Cultivar × Environment Interactions in Switchgrass

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ABSTRACT

Switchgrass (*Panicum virgatum* L.) is a widely adapted warm-season perennial that has potential as a bioenergy feedstock. The objectives of this study were to estimate the effect of harvest date on switchgrass cultivars at two locations in the north central USA and to determine the relative importance of cultivar × environment interactions for agronomic and biofuel traits of switchgrass. Six switchgrass cultivars were grown in southern Wisconsin and eastern South Dakota for 4 yr and harvested each year at three harvest dates (August, September, and October). Cultivars differed widely in biomass yield, but interacted with all environmental factors. Biomass yield did not respond consistently to harvest date, varying with cultivar, location, and year. Despite these interactions, cultivar rankings for biomass yield was consistent across harvest dates and years, but not locations. There was some preferential adaptation to either Wisconsin or South Dakota, related to longitude of the original germplasm collection site, also reflected by ground cover data. Reduced stands and biomass yields for the August harvest date in later years suggested that harvests delayed to late summer or early autumn may be beneficial in the long term. Mean dry matter, forage fiber, and lignin concentrations also varied among cultivars, consistently across locations and years. These three traits all increased with later harvest consistently across locations and years, but inconsistently among cultivars. It should be possible, through selection and breeding, to develop switchgrass germplasm with increased fiber and decreased lignin and ash, increasing the availability of fermentable sugars and decreasing the unfermentable and/or incombustible residues.

Switchgrass is a widely adapted warm-season perennial that has potential as a feedstock for bioenergy production. Switchgrass can produce a high yield of biomass across a wide geographic range; it is suitable for use on marginal, highly erodible, and droughty soils; it has potential for sequestering large amounts of atmospheric carbon in permanent grasslands; and it provides excellent nesting habitat for migratory birds (Moser and Vogel, 1995; Paine et al., 1996; Sanderson et al., 1996). The combination of heat, cold, and drought tolerance within the species results in an adequate level of adaptation for nearly all of the USA east of the Rocky Mountains and much of eastern Canada.

The large natural distribution of switchgrass has provided a wide array of germplasm, divided into a ploidy series from $2n = 2x = 18$ to $2n = 12x = 108$ and two cytotypes, upland and lowland. Upland and lowland types tend to be genetically and phenotypically distinct from each other (Gunter et al., 1996; Sanderson et al., 1996). Most switchgrass cultivars are either seed increases of source-identified collections or products of a limited number of breeding cycles (Alderson and Sharp, 1994). Therefore, much of the variation observed among cultivars is likely the result of natural selection and evolution within diverse edaphic and climatic zones. For example, latitude-of-origin has a large impact on biomass yield in extreme environments such as central Texas, where germplasms from more northern origins have progressively lower biomass yield (Sanderson et al., 1999).

Switchgrass biomass can be converted into energy by fermentation, gasification, or combustion (McLaughlin et al., 1999). A high fiber content, consisting largely of fermentable or combustible sugars, would be beneficial for each of these processes. Lignin is detrimental for fermentation, because it cannot be broken down during the process. Ash is detrimental for combustion, causing slagging and fouling of biomass boilers, increasing maintenance costs and creating a disposal problem for flyash (Miles and Miles, 1994). Switchgrass cultivars with high biomass production, combined with a high fiber concentration, low lignin, and low ash would be most desirable as general-purpose bioenergy feedstocks.

Cultivar × environment interactions are a frequent occurrence in biomass evaluations of switchgrass cultivars. Cultivar rankings and relative differences in biomass yield are frequently inconsistent across years, locations, and harvest managements (Hopkins et al., 1995a, b; Koshi et al., 1982; Sanderson et al., 1999). In some cases, cultivar × location interactions can be partly explained by the origin of a cultivar or germplasm (Hopkins et al., 1995a,b; Sanderson et al., 1999). However, while some germplasms are specifically adapted to certain environments, often reflecting characteristics of the environment, such as temperature or daylength (Sanderson et al., 1999), others have wider adaptations, unpredicted by their selection and/or collection history (Hopkins et al., 1995a,b).

The objectives of this study were to estimate the effect of harvest date on switchgrass cultivars at two locations in the north central USA and to determine the relative importance of cultivar × environment interactions for agronomic and biofuel traits of switchgrass.

MATERIALS AND METHODS

Six switchgrass cultivars were chosen for this study: Cave-in-Rock, Dacotah, Forestburg, Shawnee, Sunburst, and Trail-

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Abbreviations: ADF, acid detergent fiber; ADL, acid detergent lignin; NDF, neutral detergent fiber; SEP, standard error of prediction.

blazer. All are upland cytotypes (Hultquist et al., 1996). The cultivars were planted at Brookings, SD, and Arlington, WI, in May 1997. Soil types were Vienna silt loam (fine-loamy, mixed, frigid Calcic Hapludoll) at Brookings and Plano silt loam (fine-silty, mixed, mesic Typic Argiudoll) at Arlington. Plot sizes were 1.6 by 3.0 m at Brookings and 1.6 by 1.8 m at Arlington. Plots were seeded at a rate of 400 PLS m^{-2}, with a drill with press-wheel row openers and a seeding depth of 5 to 10 mm. Plots consisted of 10 rows spaced 15 cm apart.

