392; L.E. Moser, Agron. and Hortic. Dep., 279 Plant Sci., P.O. Box 830915, and K.P. Vogel, USDA-ARS, 344 Keim Hall, Univ. of Nebraska, P.O. Box 830937, Lincoln, NE 68583. A contribution of the University of Nebraska Agricultural Research Division, Lincoln, NE 68583. Journal Series No. 14074. Received 15 Apr. 2003. *Corresponding author (alexander_smart@sdstate.edu).

Published in Crop Sci. 44:607–613 (2004).

677 S. Segoe Rd., Madison, WI 53711 USA

Abbreviations: BMT, big bluestem high seedling weight, multiple tiller; BST, big bluestem high seedling weight, single tiller; SMT, switchgrass high seedling weight, multiple tiller; SST, switchgrass high seedling weight, single tiller.

MATERIALS AND METHODS

Mature Plant Morphological Characteristics

The breeding procedures used to develop the divergently selected plant populations have been described previously by Smart et al. (2003a). Seedlings were grown in a greenhouse during the winter of 1999 and 2000 in super-cell cone-tainers[1] (Stuewe & Sons, Inc., Corvallis, OR) containing a potting mixture of soil, peat, and vermiculite in a volume ratio of 2:1:1, respectively. Specific seedling types were selected from each of four populations for use in the study. These were BMT, BST, SMT, and SST (Smart et al., 2003a). Seedlings were selected each year by use of visual ratings from each population that were representative of the specific population. Seedlings from multiple-tiller Cycle 2 populations had three tillers each, and seedlings from single-tiller Cycle 2 populations had one tiller each.

On 19 May 1999 and 10 May 2000, 50 seedlings from each population were transplanted to the field on the East Campus (40°49′ N, 96°42′ W) and 10 km east at the Havelock Agronomy Farm of the University of Nebraska at Lincoln, respectively. The soil was a Kennebec silt loam soil at both sites. Seedlings were 16 and 12 wk old in 1999 and 2000 at time of transplanting, respectively. Four plants per row were spaced-planted into 50 rows equally spaced at 1 m between and within rows. Experiments were kept weed free by rototilling, hand weeding, and a single postemergence application of atrazine [6-chloro-*N*-ethyl-*N*′-(1-methylethyl)-1,3,5-triazine-2,4-diamine] at 2.24 kg ha^{-1}. No fertilizer applications were made. The experimental design was a randomized complete block with 50 replications. A single plant served as the experimental unit and a group of four plants within one row served as a block. Treatments consisted of a two-by-two factorial with species being the first factor and seedling type (seedling consisting of one or three tillers) as the second factor. No irrigation was used in 1999, but in 2000, seedlings were irrigated frequently by hand after transplanting because of low spring rainfall. On 20 Aug. 1999 and 17 Aug. 2000, plant height, number of tillers, leaf length, and leaf width were measured on each plant. Plant height was measured from the soil surface to the tip of the inflorescence. Length and width of leaves were measured on the most recent fully collared leaf from 10 and five randomly selected vegetative tillers from each plant in 1999 and 2000, respectively.

Harvest Management

Multiple Harvests

A three-cut harvest system was imposed on Rows 1 through 25 during the second production year from the 1999 transplants. First-year residue was removed on 13 Mar. 2000 by a prescribed burn and plants were not irrigated or fertilized. First, second, and third cuts occurred on 25 May, 13 July, and 1 Sept. 2000, respectively. Cutting height was 15 cm from the soil surface and tillers were harvested by hand with grass shears. All tillers were counted 1 d before each harvest date. Harvested plants were dried in a forced-air drier at 60°C for 72 h, weighed, and separated into leaf blade and stem (including leaf sheaths).

[1] Names of products are included for the benefit of the reader and this does not imply endorsement by the USDA or the University of Nebraska.

Single End-of-Season Harvest

A single harvest was taken on Rows 26 through 50 of the 1999 transplants during the second production year on 10 Oct. 2000. Transplants from 1999 were allowed to grow without any defoliation during the growing season of 2000 and were not irrigated or fertilized. First-year residue was removed on 13 Mar. 2000 by a prescribed burn. Cutting height was 2.5 cm above the soil surface and tillers were harvested by hand with grass shears. Number of tillers and fresh weight of each plant were recorded. A subsample (approximately 250 g fresh weight) was taken from each plant, dried in a forced-air oven at 60°C for 72 h and weighed to determine moisture concentration. Yield per plant and yield per tiller were adjusted to 100% dry matter.

