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ABSTRACT

Switchgrass (*Panicum virgatum* L.) is a widely adapted warm-season perennial that has considerable potential as a biofuel crop. Evolutionary processes and environmental factors have combined to create considerable ecotypic differentiation in switchgrass. The objective of this study was to determine the nature of population × location interaction for switchgrass, quantifying potential differences in latitudinal adaptation of switchgrass populations. Twenty populations were evaluated for biofuel and agronomic traits for 2 yr at five locations ranging from 36 to 46° N lat. Biomass yield, survival, and plant height had considerable population × location interaction, much of which (53–65%) could be attributed to the linear effect of latitude and to germplasm groups (Northern Upland, Southern Upland, Northern Lowland, and Southern Lowland). Differences among populations were consistent across locations for maturity, dry matter, and lodging. Increasingly later maturity and the more rapid stem elongation rate of more southern-origin ecotypes (mainly lowland cytotypes) resulted in high biomass yield potential, reduced dry matter concentration, and longer retention of photosynthetically active tissue at more southern locations. Conversely, increasing cold tolerance of more northern-origin ecotypes (mainly upland cytotypes) resulted in higher survival, stand longevity, and sustained biomass yields at more northern locations, allowing switchgrass to thrive at cold, northern latitudes. Although cytotype explained much of the variation among populations and the population × location interaction, ecotypic differentiation within cytotypes accounted for considerable variation in adaption of switchgrass populations.

Switchgrass is a widely adapted warm-season perennial that has considerable potential as a biofuel crop. 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 the potential of 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 ecosystems east of the Rocky Mountains and south of Hudson Bay, including arid conditions in the shortgrass prairie to marshland and open woodland (Hitchcock, 1951).

Evolutionary processes including gene migration, random genetic drift, mutation, and natural selection combined with environmental variation due to latitude, altitude, soil type, and precipitation have resulted in significant genetic and phenotypic variation in switchgrass. Switchgrass has a ploidy series from $2n = 2x = 18$ to $2n = 12x = 108$ (Nielsen, 1944) and two distinct cytotypes, upland and lowland (Hultquist et al., 1996). Upland and lowland cytotypes tend to be genetically and phenotypically distinct from each other (Gunter et al., 1996; Sanderson et al., 1996). Latitude-of-origin has a large impact on productivity and survival of switchgrass strains that are evaluated in extreme environments, such as eastern Texas (Sanderson et al., 1999), suggesting genetic variation in adaptation. Genetic responses to latitude may be complex, resulting from genetic variation for photoperiodism, cold tolerance, or heat tolerance.

Despite the spread and duration of agriculture in eastern North America, there remain hundreds of remnant prairie sites, protected by public or private organizations (Hopkins et al., 1995b; Hultquist et al., 1997). Most switchgrass cultivars are either seed increases of source-identified collections or products of a limited number of breeding cycles tracing to many of these remnant prairie sites (Alderson and Sharp, 1994). Intensive selection and breeding of switchgrass began only during the last quarter of the 20th century (Moser and Vogel, 1995). Thus, the variability present among most cultivars and ecotypes should largely reflect natural variation for adaptation to specific climatic and edaphic conditions under which these local populations evolved.

The objective of this study was to determine the nature of population × location interaction for agronomic and biofuel traits of switchgrass, quantifying potential differences in latitudinal adaptation of switchgrass populations.

MATERIALS AND METHODS

Twenty switchgrass populations, originating from Texas to South Dakota (Table 1), were planted at five locations in spring 1998. Plot sizes were 1.4 × 1.7 m at Spooner, WI (45°49′ N, 91°54′ W); 1.7 × 1.8 m at Arlington, WI (43°20′ N, 89°23′ W); 1.5 × 3.8 m at Mead, NE (41°13′ N, 96°29′ W); 1.5 × 3.4 m at Manhattan, KS (39°25′ N, 96°35′ W); and 1.5 × 4.6 m at Stillwater, OK (36°7′ N, 96°5′ W). Soil types were Omega loamy sand (sandy, mixed, frigid Typic Haplorthod) at Spooner, Plano silt loam (fine-silty, mixed, superactive, mesic Typic Argiudoll) at Arlington, Sharpsburg silt loam (fine, smectitic, mesic Typic Argiudoll) at Mead, Haynie very fine sandy loam (coarse-silty, mixed, superactive, calcareous, mesic Mollic Udifluvent) at Manhattan, and Kirkland silt loam (fine, mixed, superactive, thermic Udertic Paleustoll) at Stillwater. Plots were seeded at a rate of 400 pure live seed m^{-2}. The experimental design at each location was a randomized com-

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Abbreviations: ADL, acid detergent lignin; IVDMD, in vitro dry matter digestibility; NDF, neutral detergent fiber.

Table 1. Source and origin of 20 switchgrass populations.