The experimental design at each location was a split-plot in randomized complete blocks with five replicates at Arlington and four replicates at Brookings. Harvest dates were whole plots and cultivars were subplots. Three harvest dates generally corresponded to post-heading, based on the latest-heading cultivar (mid- to late August), about 1 mo later, and about 2 mo later. Weeds were controlled by occasional clipping and application of 0.45 kg a.i. ha^{-1} 2,4-D amine [(2,4-dichlorophenoxy) acetic acid] during the establishment year and by hand weeding in subsequent years.

Plots were fertilized in spring 1998 to 2001 with 112 kg N ha^{-1}. A swath was harvested from the center of each plot with a flail harvester (0.9 m wide at Arlington) or a sickle-bar mower (1 m wide at Brookings) at the designated harvest date. Plots were harvested for 4 yr. Dry matter concentration (hereafter referred to as dry matter) was determined on each plot using 0.5- to 1.0-kg samples dried at 60°C and used to adjust plot yields to a dry matter basis. Immediately following harvests at Arlington, dry-matter samples were clipped by hand from the edges of the harvested portion of the plot. Grab-samples of harvested biomass were used at Brookings. Ground cover, defined as ground area covered by crown tissue, was visually rated on all plots in early spring, approximately 2 wk following tiller emergence. Establishment was nearly 100% for all plots, so ground cover ratings were used as a measure of survival.

All dried samples from 1998 to 2000 were ground through a 1-mm screen of a Wiley-type mill, and then scanned with a near-infrared reflectance spectrophotometer. A calibration subset of 48 samples was drawn from the population of 486 samples by cluster analysis of the spectral reflectance values (Shenk and Westerhaus, 1991). The calibration samples were sequentially analyzed for neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), and ash by the procedures of Van Soest et al. (1991) with the exceptions that sodium sulfite and α-amylase were excluded from the NDF analysis. Values of NDF, ADF, ADL, and ash were predicted for all samples using a single calibration equation per variable, respectively: SEP = 8.4, 9.7, 4.6, and 3.1 g kg^{-1}; R^2 = 0.97, 0.97, 0.95, and 0.95. Ash was expressed on a dry matter basis, ADL was expressed on a NDF basis, and ADF data were not presented because of redundancy with NDF.

Data were analyzed by mixed models analysis, assuming all effects to be fixed, except replicates and all split-plot error terms. Year was considered as a repeated measure and modeled according to the appropriate covariance structure, as determined by the data (Littel et al., 1996). The effect of harvest date was split into two single-degree-of-freedom contrasts: linear and nonlinear. Principal components analysis of means over harvest dates and years was used to characterize the phenotypic relationship among the six cultivars at the South Dakota and Wisconsin locations. Rank correlation coefficients and Kendall's coefficient of concordance were used to assess the agreement in cultivar rankings across harvest dates (Conover, 1971).

RESULTS AND DISCUSSION

The six switchgrass cultivars varied for mean biomass yield, but their interactions with environmental factors were highly complex (Table 1). Six of 11 cultivar × environment interactions were significant ($P < 0.05$) for biomass yield, including interactions with all three environmental factors (locations, years, and harvest dates). These six switchgrass cultivars were highly unstable across the range of growing conditions encountered in this study.

The linear response to harvest date accounted for 75% of the cultivar × date interaction and approximately half of the higher order interactions for biomass yield shown in Table 1. Most of the individual regressions were linear for biomass yield, with very few showing significant deviations from linearity (Fig. 1). Therefore, all regressions were limited to the linear model for comparative purposes. Five of the six cultivars had both positive and negative responses to harvest date, depending on the location or year of harvest (Table 2; Fig. 1). These responses were not closely related to heading date of these five cultivars: Forestburg and Sunburst (2–10 August), Cave-in-Rock (8–12 August), and Shawnee and Trailblazer (10–20 August). For these cultivars, the harvest date response was highly unpredictable, more a function of location and year than of cultivar. Harvest date responses were so variable that average responses across locations and years were not significant for these five cultivars.

There was a general tendency for biomass response

Table 1. *P*-values for partial analyses of variance of six variables (NDF = neutral detergent fiber; ADL = acid detergent lignin) measured on six switchgrass cultivars evaluated at three harvest dates for 3 yr at two locations (Arlington, WI, and Brookings, SD).