Greenhouse Experiments

Leaf elongation and leaf appearance rate experiments were conducted at the USDA-ARS Forage Research Laboratory greenhouse in Lincoln, NE. Plants for study were selected from plants grown in cone-tainer cells planted in the greenhouse in January 1999 and March 2000. Seedlings were grown in a potting mixture containing soil, peat, and vermiculite in a volume ratio of 2:1:1, respectively. Ten big bluestem and switchgrass seedlings from each population described earlier were used for study based on a visual rating for large plant size and tiller number. Seedlings used in the studies from multiple-tiller Cycle 2 populations had three tillers each and seedlings from single-tiller Cycle 2 populations had one tiller each at 8 wk after planting.

In Exp. I (1999), 16-wk-old seedlings were transplanted on 21 May 1999 to pots 15 cm tall and 7.5 cm in diam. filled with the same potting mixture described earlier. Pots were arranged in the greenhouse as a randomized complete block design with 10 replications. Treatments consisted of a two-by-two factorial with species being the first factor and seedling type (seedling consisting of one or three tillers) as the second factor. Pots were well watered and fertilized once with 25 g of 20-9-16 (N-P-K) fertilizer. In August 1999, tiller number and plant height were measured. Pots then were moved to the field and inserted into the ground such that the pots were level with the soil surface. Plants were watered as needed during the fall and allowed to go dormant under natural conditions. On 29 Dec. 1999, pots were removed from the field and moved back into the greenhouse in the same experimental design arrangement and residual material was clipped at 2.5 cm above the soil surface and removed. Plants were well watered but no fertilizer was added.

Three tillers in each pot were marked, and leaf elongation measurements began when the third leaf became visible, starting on 21 Jan. 2000. Each leaf was measured daily from the collar of the second oldest collared leaf to the leaf blade tip of the emerging leaf. Leaf appearance rate was calculated as the difference in days between appearance of the third and fourth leaves. Leaf length and leaf width were measured on the third leaf after the collar was fully formed. Leaf width was measured at the widest portion of the leaf blade. Plant height was measured from the soil surface to the extended tip of the last leaf of the tallest tiller. Thirty days after initial measurements, tillers in all pots were cut at a 2.5-cm height and the number of tillers was recorded. The harvested material from each pot was dried at 60°C in a forced-air oven for 72 h. Samples were separated into leaf and stem components by separating leaf blades at the collar. Leaf sheaths were left with the stem fraction.

In Exp. II (2000), 12-wk-old seedlings were transplanted into the field in 1-m spaced rows in a Kennebec silt loam soil on 10 May 2000. On 25 August, plant height was measured and tillers were counted for each plant. On 20 November, plants were excavated from the soil and placed in the same-sized pots as used in Exp. I, with little disturbance of the root–soil interface, and moved into the greenhouse. Pots were well watered and fertilized with 5 g (equivalent to 50 kg ha^{-1}) of 20-9-16 (N-P-K) fertilizer once per week when new growth initiated, beginning 11 Dec. 2000. Measurements of leaf elongation rate, leaf appearance rate, leaf width, leaf length, plant height, number of tillers per plant, and yield were made by the same procedure described for Exp. I. The greenhouse temperatures were kept at 20/30°C night/day and plants were grown under natural light conditions for both experiments. Daylength ranged from 9.9 to 11 h and 9.5 to 9.7 h for Exp. I and II, respectively.

Statistical Analysis

Analysis of variance was performed on all variables using SAS (1999) PROC MIXED. Mean differences were considered statistically significant at the $\alpha = 0.05$ level. Species were analyzed separately because the species used are very different in morphological characteristics and the main emphasis of this study was to compare the two different plant types. Combined analysis across years was conducted on mature plant morphological characteristics measured in the field and greenhouse experiments. Response variables included plant height, leaf width, leaf length, number of tillers per plant, leaf elongation rate, and leaf appearance rate. The following linear additive model describes the independent variables which were used to analyze the response variables for each species:

$$Y_{ijk} = \mu + \text{Exp}_i + \text{block} \times \text{Exp}_{ij} + \text{population}_k + \text{Exp} \times \text{population}_{ik} + \text{error}_{ijk}, \quad [1]$$

where Y_{ijk} is the response variable in the experimental unit from the ith experiment, jth block, and kth population. The overall mean is μ, Exp_i is the ith experiment, block × Exp_{ij} is the jth block nested in the ith experiment, population_k is the kth population, Exp × population_{ik} is the ith experiment × kth population interaction, and error_{ijk} is the error from the ith experiment, jth block, and kth population.