Population	Pedigree†	Origin	Cytotype	Latitude‡
'Trailblazer'	Ey × FF	NE, KS ecotypes	upland	N
HZ4 Syn2	ecopool	Zone-4 ecotypes	upland	N
HZ5 Syn2	ecopool	Zone-5 ecotypes	upland	N
EyxFF(HDMD)C3	Ey × FF	NE, KS ecotypes	upland	N
EyxFF(HYLD)C3	ecopopulation	NE, KS ecotypes	upland	N
'Summer'	ecotype	Nebraska City, NE	upland	N
'Sunburst'	ecopopulation	southeastern SD	upland	N
'Shelter'	ecotype	St. Mary's, WV	upland	N
'Forestburg'	ecotype	Forestburg, SD	upland	N
'Cave-in-Rock'	ecotype	Cave-in-Rock, IL	upland	S
'Shawnee'	Cave-in-Rock	Cave-in-Rock, IL	upland	S
'Blackwell'	ecotype	Blackwell, OK	upland	S
SU94-1	ecopopulation	southern OK and northern TX	upland	S
NU94-2	ecopopulation	northern OK to southern NE	upland	S
'Kanlow'	ecotype	Wetumka, OK	lowland	N
NL92-1	Kanlow	Wetumka, OK	lowland	N
NL94-1	Kanlow	Wetumka, OK	lowland	N
SL92-1	ecopopulation	central to southern TX	lowland	S
SL93-3	ecopopulation	central to southern TX	lowland	S
SL94-1	ecopopulation	central to southern TX	lowland	S

† Ecotypes are seed increases of accessions collected from prairie remnants. Ecopopulations are selections only one or two generations removed from wild ecotypes. Ecopools were developed by intercrossing unselected accessions collected from remnant prairies within a specific USDA plant hardiness zone (HZ).

‡ Northern and southern groups were defined according to their origin north or south of 40° N lat (Nebraska–Kansas border) for upland cytotypes or 34° N lat (the Red River border between Texas and Oklahoma) for lowland cytotypes.

plete block with three replicates at Spooner, four replicates at Manhattan, five replicates at Arlington and Stillwater, and six replicates at Mead.

Weeds were controlled at Arlington and Spooner by clipping and application of 0.45 kg a.i. ha^{-1} 2,4-D [(2,4-dichlorophenoxy) acetic acid] in 1998 and by an application of 0.69 kg a.i. ha^{-1} pendimethalin [N-(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzenamine] in May 1999 and 2000. At Stillwater, 0.28 kg ha^{-1} a.i. of dicamba (3,6-dichloro-o-anisic acid) + 0.80 kg ha^{-1} a.i. of 2,4-D was applied in 1998 and in late winter or early spring 1999 and 2000 for broadleaf weed control. At Mead and Manhattan, 2.2 kg ha^{-1} a.i. of atrazine [6-chloro-*N*-ethyl-*N*′-(1-methylethyl)-1,3,5-triazine-2,4-diamine] was applied preemergence in 1998. At Manhattan, 1.47 kg ha^{-1} a.i. of atrazine + 2.45 kg ha^{-1} a.i. of alachlor [2-chloro-*N*-2,6-diethylphenyl)-*N*-(methoxymethyl)-acetamide] was applied in the springs of 1999 and 2000. At Mead, 2.2 kg ha^{-1} a.i. of atrazine + 2.2 kg ha^{-1} metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl acetamide] + 1.1 kg ha^{-1} a.i. of 2,4-D were applied in May of 1999 and 2000.

Plots were fertilized in spring with 112 kg N ha^{-1}. Heading date of each plot was determined when a minimum of 10 heads had fully emerged from the boot. Plant height was measured to the top of the tallest stem just before harvest. Lodging was visually rated on each plot as a weighted-average deviation of tillers from vertical. Maturity of each plot was rated just before harvest by the visual numerical index of Moore et al. (1991).

A 0.9-m swath was harvested from the center of each plot with a flail harvester in late summer 1999 and 2000 after most populations had completed anthesis. Dry matter was determined on each plot with 0.5- to 1.0-kg samples. Data were not collected from Manhattan in 1999 due to low and nonuniform growth. Survival was measured as the percentage of 50 grids that contained living switchgrass following harvest in 2000. Grids were achieved by two random placements of a 0.75- × 0.75-m frame divided into 25 15- × 15-cm squares (Vogel and Masters, 2001). The frame was made from plastic-coated 5-mm steel rebar. Grid counts were equated to survival from the time of establishment to the time of measurement 28 mo later. Establishment was nearly 100% for all plots; therefore, loss of stand during that time can be attributed to tiller and/or plant mortality.

Dry-matter samples were ground through a 2-mm screen of a Wiley-type mill and a 1-mm screen of a cyclone mill and scanned on a near-infrared reflectance spectrophotometer (NIRS) at Lincoln, NE. A calibration set of 132 samples was chosen by cluster analysis of the reflectance data (Shenk and Westerhaus, 1991). Calibration samples were sequentially analyzed for neutral detergent fiber (NDF), acid detergent fiber, and acid detergent lignin (ADL) with the ANKOM Fiber Analyzer (ANKOM Technology Corp., Fairport, NY)[1] and the procedures described by Vogel et al. (1999). Samples were analyzed in duplicate for in vitro dry matter digestibility (IVDMD) with the ANKOM Rumen Fermenter and the procedures described by Vogel et al. (1999). Nitrogen concentration was determined by the LECO combustion method (Model FP 428, LECO Corp., St. Joseph, MI) (Watson and Isaac, 1990; Bremner, 1996). Laboratory mean values were used to develop calibration equations by partial least squares (Shenk and Westerhaus, 1991). Following calibration, holocellulose (cellulose + hemicellulose ≈ total structural sugars) was estimated as the difference between NDF and ADL, and lignin was expressed on an NDF basis. Values of NDF, ADL, IVDMD, and N were predicted for all samples with a single calibration equation per variable, respectively: SEP = 9.4, 3.2, 17.8, and 0.6 g kg^{-1}; R^2 = 0.92, 0.96, 0.96, and 0.99.