Source of variation†	df‡	Biomass yield	Ground cover	Dry matter	NDF	ADL	Ash
Cultivar (C)	5	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
C×L	5	0.0004	<0.0001	0.0023	0.0025	0.5726	0.0325
C×Y	10	<0.0001	0.1912	0.2569	0.0552	0.0724	0.0207
C×L×Y	10	<0.0001	0.0002	0.1474	0.0019	0.3711	0.0182
C×D_L	5	0.0003	0.5937	<0.0001	<0.0001	0.0114	0.0953
C×D_N	5	0.1708	0.0001	0.9312	0.0002	0.0182	0.0306
C×D_L×L	5	0.4350	0.7033	0.6379	0.1136	0.0268	0.1364
C×D_N×L	5	0.0304	0.1490	0.5465	0.0831	0.0502	0.0609
C×D_L×Y	10	0.0592	0.2152	0.4338	0.1627	0.6089	0.0211
C×D_N×Y	10	0.0326	0.9172	0.1967	0.5801	0.6373	0.5568
C×D_L×L×Y	10	0.8644	0.9941	0.0049	0.0324	0.7322	0.1271
C×D_N×L×Y	10	0.4002	0.9919	0.0736	0.1846	0.4790	0.9180

† L = location, Y = year, D_L = harvest date:linear, and D_N = harvest date:non-linear.
‡ All terms involving 'Y' have 15 df for Biomass yield and Dry matter (4 yrs).

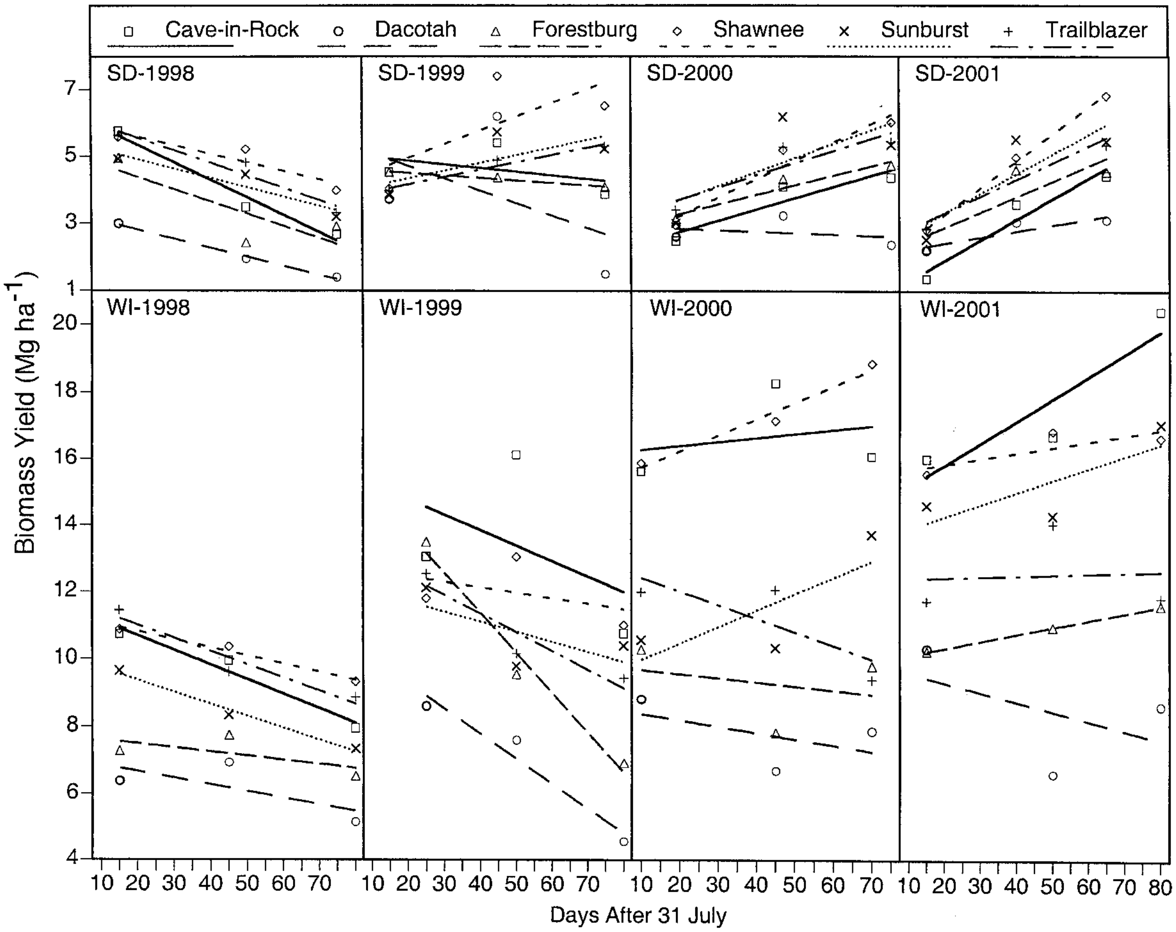

Fig. 1. Linear regressions of biomass yield on harvest date for six switchgrass cultivars evaluated at two locations (SD = Brookings, SD, and WI = Arlington, WI) for 4 yr.