Multiple harvest response variables included number of tillers per plant, leaf-to-stem ratio, yield per plant, leaf yield per plant, stem yield per plant, yield per tiller, leaf yield per tiller, and stem yield per tiller. The following linear additive model describes the independent variables which were used to analyze the response variables for each species:

$$Y_{ijk} = \mu + \text{block}_i + \text{population}_j + \text{cutting date}_k + \text{population} \times \text{cutting date}_{jk} + \text{error}_{ijk}, \quad [2]$$

where Y_{ijk} is the response variable in the experimental unit from the ith block, jth population, and kth cut. The overall mean is μ, block_i is the ith block, population_j is the jth population, cutting date_k is the kth cutting date, population × cutting date_{jk} is the jth population × kth cutting date interaction, and error_{ijk} is the error from the ith block and jth population. Cutting dates were analyzed as a repeated measure. The analyses were computed using PROC MIXED (SAS Institute, 1999) with a compound symmetry model that adequately accounted for error correlation during the three cutting dates.

The single end-of-season harvest response variables included plant height, number of tillers per plant, yield per plant, and yield per tiller. The following linear additive model describes the independent variables which were used to analyze the response variables for each species:

$$Y_{ij} = \mu + \text{block}_i + \text{population}_j + \text{error}_{ij}, \quad [3]$$

where Y_{ij} is the response variable in the experimental unit from the ith block and jth population. The overall mean is μ, block_i is the ith block, population_j is the jth population, and error_{ij} is the error from the ith block and jth population.

RESULTS AND DISCUSSION

Mature Plant Morphological Characteristics

Experiment × plant type interaction effects for plant height, leaf width, and leaf length were not significant on big bluestem and switchgrass transplants measured in August, approximately 100 d after transplanting. Experiment × plant type interaction for number of tillers per plant was significant only for switchgrass; however, it only accounted for 3% of the total variation. Mature BMT plants were not different from BST plants in plant height (Table 1). Leaf length measured from vegetative tillers was similar between plant types. However, BST plants had 2 mm wider leaves from vegetative tillers and 32 fewer tillers $plant^{-1}$ than BMT plants. Switchgrass single-tiller types were taller, had longer and wider leaves, and had 39 fewer tillers $plant^{-1}$ than SMT types.

These results with switchgrass and big bluestem were consistent with morphological differences that have been shown in other grasses with genotypes differing in number of tillers per plant. Leaf width and leaf length have been negatively correlated with tiller number in perennial ryegrass, reed canarygrass, and tall fescue (Edwards and Cooper, 1963; Nelson et al., 1977; Zarrough et al., 1984). Multiple-tiller plant types had more tillers than single-tiller plants, which also was consistent with similar research with other grass species (Edwards and Cooper, 1963; Nelson et al., 1977; Topark-Ngram et al., 1977; Jones et al., 1979; Zarrough et al., 1984).

Harvest Management

Multiple Harvests

Big bluestem plant types were similar in total yield per plant or total leaf and stem yield per plant at each harvest except for greater stem yield per plant at the

Table 1. August plant height, leaf width, leaf length, and number of tillers per plant averaged across two experiments, measured on big bluestem and switchgrass mature plants from populations developed by divergent selection for seedling tiller number and high shoot weight at Lincoln, NE.

Species	Type†	Plant height	Leaf width	Leaf length	Tillers per plant
		cm	mm	mm	
Big bluestem	BMT	100	7	33	60
	BST	100	9	34	28
P		0.51	<0.01	0.33	<0.01
SE		5	0.2	1.1	3.1
Switchgrass	SMT	80	9	33	119
	SST	90	11	38	80
P		0.02	<0.01	<0.01	<0.01
SE		3	0.2	0.9	5.2

† Plant type BMT is big bluestem multiple-tiller Cycle 2, BST is big bluestem single-tiller Cycle 2, SMT is switchgrass multiple-tiller Cycle 2, and SST is switchgrass single-tiller Cycle 2.