Data were analyzed by ANOVA assuming replicates and years to be random effects, locations and populations to be fixed effects. Population means were computed for each location, averaged across all replicates and years. Location means were subtracted from these means to provide deviations from location means for each population. For each population, these deviations were regressed on location latitude. Regressions were computed as linear contrasts using coefficients computed according to Carmer and Seif (1963) and tested according to Steel et al. (1996). Latitude and longitude are partially confounded in this experiment: the two northernmost locations are between 89 and 92°W and the three southernmost locations are between 96 and 97°W. Thus, the linear regression on latitude also includes some effect of longitude. However,

[1] Mention of trademark or brand names does not constitute an endorsement over any other product by USDA-ARS, USDA-NRCS, the University of Wisconsin, the University of Nebraska, or Oklahoma State University.

longitudinal variation per se between Wisconsin and the three southernmost locations likely represents little change in edaphic or climatic conditions; soils, humidity, and precipitation are generally similar. All five sites are located on soils that evolved under permanent grassland or, for Spooner, mixed grassland-woodland. The greatest gradients among these five locations are for temperature, daylength, and length of the growing season, all of which are consequences of latitude.

Populations were divided into four groups: Northern-Upland, Southern-Upland, Northern-Lowland, and Southern-Lowland. Northern and southern groups were defined according to their origin north or south of 40° N lat (Nebraska–Kansas border) for upland cytotypes or 34° N lat (the Red River border between Texas and Oklahoma) for lowland cytotypes. Among-group comparisons for means and linear regressions on latitude were made by orthogonal contrasts.

For each variable, the 5 × 20 matrix of population means for five locations was analyzed by Kendall's coefficient of concordance, which provides an overall measure of correlation among population rank values across the five locations (Conover, 1971). Principal components analysis was used to describe the overall differences among populations at each location by means for 10 traits: biomass yield, survival, plant height, maturity, lodging, dry matter, holocellulose, lignin, IVDMD, and N. Phenotypic correlations among traits were computed for each location and compared across locations by the homogeneity chi-square test (Steel et al., 1996). Path analysis (Wright, 1921) of biomass yield was conducted for each location, providing a measure of the direct effect of survival, maturity, plant height, lodging, dry matter, holocellulose, and lignin on biomass yield. Two traits, IVDMD and N, were excluded from the path analyses because they could not be inferred to have a unilateral direct causal effect on biomass yield. Path analysis was not conducted for Manhattan data because plant height and lodging were not measured at that location.

RESULTS AND DISCUSSION

Population × year interactions were generally nonsignificant. Phenotypic correlation coefficients between years were generally high within each location, indicating that relative population performance and ranking did not change significantly across years. This result is similar to other switchgrass results of Hopkins et al. (1995a and 1995b) and Sanderson et al. (1999). The population × year interaction accounted for <5% of the variance of a population mean for each variable (data not shown). Therefore, all further analyses and results are presented as means across years (Table 2).

The 10 traits fell into three categories based on the characteristics of their Population × Latitude (P × L) interaction (Table 2). Biomass yield, survival, and plant height all had P × L interaction that accounted for 25 to 48% of the variance of a population mean (Table 3). The linear effect of latitude accounted for a large portion of the P × L interaction for these three traits: 53 to 65% in the three degrees of freedom associated with origin and cytotype (4% of the P × L interaction df), plus an additional 4 to 9% associated with variation among populations within germplasm groups. At least 12 populations had significant linear regressions on latitude for these three variables. Finally, there was little concordance in population rank values across locations for these three variables.

Maturity, lodging, and dry matter all had very low P × L interaction, accounting for <7% of the variance of a population mean (Table 3). These three traits each had only one population with a significant linear regression on latitude and all had a high coefficient of concor-

Table 2. Mean squares from analyses of variance of 20 switchgrass populations evaluated at five locations.

Source of variation†	df	Biomass yield	Survival	Plant height	Maturity	Lodging
Origin (O)	1	31.9**	9 315.2**	7 922.9**	1.68**	450.1
Cytotype (C)	1	257.4**	34 119.4**	36 623.1**	71.24**	12 890.3**
O × C	1	281.5**	7 629.1**	1 383.4**	2.28**	2 191.8**
Population (P)/O × C	16	18.6**	172.8**	860.6**	0.35**	1 596.9**
Latitude × O	1	99.8**	7 923.5**	1 039.2**	0.69**	419.3
Latitude × C	1	512.8**	41 818.4**	26 104.6**	7.73**	0.3
Latitude × O × C	1	4.2	6 720.8**	2 591.5**	4.31**	1 183.5*
Latitude × P/O × C	16	4.1**	235.4**	252.3*	0.09**	514.0**
Location × O	3	7.0*	1 236.1**	380.4	0.35**	645.9*
Location × C	3	177.1**	5 644.2**	427.3*	1.42**	2 297.9**
Location × O × C	3	36.2**	1 909.5**	4 473.5**	0.03	1 201.6**
Location × P/O × C	48	3.1**	57.4	201.4	0.10**	536.6**
Error	342	1.6	51.1	137.5	0.03	201.9
		Dry matter conc.	Holocellulose conc.	Lignin conc.	IVDMD‡	N conc.
Origin (O)	1	1 506.5**	5 959.7**	9.6	37 523.6**	7.63**
Cytotype (C)	1	4 557.2**	2 026.4**	6 020.4**	33 689.3**	1.82
O × C	1	42.5	3 456.8**	223.9**	81.2	6.78*
Population (P)/O × C	16	55.0**	2 122.3**	110.6**	3 825.2**	1.56
Latitude × O	1	1.0	1 395.2**	181.0**	3 950.6**	16.91**
Latitude × C	1	1.0	12 283.4**	416.1**	22 181.5**	37.51**
Latitude × O × C	1	65.5*	187.5	16.3	554.0	13.43**
Latitude × P/O × C	16	33.2**	323.1**	36.7	801.2*	3.16**
Location × O	3	5.3	936.7**	180.4**	2 202.6**	2.26
Location × C	3	83.2**	1 386.4**	536.3**	7 253.5**	13.66**
Location × O × C	3	31.1*	493.9*	18.7	721.7	2.15
Location × P/O × C	48	12.6	232.6*	49.6**	907.4**	2.05**
Error	342	11.5	158.8	22.4	463.9	1.16

* MS significant at $P = 0.05$.
** MS significant at $P = 0.01$.
† *Latitude* is the linear effect of latitude. *Location* is the residual effect of location after accounting for the linear effect of latitude.
‡ IVDMD, in vitro dry matter digestibility.