to harvest date to become more positive with advancing years at each location (Table 2; Fig. 1). This observation could be explained partly by differential changes in ground cover. August-harvested plots suffered more severe ground cover loss (33% ground cover in 2001) than did September- and October-harvested plots (47 and 44% ground cover in 2001, respectively). Switchgrass plants in the August-harvested plots were apparently incapable of producing sufficient numbers of tillers or sufficiently large tillers to compensate for the stand losses imposed by this relatively early harvest date. Vogel et al. (2002) observed maximum biomass yields of switchgrass when the first harvest of a two-harvest system was taken between panicle emergence and postanthesis at locations between 41 and 42°N latitude. They did not observe differential ground cover responses to first-harvest date. Our observations suggest that, for more northern latitudes (43–44°N latitude), harvesting switchgrass preanthesis can have a severe long-term effect on ground cover, reducing stands and biomass yields over time. Switchgrass suffers from winter mortality at northern latitudes (Casler et al., 2002), an effect that may be enhanced by depletion of carbohydrate reserves following a mid-August harvest date. The minimal re-

Table 2. Linear regression coefficients for biomass yield regressed on harvest date of six switchgrass cultivars evaluated at two locations (Brookings, SD, or Arlington, WI) for 4 yr.

Cultivar	**SD 1998**	**SD 1999**	**SD 2000**	**SD 2001**	**WI 1998**	**WI 1999t**	**WI 2000t**	**WI 2001**	**Mean**
					kg ha^{-1} d^{-1}				
Cave-in-Rock	**−53.9****	**−10.4**	**32.1****	**57.0**	**−43.6***	**−42.7**	**10.0**	**66.4†**	**1.9**
Dacotah	**−27.9***	**−35.5**	**−4.5**	**17.0**	**−19.9**	**−73.8****	**−16.8**	**−28.0**	**−23.7***
Forestburg	**−37.7***	**−7.3**	**27.4****	**43.2**	**−12.2**	**−119.5****	**−10.3**	**20.9**	**−11.9**
Shawnee	**−26.2†**	**43.2†**	**52.3****	**74.1**	**−24.3**	**−14.8**	**46.7**	**17.6**	**21.1**
Sunburst	**−28.6***	**24.3**	**38.7***	**55.0**	**−35.8***	**−31.1**	**48.1†**	**36.5**	**13.4**
Trailblazer	**−38.3****	**22.5**	**34.2****	**46.7**	**−39.7***	**−56.1†**	**−39.4†**	**3.3**	**−8.3**
Mean	**−35.4****	**6.1**	**30.0****	**48.8**	**−29.2***	**−56.3***	**6.4**	**19.4**	

† Slope significantly different from zero at $P < 0.10$.
*** Slope significantly different from zero at $P < 0.05$.**
**** Slope significantly different from zero at $P < 0.01$.**

Table 3. Rank correlation coefficients between mean biomass yield at three harvest dates for six switchgrass cultivars evaluated at two locations (Brookings, SD, and Arlington, WI) for 4 yr.

Harvest dates	SD-1998	SD-1999	SD-2000	SD-2001	WI-1998	WI-1999	WI-2000	WI-2001
August vs. September	0.49	−0.54	0.66	0.71	0.83*	0.26	0.94**	0.89*
August vs. October	0.31	0.14	0.54	0.77	0.94**	0.03	0.83*	0.89*
September vs. October	0.94**	0.14	0.77	0.94**	0.94**	0.89*	0.77	0.83*
Kendall's Tau	0.72*	0.28	0.77*	0.87*	0.94*	0.59	0.90*	0.91*

* Rank correlation coefficient different from zero at $P < 0.05$. Kendall's Tau significant at $P < 0.05$, indicating concordance in cultivar ranking among the three harvest dates.

** Rank correlation coefficient different from zero at $P < 0.01$. Kendall's Tau significant at $P < 0.01$, indicating concordance in cultivar ranking among the three harvest dates.

growth following the September harvest and absence of regrowth following the October harvest would act to preserve carbohydrate reserves.

Dacotah was the only cultivar that showed any level of consistency in the harvest date response, with negative responses at seven of eight location–year combinations and a significant average response for biomass yield (Table 2; Fig. 1). Dacotah was extremely early in heading, generally about 2 to 3 wk earlier than the earliest of the other cultivars. This early heading date may have been responsible for the fairly consistent negative heading date response, with the earliest harvest date generally occurring after seed ripening of Dacotah.

Variation in linear responses to harvest date resulted in significant changes in ranking of the cultivars across harvest dates for biomass yield (Fig. 1; Table 3). However, Kendall's Tau, a measure of concordance in cultivar rank values across the three harvest dates, was significant for 3 of 4 yr at both locations, indicating a general agreement in cultivar rankings for these location–year combinations. This can also be observed in the relative lack of crossover among the harvest date regressions for the six cultivars (Fig. 1). While the linear responses to harvest date were highly variable among cultivars, locations, and years, this variability did not, on a broad scale, significantly alter cultivar rankings.