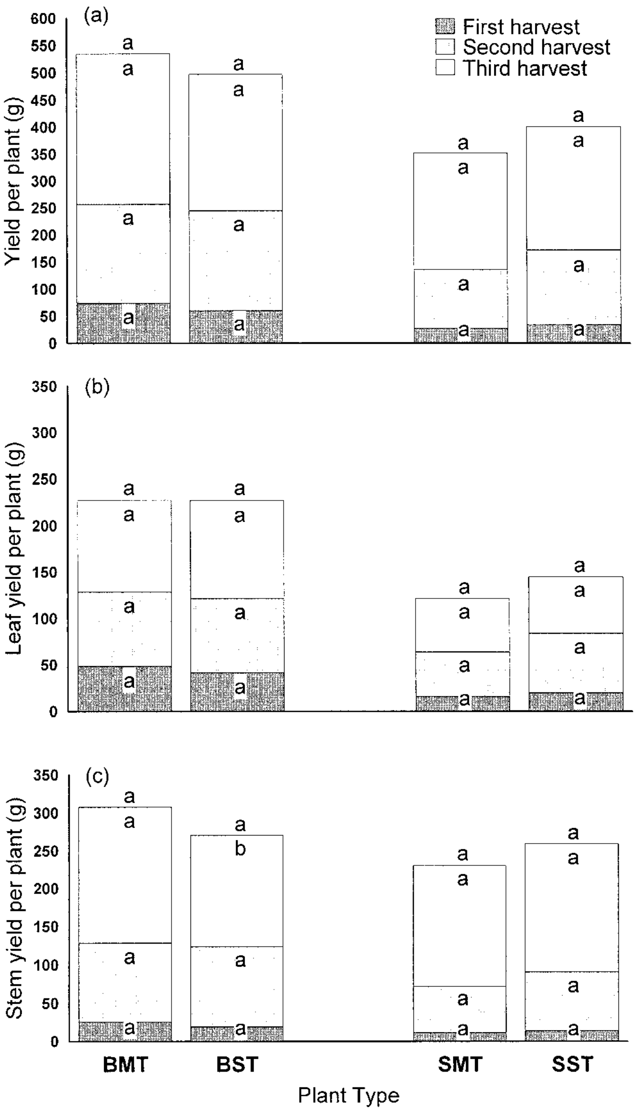

Fig. 1. (a) Yield per plant, (b) leaf yield per plant, and (c) stem yield per plant of a three-cut harvest management schedule on spaced-planted big bluestem and switchgrass plants from populations developed by divergent selection for seedling tiller number and high shoot weight. The first, second, and third harvests were on 25 May, 13 July, and 1 Sept. 2000, respectively. Similar letters within a harvest and species indicate no significant difference at $P > 0.05$. Plant type BMT is big bluestem multiple tiller Cycle 2, BST is big bluestem single-tiller Cycle 2, SMT is switchgrass multiple-tiller Cycle 2, and SST is switchgrass single-tiller Cycle 2.

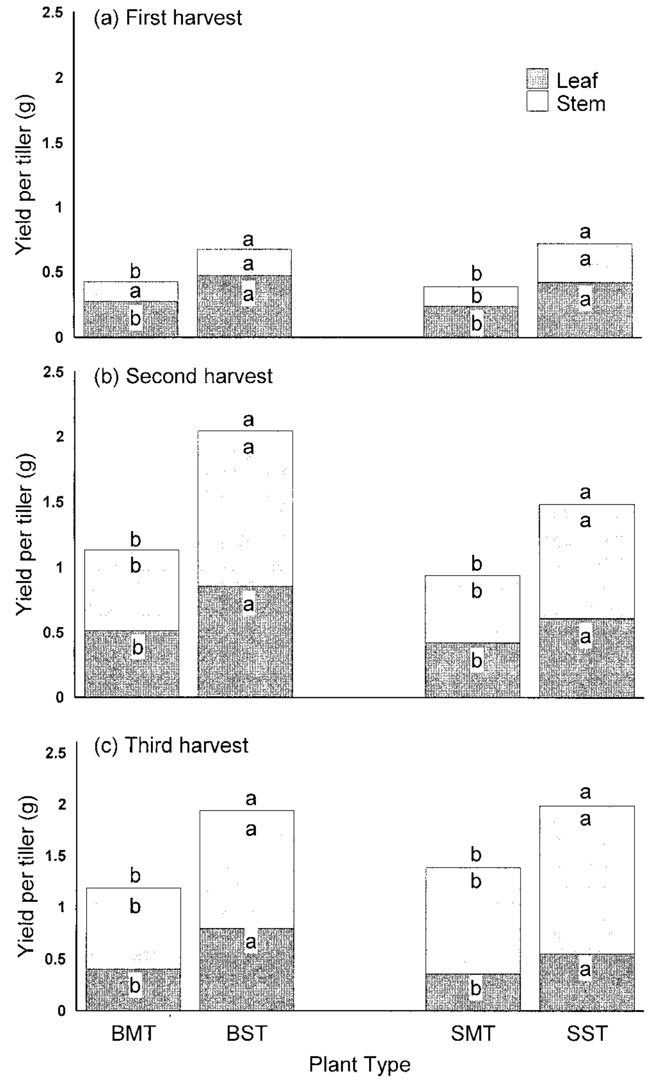

Fig. 2. Yield per tiller, stem yield per tiller, and leaf yield per tiller for the (a) first harvest, 25 May 2000; (b) second harvest, 13 July 2000; and (c) third harvest, 1 Sept. 2000 of a three-cut harvest management schedule on spaced-planted big bluestem and switchgrass plants from populations developed by divergent selection for seedling tiller number and high shoot weight. Similar letters within a plant fraction (stem or leaf) among plant types and species indicate no significant difference at $P > 0.05$. Plant type BMT is big bluestem multiple-tiller Cycle 2, BST is big bluestem single-tiller Cycle 2, SMT is switchgrass multiple-tiller Cycle 2, and SST is switchgrass single-tiller Cycle 2.