Table 3. Characteristics of the population × location interaction for 20 switchgrass populations evaluated at five locations.

Variable	σ^2_{PL}†	Origin × Cytotype × Latitude (linear)‡	Population × Latitude (linear)§	No. regressions with $P < 0.05$¶	Coefficient of concordance
	%				
Biomass yield	50.2	52.8	58.4	12	0.29
Survival	35.1	63.2	67.4	17	0.38
Plant height	25.5	64.8	73.6	13	0.49
Maturity rating	6.6	52.4	58.2	1	0.78**
Lodging	1.8	4.5	27.8	1	0.71*
Dry matter	0.0	4.3	38.2	1	0.84**
Holocellulose conc.	16.8	35.9	49.2	10	0.50*
Lignin conc.	12.6	10.6	17.7	6	0.53*
IVDMD	14.2	23.5	34.8	6	0.48*
N conc.	33.2	25.0	43.7	9	0.16

* Coefficient of concordance significant at $P = 0.05$.
** Coefficient of concordance significant at $P = 0.01$.
† Variance component for population × location interaction expressed as a percentage of the variance of a population mean (76 df).
‡ Origin × Latitude (linear) + Cytotype × Latitude (linear) + Origin × Cytotype × Latitude (linear) with 3 df, as a percentage of the Population × Location interaction with 57 df.
§ Population × Latitude (linear) had 19 df, as a percentage of the Population × Location interaction with 57 df.
¶ Maximum of 20 significant regressions, one per population.

dance. The quantitative variation observed among populations for these three traits was relatively insensitive to environmental effects. Observations made on these populations for these three traits could be considered to be general characteristics of the populations, not dependent on the location in which they were made.

For maturity and dry matter, the main effect of populations was largely due to germplasm groups, accounting for 93 and 87% of the sum of squares for populations, respectively (Table 2). Germplasm group means for maturity were 4.3 for Northern Upland, 4.2 for Southern Upland, 3.3 for Northern Lowland, and 3.2 for Southern Lowland. Heading date data could not be uniformly analyzed and compared across all populations and locations because of the extreme late maturity of some lowland populations that showed no heading at some locations. For the upland types, the mean difference of 0.1 was equivalent to 4 d, which was consistent across locations. Lowland cytotypes were at least 2 to 4 weeks later in heading than upland cytotypes, observations supported by previous studies of ecotypic differentiation (McMillan, 1965).

Germplasm group dry matter means were 470 g kg^{-1} for Northern Upland, 436 g kg^{-1} for Southern Upland, 396 g kg^{-1} for Northern Lowland, and 378 g kg^{-1} for Southern Lowland. For lodging, germplasm groups accounted for 38% of the population sum of squares. Germplasm group lodging means were 28% for Northern Upland, 23% for Southern Upland, 9% for Northern Lowland, and 22% for Southern Lowland. The minimum and maximum for individual populations were 8 to 42% for upland cytotypes and 6 to 23% for lowland cytotypes. Lodging was not consistently related to lignin or holocellulose concentration ($r = -0.11$ to 0.63), but was partially related to maturity ($r = 0.38$ to 0.54) and to plant height ($r = -0.82$ to -0.47). However, the phenotypic correlations of lodging with maturity and plant height were largely due to differences between cytotypes for these two traits.

Finally, the concentration of holocellulose, lignin, N, and IVDMD fell into the third category, characterized by a moderate amount of P × L interaction (Table 3). This interaction accounted for 12 to 33% of the variance of a population mean. The linear effect of latitude accounted for a moderate amount of the P × L interaction, considerably less than that for biomass yield, survival, and plant height. Thus, the P × L interaction for these four variables was more a characteristic of the entire group of populations rather than of the four germplasm groups, as observed for biomass yield, survival, and plant height. There was also only a moderate agreement in population rankings across locations, as indicated by the presence of several significant linear regressions on latitude and only moderately high coefficients of concordance for three of the four traits in this group.

Linear regressions of biomass yield, expressed as deviations from location means, on latitude were separated into three discrete groups with either positive, negative, or nonsignificant slope (Fig. 1; Table 4). Upland cytotypes all had positive or nonsignificant slopes, indicating preferential adaptation to northern latitudes, or no preferential adaptation. Lowland cytotypes all had negative slopes, indicating preferential adaptation to southern latitudes. Within cytotypes, responses to latitude were differentiated by northern vs. southern origins. Northern-Upland populations had steeper slopes than Southern-Upland populations, resulting in similar biomass yields at the northernmost sites, but lower biomass yields at the southernmost sites. None of the Southern-Upland populations had a significant slope, while three of the six Northern-Upland populations with a significant slope (HZ4-Syn2, 'Sunburst', and 'Forestburg', originated in the northernmost portion of the range; Table 1). Southern-Lowland populations had a steeper negative slope than Northern-Lowland populations, resulting in similar biomass yields at the southernmost sites, but lower biomass yields at the northernmost sites. Relative to the experiment mean, Northern-Upland populations increased in biomass yield by an average of 3.0% for each degree of latitude, while Southern-Upland populations increased in biomass yield by an average of 1.2%. Northern-Lowland populations decreased in biomass yield by an average of 4.5% for each degree of latitude, while Southern-Lowland populations decreased in biomass yield by an average of 6.5%.