The extreme interactions between cultivars and harvest dates mirror the interactions between cultivars and harvest frequency observed in other studies. While a one-harvest management typically results in higher biomass production than a two-harvest management, cultivars do not always show a consistent harvest frequency effect (Koshi et al., 1982; Sanderson et al., 1999). Cultivar rankings changed dramatically between one- and two-harvest management systems, resulting in a few cultivars that had higher biomass yield under the two-harvest system (Sanderson et al., 1999). Furthermore, in the latter study, these interaction effects were inconsistent across locations and years, much as observed in our study (Tables 2 and 3; Fig. 1). Koshi et al. (1982) also observed a differential response to harvest frequency for three switchgrass strains.

Averaged over harvest dates, there was also broad concordance in cultivar rankings for biomass yield (Table 4). Dacotah ranked last for biomass yield in all location–year combinations. Forestburg ranked fifth for six of eight location–year combinations. Cave-in-Rock ranked first twice, Shawnee ranked first five times, and Sunburst ranked first once in biomass yield. Shawnee never ranked lower than second for biomass yield for all location–year combinations, demonstrating broad relative adaptation to both locations. Conversely, Cave-in-Rock ranked first, second, or third in biomass yield in Wisconsin, but fourth or fifth in South Dakota. Cave-in-Rock is a natural population collected in southern Illinois. Similarly, Trailblazer ranked second or third in South Dakota, but second or fourth in Wisconsin. Trailblazer derives from germplasm collected in Nebraska. These observations are supported by previous studies. Hopkins et al. (1995a) found Cave-in-Rock to rank higher in biomass yield at locations east of the Great Plains, compared with a location within the Great Plains. Similarly, Hopkins et al. (1995b) found Cave-in-Rock to rank higher in biomass yield than Trailblazer at locations east of the Great Plains, but lower than Trailblazer at a location within the Great Plains. Madakadze et al. (1998) also found that biomass yield of switchgrass in eastern Canada was higher for populations originating in the eastern USA than with those originating in central USA.

Cultivar × environment interactions for ground cover were relatively simple to interpret (Table 1). The cultivar × location interaction for ground cover reflected differential adaptation of the cultivars, while the cultivar × location × year interaction indicated a differential rate of ground cover loss for various cultivars at

Table 4. Mean biomass yield of six switchgrass cultivars evaluated at two locations (Brookings, SD, and Arlington, WI) for 4 yr.

Cultivar†	SD-1998	SD-1999	SD-2000	SD-2001	WI-1998	WI-1999	WI-2000	WI-2001	Mean
					Mg ha^{-1}				
Cave-in-Rock	3.97	4.60	3.67	3.14	9.55	13.32	16.66	17.71	9.08
Dacotah	2.12	3.81	2.75	2.81	6.16	6.93	7.81	8.53	5.11
Forestburg	3.44	4.34	4.08	3.83	7.19	10.00	9.32	10.95	6.64
Shawnee	4.93	5.99	4.73	4.89	10.20	11.96	17.31	16.36	9.55
Sunburst	4.19	4.93	4.86	4.51	8.45	10.77	11.55	15.33	8.07
Trailblazer	4.58	4.73	4.72	4.34	9.98	10.72	11.16	12.55	7.85
Mean	3.87	4.74	4.13	3.92	8.59	10.62	12.30	13.57	

† LSD(0.05) values for comparing cultivar means within columns are: 1.75 for SD, 1.57 for WI, and 0.58 for the overall mean. Means are over three harvest dates and four or five replicates.

Table 5. Mean ground cover of six switchgrass cultivars evaluated at two locations (Brookings, SD, and Arlington, WI) for 3 yr.

Cultivar†	SD-1998	SD-1999	SD-2000	WI-1998	WI-1999	WI-2000
	%					
Cave-in-Rock	100	100	60	100	82	76
Dacotah	100	100	87	100	63	48
Forestburg	100	100	80	100	69	47
Shawnee	100	100	76	100	67	64
Sunburst	100	100	81	100	86	70
Trailblazer	100	100	74	100	62	39

† LSD(0.05) values for comparing cultivar means within columns are: 8 for SD-2000, 7 for WI-1999 and WI-2000. Means are over three harvest dates and four or five replicates.

the two locations. Ground cover began to decline during or after the 1999 growing season in South Dakota and the 1998 growing season in Wisconsin (Table 5). Changes in ground cover were inconsistent across cultivars. Cave-in-Rock showed the largest ground cover reduction in South Dakota, while Dacotah, Forestburg, and Trailblazer showed the largest ground cover reductions in Wisconsin. These changes reflect the cultivar × location interaction for biomass yield, suggesting that Cave-in-Rock is better adapted to the Wisconsin location, while Trailblazer is better adapted to the South Dakota location. While the nonlinear portion of the cultivar × harvest date interaction was significant (Table 1), it made up only 3.4% of the total sum of squares for ground cover and consisted largely of apparently random changes in cultivar rankings. Rank correlations between harvest dates for ground cover ranged from $r = 0.60$ to 0.94, with a Kendall's Tau = 0.82 ($P < 0.05$), indicating concordance in cultivar ranking among harvest dates.