third harvest (Fig. 1). Yield per tiller was greater for BST plants than BMT plants at every harvest (Fig. 2). At the first harvest, big bluestem tillers had not elongated; therefore, yield per tiller difference was a result of greater leaf yield per tiller for BST plants than BMT plants. At later harvests, leaf and stem yield per tiller were greater for BST plants than BMT plants because plants were in the stem elongation growth phase. Number of tillers per plant was greater for BMT plants than BST plants at all three harvest dates (Table 2). Leaf-to-stem ratio was greater for BST plants than BMT plants at first and third harvests; however, the reverse was the case at second harvest.

Switchgrass plant types were similar in total yield per plant or total leaf and stem yield per plant at each harvest (Fig. 1). Switchgrass single-tiller plant types were consistently greater in yield per tiller at all three harvests than multiple-tiller plants (Fig. 2). Also, stem and leaf yield per tiller were greater for SST plants than SMT plants at each harvest. Number of tillers per plant was similar between SMT and SST types for the first two harvests, but SMT had 48 more tillers plant^{-1} than SST plants at the third harvest (Table 2). Leaf-to-stem ratio was similar between switchgrass plant type at all three harvests. It is unclear why tiller number was not greatly different between switchgrass plant types during the first two harvests. One possible explanation could

Table 2. Number of tillers per plant and leaf-to-stem ratio measured for three harvests during 2000 from second production year of big bluestem and switchgrass spaced-planted plants from populations developed by divergent selection for seedling tiller number and high shoot weight at Lincoln, NE.

		Number of tillers per plant			Leaf-to-stem ratio		
		Harvest date					
Species	Type†	25 May	13 July	1 Sept.	25 May	13 July	1 Sept.
Big bluestem	BMT	180	166	240	1.9	1.3	0.6
	BST	92	100	143	2.5	0.9	0.9
P		<0.01	<0.01	<0.01	<0.01	0.17	0.13
SE		17.6	17.6	17.6	0.21	0.21	0.21
Switchgrass	SMT	45	104	166	1.6	1.0	0.4
	SST	31	88	118	1.4	0.8	0.4
P		0.54	0.48	0.03	0.10	0.09	0.95
SE		22.6	22.0	21.6	0.12	0.11	0.11

† Plant type BMT is big bluestem multiple-tiller Cycle 2, BST is big bluestem single-tiller Cycle 2, SMT is switchgrass multiple-tiller Cycle 2, and SST is switchgrass single-tiller Cycle 2.

be that a 15-cm cutting height promoted tillering for the switchgrass single-tiller types.

In this study, plants were individually spaced-planted such that interplant competition for light, water, and nutrients was minimized. Thus, plant tillering was not hindered which resulted in similar yield per plant among the two plant types. This was especially evident in big bluestem because multiple-tiller types had almost 100 more tillers per plant at each cutting than single-tiller types (Table 2). These results were similar to results of tall fescue genotypes differing in yield per tiller (Zarrough and Nelson, 1980; Zarrough et al., 1983). Number of tillers has been shown to be more important in determining yield per plant under low competition than yield per tiller (Nelson et al., 1977). Such was the case in the three-cut harvest management system. However, under high competition (e.g., swards), yield per tiller of tall fescue became more important in determining yield than number of tillers (Zarrough et al., 1983). In tall fescue, frequency of tiller weight was evenly distributed for the high yield per tiller genotypes compared with a skewed distribution of tiller weights for the low yield per tiller genotypes, which was characterized by a large number of small tillers that contributed little to the overall yield of the plant (Jones et al., 1979). Although individual tillers were not measured in our study, similar tiller size distributions to that of tall fescue were observed in big bluestem and switchgrass.

Forage nutritive value might be improved by selecting for increased seedling tiller number in switchgrass and big bluestem because average mature plant tiller size was reduced in the multiple-tiller plant types. A negative relationship between tiller length and digestibility has been shown in the hybrid pearl millet [*Pennisetum glaucum* (L.) R. Br.] × elephantgrass (*Pennisetum purpureum* Schumach.) (Warndorf et al., 1987). Decline in stem digestibility was faster than leaf digestibility of big bluestem and switchgrass when the plant was in the rapid stem elongation period (Griffin and Jung, 1983). Plants with high yield per tiller and high yield potential (Zarrough and Nelson, 1980; Zarrough et al., 1983) may be of low digestibility because of high concentrations of lignin and other structural constituents needed to support large plant parts (Christensen et al., 1984). This might be more likely in the case of switchgrass than big bluestem because tiller number was not greatly different between plant types (Table 2), but yield per tiller was different (Fig. 2).