The convergence point, at which most of the crossover

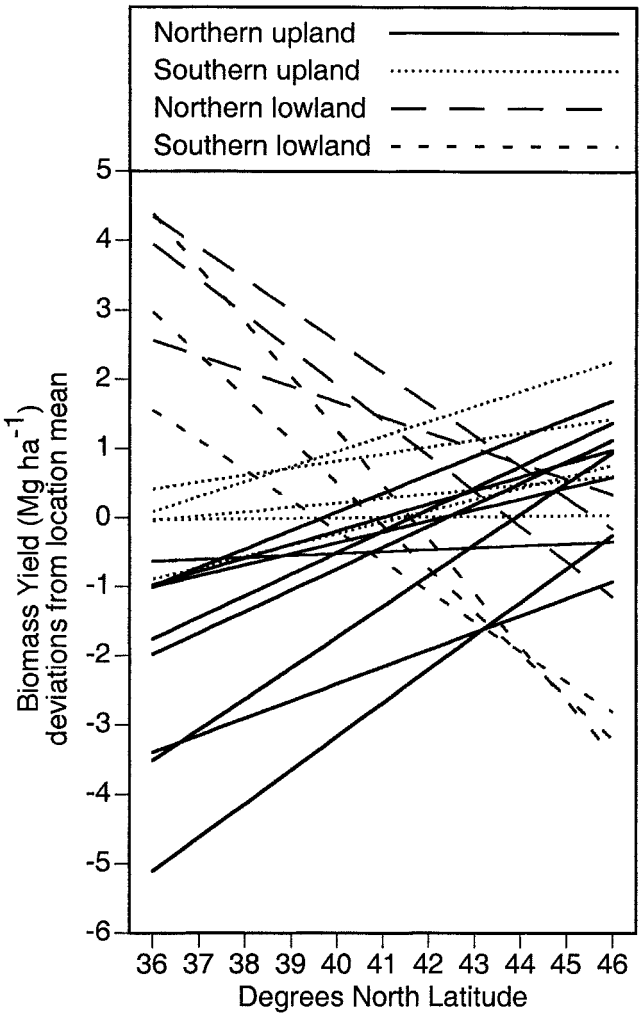

Fig. 1. Linear regressions of mean biomass yield, expressed as deviations from location means, on location latitude for 20 switchgrass populations belonging to four germplasm groups. Linear regression coefficients for each population and group are listed in Table 4.

interactions occurred for biomass yield, was between Mead, NE, and Arlington, WI (Fig. 1). This resulted in greater variability among population means at the southernmost locations and suggested that the warmer temperatures and/or longer growing season of the more southern locations were likely the most important factors in determining this P × L interaction for biomass yield. Although switchgrass is a warm-season grass and has a high level of inherent heat tolerance, this result raises the possibility that upland cytotypes may be limited in their southern adaptation by reduced heat tolerance or reduced ability to utilize the longer growing season compared with lowland cytotypes. The Southern-Upland group ranked first or second in biomass yield only at the two northernmost locations, while the Northern-Upland group ranked high only at the northernmost location (Table 5). These observations support our earlier contention that latitude is the greatest environmental determinant among these five locations and that its confounding with longitude is of relatively minor importance for the purpose of this study. Most of these upland populations originate in the northern Great Plains, at longitudes similar to Mead, Manhattan, and Stillwater. Thus, their superior relative adaptation, as measured by biomass yield, was expressed at longitudes well east of their environmental origin.

The Southern-Lowland group ranked first or second in biomass yield at each of the three southernmost locations (Table 5). The Northern-Lowland group ranked first or second in biomass yield at these three locations and at Arlington. Lowland populations appeared to be limited in adaptation by lack of cold tolerance, expressed largely at the two northernmost locations.

Switchgrass is highly photoperiod-sensitive (Benedict, 1941). Moving northern strains south reduces the daylength to which they are exposed, prompting them to flower early, reducing biomass yields. When evaluated for biomass yield in eastern Texas (30 to 32° N lat), switchgrass cultivars declined by 0.72 Mg ha^{-1} for each additional degree of northern latitude from which they originated (Sanderson et al., 1999). Lowland cytotypes had considerably higher biomass yield than upland cytotypes in Texas (Sanderson et al., 1999). Conversely, moving southern strains north delays their reproductive maturity, extending their growing season and increasing biomass yields (Newell, 1968). Many forage yield gains in switchgrass have derived from this practice (Vogel et al., 1985).

'Kanlow', collected in east-central Oklahoma, had the lowest response to latitude among the six lowland cytotypes (Table 4; Fig. 1). The two populations selected directly from Kanlow, NL92-1 and NL94-1, had biomass yield responses to latitude intermediate between Kanlow and the Southern-Lowland populations. This suggests that selection for high biomass yield and other agronomic traits at Stillwater, OK (C.M. Taliaferro, 2001, unpublished data) may have moved the adaptation characteristics of these populations closer to those of the Southern-Lowland type.