Although there was a cultivar × location interaction for dry matter (Table 1), it was largely due to changes in magnitude of cultivar means and involved only minor changes in ranking of cultivars, accounting for less than 1% of the sum of squares for dry matter. Most of the variation in dry matter was explained by cultivar means and the cultivar × harvest date interaction (Table 6; Fig. 2). The linear response to harvest date accounted for 97% of the cultivar × harvest date interaction (data not shown). Cultivar means and linear responses were highly correlated with each other and reflected, nearly perfectly, relative differences in heading date among cultivars. Early heading cultivars had the highest mean dry matter and the greatest response to harvest date. Early heading would be an advantage for production of field-dry biomass, but only if combined with rapid dry matter accumulation to produce a high biomass yield.

The negative correlation between dry matter and biomass yield (Tables 4 and 6) suggests that combining high biomass yield with high dry matter represents a formidable challenge for plant breeders. The number of phytomers (node + internode + leaf) is positively correlated with tiller biomass (Boe et al., 2000), suggesting that an increase in the number of phytomers may be a mechanism for increasing biomass yield of grasses. Late-heading cultivars have more phytomers than early heading cultivars of switchgrass (A. Boe, 2002, unpublished data). Late-heading cultivars tend to have higher biomass yields than early-heading cultivars of switchgrass (Madakadze et al., 1998; Newell, 1968; Sanderson et al., 1999). Early heading represents a developmental threshhold to the number of phytomers (Moore and Moser, 1995), limiting the mechanisms for continued biomass accumulation to dry matter accumulation in the developing caryposes and/or the production of new tillers. The optimal heading date for a switchgrass cultivar used as a bioenergy feedstock may be that which allows complete development of the maximum number of phytomers per tiller. Maintenance of a low dry matter concentration throughout the growing season (i.e., late heading) would also have the advantage of increasing total photosynthesis and carbon fixation, potentially increasing biomass production.

The cultivar × harvest date interaction for NDF concentration was largely consistent across locations and years, despite the statistical significance of a higher-order interaction term (Table 1), which only accounted for 13% of the sum of squares for interactions involving cultivars and harvest dates. Means and linear responses to harvest date for NDF followed the pattern observed for dry matter, with the exception of Dacotah (Table 6; Fig. 2). For the other five cultivars, mean NDF and linear response to harvest date were highly correlated with relative maturity, with late-heading cultivars having lower mean NDF concentration and lower NDF accumulation rates. Dacotah, the most early heading of the

Table 6. Means and linear responses to harvest date for dry matter, neutral detergent fiber (NDF), and acid detergent lignin (ADL) of six switchgrass cultivars. All values are averages over two locations (Brookings, SD, and Arlington, WI) and 3 yr.

Cultivar	Dry matter		NDF		ADL	
	Mean	Slope	Mean	Slope	Mean	Slope
	g kg^{-1}	g kg^{-1} d^{-1}	g kg^{-1}	g kg^{-1} d^{-1}	g kg^{-1} NDF	g kg^{-1} NDF d^{-1}
Cave-in-Rock	488	3.40	760	0.408	95	0.357
Dacotah	577	4.94	775	0.761	101	0.212
Forestburg	560	4.42	784	1.093	102	0.280
Shawnee	503	3.93	769	0.538	99	0.325
Sunburst	574	4.51	784	1.067	101	0.247
Trailblazer	506	3.74	777	0.724	101	0.268
LSD(0.05)	28		13		3	