Single End-of-Season Harvest

Mature BMT plants averaged 130 more tillers per plant than BST plants at the end of the growing season (Table 3). Plant types were not significantly different in yield per plant, but BST plants had 2.2 times more yield per tiller than BMT plants. Switchgrass multiple-tiller plants had 60 more tillers than SST plants. Yield per plant was 200 g plant^{-1} greater for SST types than SMT types. Yield per tiller was 1.8 times greater for SST plants than SMT plants.

Big bluestem produced an average of 220 g plant^{-1} more ($P < 0.01$) when harvested once in October vs. being harvested three times during the growing season. Switchgrass produced an average of 510 g plant^{-1} more ($P < 0.01$) when harvested once in October vs. being harvested three times during the growing season. These results were consistent to reported harvest management of warm-season grasses (Sanderson, 2000).

Although yield per plant was not significantly different ($P > 0.05$) in this study among big bluestem plant types in spaced-planted plots, prior research in tall fescue showed that high yield per tiller genotypes planted

Table 3. Number of tillers per plant, yield per plant, and yield per tiller measured with a single end-of-season harvest on 10 Oct. 2000 from second production year of big bluestem and switchgrass spaced-planted plants from populations developed by divergent selection for seedling tiller number and high shoot weight at Lincoln, NE.

Species	Type†	Tillers per plant	Yield per plant	Yield per tiller
			g	
Big bluestem	BMT	226	680	4
	BST	96	740	9
P		<0.01	0.58	<0.01
SE		26.3	98	1.0
Switchgrass	SMT	293	840	3
	SST	233	1040	5
P		0.02	0.03	<0.01
SE		24.1	84	0.5

† Plant type BMT is big bluestem multiple-tiller Cycle 2, BST is big bluestem single-tiller Cycle 2, SMT is switchgrass multiple-tiller Cycle 2, and SST is switchgrass single-tiller Cycle 2.

in swards under infrequent harvests had higher yields than low yield per tiller genotypes (Zarrough and Nelson, 1980; Zarrough et al., 1983). Differences in yield per tiller between multiple-tiller plant types and single-tiller plant types may be caused by rate of tiller production, rate of tiller maturation, tiller size at maturation, and mortality rate of tillers (Jones et al., 1979). In yield analysis research with switchgrass, high-yielding switchgrass cultivars had a slow leaf appearance rate (Van Esbroeck et al., 1997) and an extended period of vegetative growth (Evans, 1993). Earlier-maturing switchgrass cultivars reached maximum leaf number at fewer growing degree-days and yielded less than later-maturing cultivars (Madakadze et al., 1998). Van Esbroeck et al. (1998) showed that by divergent selection for phyllochron (inverse of leaf appearance rate), they changed panicle emergence in switchgrass to 7 d earlier or 12 d later than the original population. Tiller size at maturation would seem to be very important in determining yield per tiller and thus overall plant yield in a single year-end harvest. Thus, a single-cut harvest management system suggested for biomass production (Sanderson, 2000) would favor high yield per tiller genotypes such as BST and SST plants.

Greenhouse Experiments

Number of tillers per plant and plant height were different among the two plant types in the autumn before the initiation of the two greenhouse experiments conducted to measure leaf elongation rate (Table 4). At the end of the two greenhouse experiments, approximately 60 d after plants were moved into the greenhouse, plant type effects explained the majority of the variation associated with leaf elongation rate and leaf appearance rate on big bluestem and switchgrass (Table 5). Leaf elongation rate averaged 22% greater for BST plants than BMT plants; however, leaf appearance rate was not different between plant types. Leaf elongation rate was 28% greater for SST plants than SMT plants, but leaf appearance rate was not different between plant types.

There have been similar findings for leaf elongation rate between genotypes that differed in number of tillers for tall fescue (Zarrough et al., 1984), perennial and Italian ryegrasses (Edwards and Cooper, 1963), and reed canarygrass (Topark-Ngram et al., 1977). Although not significantly different in this experiment, leaf appearance rate has been shown to be faster for genotypes with more tillers than genotypes with less tillers (Edwards and Cooper, 1963; Topark-Ngram et al., 1977; Zarrough et al., 1984). Grasses selected for traits such as leaf area expansion (Reeder et al., 1984), leaf elongation (Horst et al., 1978), and specific leaf weight (Topark-Ngram et al., 1977) indirectly altered number of tillers per plant.

Table 4. Number of tillers per plant and plant height measured in August averaged across two experiments before initiation of greenhouse experiments on big bluestem and switchgrass mature plants from populations developed by divergent selection for seedling tiller number and high shoot weight at Lincoln, NE.