Linear regressions of survival, expressed as deviations from location means, on latitude showed strong separation by cytotype (Fig. 2, Table 4). All upland cytotypes had a positive response to latitude, except Sunburst and Forestburg with nonsignificant responses, and SU94-1 with a significant negative response. SU94-1 originated in southern Oklahoma and northern Texas and was selected for biomass yield and agronomic traits at Stillwater, OK, likely contributing to its preferential adaptation to more southern locations. Southern-Lowland populations had the most extreme negative response, followed by Northern-Lowland populations. Kanlow had a significant positive response, giving it the appearance of an upland cytotype for survival. As with biomass yield, the intermediate nature of populations NL92-1 and NL94-1 suggested that selection has moved the adaptation characteristics of these populations away from Kanlow and closer to the Southern-Lowland phenotype.

The convergence point for survival was between 37 and 40° N lat, resulting in much greater variability among populations at the northernmost locations (Fig. 2; Table 5). This suggested that switchgrass stand losses in this study were largely due to insufficient cold tolerance, which was likely the most important factor regulating

Table 4. Linear regression coefficients for the regressions of population means, expressed as deviations from location means, on degrees latitude (DL) for 20 populations evaluated at five locations.

Population or Group	Biomass yield	Survival	Plant height	Holocellulose conc.	Lignin conc.	IVDMD	N conc.
	Mg ha^{-1} DL^{-1}	% DL^{-1}	cm DL^{-1}	g kg^{-1} DL^{-1}			
Trailblazer	0.06	1.40**	0.44	0.53	−0.06	−0.75	0.03
HZ4 Syn2	0.31*	1.59**	1.89	2.70**	0.52	−4.05**	−0.10
HZ5 Syn2	0.18	1.42**	1.24	0.13	−0.34	1.48	0.01
EyxFF(HDMD)C3	0.28*	1.70**	1.79*	−0.15	0.37	−1.04	−0.07
EyxFF(HYLD)C3	0.24	1.80**	1.44	1.05	−0.42	1.45	0.01
Summer	0.35**	2.94**	2.61**	0.61	0.16	−0.42	−0.20*
Sunburst	0.50**	0.51	1.29	4.01**	0.43	−5.01**	−0.31**
Shelter	0.32*	2.16**	2.80**	2.10*	−0.21	−1.66	−0.20*
Forestburg	0.56**	0.98	3.14**	2.56**	0.86*	−4.70**	−0.25**
Cave-in-Rock	0.23	2.80**	1.47*	1.18	−0.03	−0.78	−0.11*
Shawnee	0.18	2.30**	2.77**	2.51**	−0.75*	−0.42	−0.05
Blackwell	0.00	1.12*	3.11**	−0.35	−0.36	0.83	−0.13
SU94-1	0.09	−2.02**	−0.81	−0.36	0.08	−0.62	0.03
NU94-2	0.11	3.71**	1.49*	1.03	0.03	−1.46	−0.07
Kanlow	−0.27*	0.79	−1.93	−1.28	−0.47	2.38	−0.14
NL92-1	−0.53**	−3.10**	−2.74**	−2.49**	−0.96**	3.14*	0.00
NL94-1	−0.60**	−1.72**	−3.12**	−3.20**	−0.03	4.36**	0.33**
SL92-1	−0.87**	−4.77**	−5.11**	−3.50**	−1.05**	4.79**	0.17*
SL93-3	−0.68**	−6.73**	−7.52**	−3.47**	0.98**	0.38	0.58**
SL94-1	−0.47**	−6.89**	−4.23**	−3.61**	1.25**	2.10	0.48**
Northern Upland	0.31**	1.61**	1.85**	1.50**	0.15	−1.63**	−0.12**
Southern Upland	0.12*	1.58**	1.61**	0.80*	−0.21	−0.49	−0.07*
Northern Lowland	−0.47**	−1.34**	−2.60**	−2.32**	−0.49**	3.29**	0.06*
Southern Lowland	−0.67**	−6.13**	−5.62**	−3.53**	0.40**	2.42**	0.41**

the P × L interaction for survival. The rapid increase in among-population variability beginning at the Mead location suggested that some switchgrass germplasm is sensitive to winter temperatures as far south as 41° N lat. Lowland cytotypes in particular, and possibly some upland-cytotype germplasm appear to be susceptible to cold winter conditions. A previous study, which recorded survival of individual switchgrass spaced plants in spring and autumn at three locations ranging from 40 to 43° N lat, showed that nearly all mortality across a 4-yr period occurred during winter months (Casler et al., 2002). Genetic variation for winter survival exists in switchgrass (Vogel et al., 2002) and appears to be a factor regulating environmental adaptation of switchgrass populations. Plants with the lowland cytotype are extremely rare north of 38° N lat (Hultquist et al., 1997), suggesting limited cold tolerance in lowland switchgrass germplasm.

Linear regressions of plant height, expressed as deviations from location means, on latitude were differentiated by cytotype and latitude of origin (Fig. 3, Table 4). Lowland cytotypes were extremely tall and upland cytotypes were extremely short at the southernmost locations. The regressions tended to converge across the northern half of the latitude range in this study, indicating that the shorter daylength and longer growing season of the southernmost locations were the primary determinants of the P × L interaction for plant height. Five of six lowland cytotypes, with the exception of Kanlow, had significant linear regressions of plant height on latitude, with Southern-Lowland populations having approximately twice the response of Northern-Lowland populations. As with biomass yield and survival, the selections from Kanlow were intermediate between Kanlow and the Southern-Lowland populations. There was little difference between Northern-Upland and Southern-Upland populations, although Southern-Upland populations had a higher frequency of significant regressions.

For the concentration of holocellulose, lignin, N, and IVDMD, linear regressions on latitude explained considerably less variation than observed for biomass yield, survival, and plant height (Table 3). Furthermore, for these four traits, less of the latitude portion of the P × L interaction could be explained by germplasm groups.