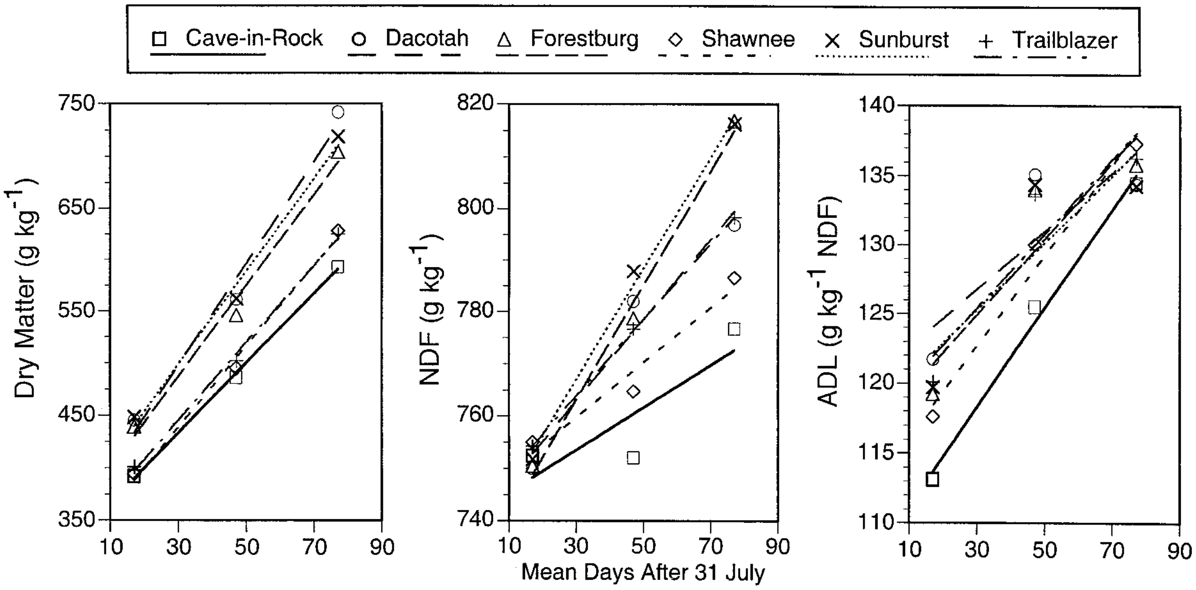

Fig. 2. Linear regressions of dry matter, neutral detergent fiber (NDF), and acid detergent lignin (ADL) concentrations on mean harvest date for six switchgrass cultivars evaluated at two locations (Brookings, SD, and Arlington, WI) for 3 yr.

cultivars, was the only exception to this, with mean NDF concentration and NDF accumulation rate similar to the late-heading cultivars. This observation probably relates to the low mean biomass yield and the rapid rate at which biomass yield of Dacotah is lost with delayed harvest date. Because NDF makes up such a large proportion of plant dry matter, whatever mechanism limits biomass yield accumulation in Dacotah at these locations, also likely limits cell-wall development. Biomass yield and NDF concentration are generally positively correlated in herbage grasses (Casler, 2001).

For NDF concentration, the interactions of cultivar with location and year were more important than the main effect of cultivar. Cultivar rankings were highly inconsistent across locations and years, with three cultivars ranking last and four cultivars ranking first at one or more location–year combinations (Table 7). The relative importance of cultivar × environment interaction for NDF concentration of switchgrass was similar to results of Hopkins et al. (1995a) for in vitro dry matter digestibility, which is often highly correlated with NDF (Casler, 2001). These observations differ from those made on forage crops that are harvested on a typical hay management scheme, in which genotype × environment interactions for NDF and other forage quality traits are generally not important (Casler, 2001; Casler and Vogel, 1999). Despite these interactions, there was some level of consistency, with Sunburst and Forestburg ranking first or second in NDF concentration for five of the six location–year combinations. These observations support the conclusions of Hopkins et al. (1995a) that the

Table 7. Mean neutral detergent fiber concentration of six switchgrass cultivars evaluated at two locations (Brookings, SD, and Arlington, WI) for 3 yr.

Cultivar†	SD-1998	SD-1999	SD-2000	WI-1998	WI-1999	WI-2000
	g kg^{-1}					
Cave-in-Rock	722	728	756	771	799	787
Dacotah	715	729	774	780	842	818
Forestburg	732	743	800	791	835	797
Shawnee	732	724	785	783	806	783
Sunburst	750	725	802	788	844	797
Trailblazer	732	751	781	787	821	790

† LSD(0.05) values for comparing cultivar means within columns are: 19 for SD and 17 for WI. Means are over three harvest dates and four or five replicates.

Table 8. Mean ash concentration of six switchgrass cultivars evaluated at two locations (Brookings, SD, and Arlington, WI) for 3 yr.

Cultivar†	SD-1998	SD-1999	SD-2000	WI-1998	WI-1999	WI-2000	Mean
	g kg^{-1}						
Cave-in-Rock	23	46	38	24	15	17	27
Dacotah	33	47	42	28	15	18	31
Forestburg	30	51	40	25	15	18	30
Shawnee	26	53	40	27	15	18	30
Sunburst	25	48	40	27	16	17	29
Trailblazer	29	50	41	27	17	20	31

† LSD(0.05) values for comparing cultivar means within columns are: 3 for SD, 3 for WI, and 2 for the overall mean. Means are over three harvest dates and four or five replicates.

Table 9. Eigenvalues of the first and second principal components (PRIN1, PRIN2) of the correlation matrix among six switchgrass variables measured at two locations (Brookings, SD, and Arlington, WI), averaged over three harvest dates and 3 or 4 yr.

	South Dakota		Wisconsin	
Variable	PRIN1	PRIN2	PRIN1	PRIN2
Biomass yield	−0.12	0.67	−0.46	−0.05
Ground cover	0.43	−0.38	0.38	0.52
Dry matter	0.51	−0.15	−0.28	0.92
NDF	0.32	0.53	0.48	0.20
ADL	0.48	0.32	0.49	0.05
Ash	0.46	0.00	0.31	−0.54
Percentage	57	31	68	24

suitability of switchgrass as a bioenergy feedstock can probably be improved by selection and breeding.

Lignin, measured as ADL in the NDF fraction, was relatively insensitive to cultivar × environment interactions (Table 1). Most of the variation in ADL among cultivars was explained by the cultivar main effect and by differences in rate of ADL accumulation with later harvest date (Table 6). Cave-in-Rock and Shawnee had the lowest mean ADL concentration, but the highest rate of ADL accumulation with later harvest date. This negative relationship between mean ADL and linear response to harvest date was caused by a compression of cultivar differences at the latest harvest date (Fig. 2). In turn, this observation appeared to be largely due to Cave-in-Rock, which had extremely low ADL at the first two harvest dates, but was more similar to the other cultivars at the third harvest date. While the relatively low lignin concentration would be advantageous for use of Cave-in-Rock as a biofuel, its relatively low NDF concentration would limit the production of fermentable sugars.