Species	Type†	Tillers per plant	Plant height
			cm
Big bluestem	BMT	50	150
	BST	21	180
P		<0.01	<0.01
SE		5.7	12
Switchgrass	SMT	83	120
	SST	53	130
P		<0.01	<0.01
SE		6.6	5

† Plant type BMT is big bluestem multiple-tiller Cycle 2, BST is big bluestem single-tiller Cycle 2, SMT is switchgrass multiple-tiller Cycle 2, and SST is switchgrass single-tiller Cycle 2.

Table 5. Leaf elongation rate and leaf appearance rate averaged over two greenhouse experiments, measured on big bluestem and switchgrass mature plants from populations developed by divergent selection for seedling tiller number and high shoot weight at Lincoln, NE.

Species	Type†	Leaf elongation rate‡	Leaf appearance rate§
		mm d^{-1}	leaf d^{-1}
Big bluestem	BBMT-C2	20	0.26
	BBST-C2	25	0.24
P		<0.01	0.41
SE		1.1	0.03
Switchgrass	SWMT-C2	30	0.15
	SWST-C2	38	0.15
P		<0.01	0.85
SE		2.3	0.01

† Plant type BMT is big bluestem multiple-tiller Cycle 2, BST is big bluestem single-tiller Cycle 2, SMT is switchgrass multiple-tiller Cycle 2, and SST is switchgrass single-tiller Cycle 2.
‡ Leaf elongation rate mean of Leaves 3 and 4.
§ Leaf appearance rate between Leaves 3 and 4.

Morphological characters such as leaf width, leaf length, and plant height were positively correlated to yield characteristics (Table 6). Leaf elongation rate was negatively correlated to leaf appearance rate, but positively correlated to plant height, stem yield, and leaf and stem yield per tiller. Leaf appearance rate was negatively correlated to all characteristics. Number of tillers was negatively correlated to yield per tiller characteristics; however, it was positively correlated to yield on a per-plant basis. In general, the leaf and stem yield were positively correlated to all characteristics except leaf appearance rate, whereas leaf and stem yield per tiller were negatively correlated to both leaf appearance rate and number of tillers.

The general inverse relationship between leaf appearance rate and leaf length was supported by this study (Table 6) and others (Cooper and Edwards, 1960; Zarrough et al., 1984). Number of tillers per plant was inversely related to yield per tiller in this study and has been shown in other species mentioned earlier. In addition, plant height was correlated to leaf elongation rate, yield per plant, and yield per tiller. Because plant height was simple to measure in this study, and can be easily measured in the field compared with counting tillers, it could be an important trait to use in cultivar development.

In summary, mature plant morphological characteristics were different between multiple-tiller and single-tiller plant types of both big bluestem and switchgrass and generally were in agreement with research con-

Table 6. Correlation coefficients among plant characteristics and herbage yield averaged across two greenhouse experiments, measured on big bluestem and switchgrass plants from populations developed by divergent selection for seedling tiller number and high shoot weight at Lincoln, NE.

Character	Leaf width†	Leaf length‡	LER§	LAPR¶	Plant height	No. tillers	Leaf yield per plant	Stem yield per plant	Leaf yield per tiller	Stem yield per tiller	Yield per plant	Yield per tiller
Leaf width	–											
Leaf length	0.43*	–										
LER	0.74*	0.37*	–									
LAPR	−0.17	−0.63*	−0.08	–								
Plant height	0.51*	0.44*	0.54*	−0.07	–							
No. of tillers	0.20	0.10	0.31*	−0.04	0.18	–						
Leaf yield per plant	0.52*	0.28*	0.41*	−0.11	0.51*	0.80*	–					
Stem yield per plant	0.64*	0.49*	0.53*	−0.27*	0.64*	0.62*	0.89*	–				
Leaf yield per tiller	0.49*	0.41*	0.20	−0.18	0.66*	−0.23*	0.28*	0.41*	–			
Stem yield per tiller	0.56*	0.59*	0.32*	−0.34*	0.71*	−0.12	0.30*	0.60*	0.82*	–		
Yield per plant	0.58*	0.36*	0.46*	−0.17	0.57*	0.76*	0.99*	0.95*	0.34*	0.41*	–	
Yield per tiller	0.54*	0.51*	0.26*	−0.26	0.71*	−0.19	0.30*	0.52*	0.97*	0.94*	0.38*	–

* Significant at $P < 0.05$.
† Leaf width of Leaf 3.
‡ Leaf length of Leaf 3.
§ LER is leaf elongation rate and is the mean of Leaves 3 and 4.
¶ LAPR is leaf appearance rate and is between Leaves 3 and 4.

ducted on cool-season grasses. Selection for seedling tiller number significantly affected mature plant characteristics. Selection at the seedling level for tiller number can be effective in developing genotypes differing in yield per tiller, which could have significant impacts on cultivar development. Forage yield and nutritive value need to be evaluated on a sward basis for big bluestem and switchgrass genotypes differing in yield per tiller. This could be especially important for grasses managed for biomass that are harvested in a single cutting at the end of the season. In addition, multiple-tiller genotypes of big bluestem and switchgrass need to be evaluated for nutritive value and regrowth in sward conditions because of their potential to be better than single-tiller genotypes for use in pastures.