Table 5. Mean biomass yield and survival for four groups of switchgrass cultivars evaluated at five locations in 1999 and 2000.

Trait and germplasm group	Stillwater, OK (36° N)	Manhattan, KS (39° N)	Mead, NE (41° N)	Arlington, WI (43° N)	Spooner, WI (46° N)
Biomass yield			Mg ha^{-1}		
Northern-Upland	10.45	7.05	12.71	10.25	7.33
Southern-Upland	12.62	7.96	14.99	11.44	7.39
Northern-Lowland	14.81	10.28	20.93	10.61	4.60
Southern-Lowland	15.13	9.26	17.46	6.46	3.81
SEM†	0.68	0.86	0.83	0.88	1.23
Survival			%		
Northern-Upland	87	98	91	86	80
Southern-Upland	87	98	90	91	76
Northern-Lowland	84	96	95	83	43
Southern-Lowland	83	97	84	10	21
SEM†	2.5	2.5	3.0	10.3	11.4

† Compute SED = SEM$[(n_1 + n_2)/n_1n_2]^{1/2}$ for comparing any two group means, where n_1 and n_2 are the numbers of cultivars in the two groups to be compared (n = 9 for Northern-Upland, n = 5 for Southern-Upland, and n = 3 for Northern-Lowland and Southern-Lowland).

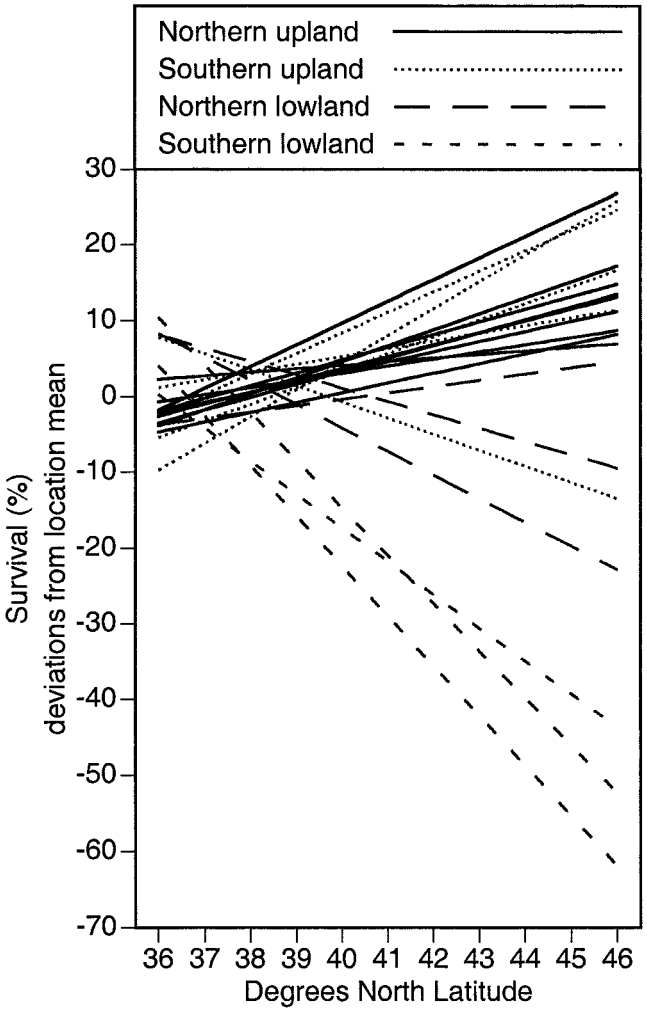

Fig. 2. Linear regressions of mean survival, expressed as deviations from location means, on location latitude for 20 switchgrass populations belonging to four germplasm groups. Linear regression coefficients for each population and group are listed in Table 4.

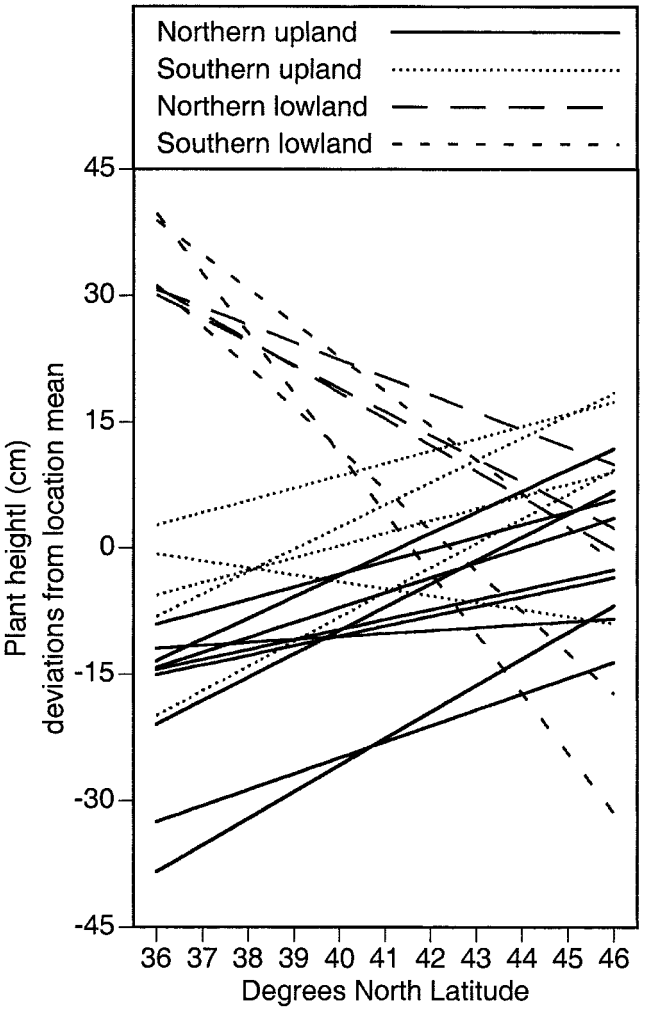

Fig. 3. Linear regressions of mean plant height, expressed as deviations from location means, on location latitude for 20 switchgrass populations belonging to four germplasm groups. Linear regression coefficients for each population and group are listed in Table 4.