Although there was a fair amount of cultivar × environment interaction for ash concentration, Cave-in-Rock was consistently low, ranking lowest or tied for lowest at all six location–year combinations (Table 8). The relatively low ash concentration would make Cave-in-Rock more suitable than the other cultivars for cofiring in coal-fired power plants. Ash concentration increased with later harvest date ($b = 0.091 \pm 0.010$ g kg^{-1} d^{-1}; $P < 0.0001$), suggesting that hay produced from later harvests would be more detrimental for the cofiring process.

The first two principal components explained 88 and 92% of the variation among the six switchgrass cultivars in South Dakota and Wisconsin, respectively (Table 9). In South Dakota, the first component described high ground cover, dry matter, NDF, ADL, and ash; the second component described high biomass yield, NDF, ADL, and ash, but low ground cover. In Wisconsin, the first component described low biomass yield and dry matter with high ground cover, NDF, ADL, and ash; the second component described high ground cover and dry matter with low ash. The differences between the two locations can be attributed to differences in covariance structure among the six traits. In South Dakota, Cave-in-Rock and Dacotah appeared unique relative to the other cultivars (Fig. 3). Neither of these cultivars had superior biomass yield or survival at this location, but likely for different reasons. Cave-in-Rock was collected in southern Illinois and Dacotah was collected in south-central North Dakota. In Wisconsin, cultivar groupings were less obvious, but Cave-in-Rock was phenotypically distinct from the other cultivars, with the exception of Shawnee, which had relatively broad adaptation to both locations, as measured by both biomass yield and ground cover.

CONCLUSIONS

Biomass yield of switchgrass is unstable, varying by harvest date, site, year, and cultivar. Interactions among these factors cause biomass yield to be relatively unpredictable, particularly with respect to harvest date. For a single harvest of switchgrass, aimed at bioenergy feedstock production, the optimal harvest date was in late summer or early autumn, when soil and air temperatures are sufficiently low to minimize the potential for regrowth. In the short term, an earlier harvest date could increase biomass yields, but this would have detrimental long-term effects on stands. In the long term, plant mortality is apparently reduced by delayed harvest and preservation of carbohydrate reserves. Delayed harvest would have the further advantage of substantially in-

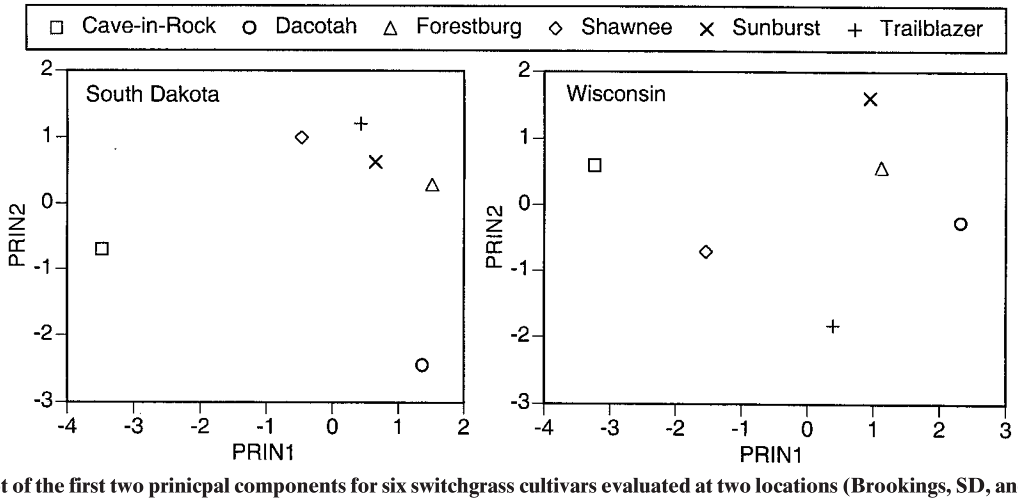

Fig. 3. Scatterplot of the first two prinicpal components for six switchgrass cultivars evaluated at two locations (Brookings, SD, and Arlington, WI).

creasing dry matter and NDF concentration. While ash concentration would increase with delayed harvest, this would only present a problem for switchgrass biomass to be cofired with coal for combustion.

The patterns of variation among switchgrass cultivars, including the cultivar × location interactions, suggest that switchgrass cultivars differ in their region of optimal adaptation. Broadly adapted, broadly unadapted, and specifically adapted germplasm of switchgrass can be identified. Cultivar differences in NDF, ADL, and ash further suggest that switchgrass cultivars vary in their suitability for bioenergy feedstock production. It should be possible, through selection and breeding, to develop switchgrass germplasm with increased NDF and decreased ADL and ash, increasing the availability of fermentable sugars and decreasing the unfermentable and/or incombustible residues.

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