REFERENCES

Christensen, D.W., D.D. Stuthman, and A.W. Hovin. 1984. Associations among morphological and digestibility characters in reed canarygrass. Crop Sci. 24:675–678.

Cooper, J.P., and K.J.R. Edwards. 1960. Selection for leaf area in ryegrass. p. 71–75. *In* Report of the Welsh Plant Breeding Station for 1959. Plas Gogerddan, Aberystwyth, UK.

Edwards, K.J.R., and J.P. Cooper. 1963. The genetic control of leaf development in Lolium. II. Response to selection. Heredity 18: 307–317.

Evans, L.T. 1993. Crop evolution, adaptation and yield. Cambridge Univ. Press, Cambridge, U.K.

Griffin, J.L., and G.A. Jung. 1983. Leaf and stem forage quality of big bluestem and switchgrass. Agron. J. 75:723–726.

Horst, G.L., C.J. Nelson, and K.H. Assay. 1978. Relationship of leaf elongation to forage yield of tall fescue genotypes. Crop Sci. 18: 715–719.

Jones, R.J., C.J. Nelson, and D.A. Sleper. 1979. Seedling selection for morphological characters associated with yield of tall fescue. Crop Sci. 19:631–634.

Madakadze, I., B.E. Coulman, K. Stewart, P. Peterson, R. Samson, and D.L. Smith. 1998. Phenology and tiller characteristics of big bluestem and switchgrass cultivars in a short growing season area. Agron. J. 90:489–495.

Nelson, C.J., K.H. Asay, and D.A. Sleper. 1977. Mechanisms of canopy development of tall fescue genotypes. Crop Sci. 17:449–452.

Reeder, L.R., Jr., D.A. Sleper, and C.J. Nelson. 1984. Response to selection for leaf area expansion rate of tall fescue. Crop Sci. 24:97–100.

SAS Institute. 1999. SAS OnLine Doc. v. 8. SAS Inst., Cary, NC.

Sanderson, M.A. 2000. Cutting management of native warm-season perennial grasses: Morphological and physiological responses. *In* K.J. Moore and B.E. Anderson (ed.) Native warm-season grasses: Research trends and issues. CSSA Spec. Publ. 30. CSSA and ASA, Madison, WI.

Skinner, R.H., and C.J. Nelson. 1994. Role of leaf appearance rate and the coleoptile tiller in regulating tiller production. Crop Sci. 34:71–75.

Smart, A.J., L.E. Moser, and K.P. Vogel. 2003b. Establishment and seedling growth of big bluestem and switchgrass populations divergently selected for seedling tiller number. Crop Sci. 43:1434–1440.

Smart, A.J., K.P. Vogel, L.E. Moser, and W.W. Stroup. 2003a. Divergent selection for seedling tiller number in big bluesem and switchgrass. Crop Sci. 43:1427–1433.

Topark-Ngram, A., I.T. Carlson, and R.B. Pearce. 1977. Direct and correlated responses to selection for specific leaf weight in reed canarygrass. Crop Sci. 17:765–769.

Van Esbroeck, G.A., M.A. Hussey, and M.A. Sanderson. 1997. Leaf appearance rate and final leaf number of switchgrass cultivars. Crop Sci. 37:864–870.

Van Esbroeck, G.A., M.A. Hussey, and M.A. Sanderson. 1998. Selection response and development basis for early and late panicle emergence in Alamo switchgrass. Crop Sci. 38:342–346.

Warndorf, M., A. Dovrat, and T. Kipnis. 1987. The effects of tiller length and age on herbage quality of hybrid pennisetum canopies. Neth. J. Agric. Sci. 35:21–28.

Zarrough, K.M., and C.J. Nelson. 1980. Regrowth of genotypes of tall fescue differing in yield per tiller. Crop Sci. 20:540–544.

Zarrough, K.M., C.J. Nelson, and J.H. Coutts. 1983. Relationship between tillering and forage yield of tall fescue. I. Yield. Crop Sci. 23:333–337.

Zarrough, K.M., C.J. Nelson, and D.A. Sleper. 1984. Interrelationships between rates of leaf appearance and tillering in selected tall fescue populations. Crop Sci. 24:565–569.