Holocellulose made up the largest component of dry matter, with a mean of 675 g kg^{-1}, so linear regressions for holocellulose concentration (Fig. 4) were patterned somewhat similar to those for biomass yield. Upland cytotypes had a greater response to latitude than lowland cytotypes and northern origins had a greater response to latitude than southern origins within both cytotypes. There was no obvious convergence point and variability among populations appeared somewhat uniform across latitudes. For lignin and IVDMD, there was little pattern to the linear regressions on latitude (Table 4). For N concentration, the linear regressions on latitude were nearly a mirror image of those for biomass yield (Table 4), suggesting that N yield was largely constant and variation in N concentration was largely due to dilution from increasing biomass accumulation. This was supported by fairly consistent negative phenotypic correlation coefficients between biomass yield and N concentration at the five locations ($r = -0.73$ to -0.47: $P < 0.05$; homogeneity chi-square: $P = 0.75$).

All traits that were significant in the path analysis regressions exceeded the residual of their respective model (Table 6). For Stillwater, the southernmost location, only plant height had a significant effect on biomass yield: the tallest populations had the highest biomass yield. Not coincidentally, the tallest populations were lowland cytotypes (mean plant height of 214 to 222 cm compared with upland cytotypes, 145 to 178 cm, at Stillwater). Biomass yield of switchgrass is largely influenced by growth and development of individual tillers (Redfearn et al., 1997). Plant height is, in turn, regulated by stem elongation rate (Madakadze et al., 1998). There is some evidence that lowland cytotypes have higher photosynthesis rates (Wullschleger et al., 1996) and lower respiration rates (Nickell, 1972; Sanderson et al., 1996) than upland cytotypes. A higher photosynthetic rate, reduced respiration losses, and more rapid stem elongation rate would allow lowland cytotypes to take fuller advantage of the longer growing season at Stillwater compared with the other locations. Such an advantage could be achieved independent of minor changes in survival.

For the three northernmost locations, plant height

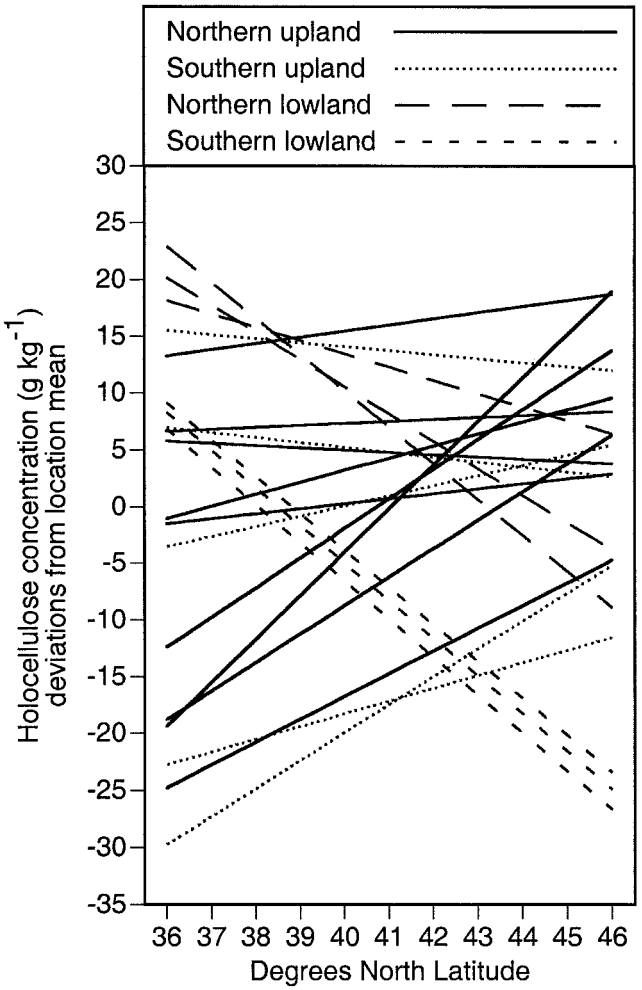

Fig. 4. Linear regressions of mean holocellulose concentration, expressed as deviations from location means, on location latitude for 20 switchgrass populations belonging to four germplasm groups. Linear regression coefficients for each population and group are listed in Table 4.

did not influence biomass yield, but survival was the most important, or nearly the most important factor (Table 6). Mead, NE, is sufficiently far north that switchgrass stands can suffer from winter mortality (Casler et al., 2002). The range in survival among populations was greater at Mead, Arlington, and Spooner than at Stillwater (Fig. 2). For these locations, particularly Arlington and Spooner, differential survival among populations was sufficiently great that tillering could not compensate for loss of stands. Thus, reduced ground cover was an important factor determining biomass yields for the more northern locations. The extreme cold of the two northernmost locations resulted in the greatest survival differential among populations (Fig. 2), eliminating any other trait from having a measurable influence on biomass yields.

Conversely, at Mead, where winter conditions are relatively mild, two other traits had a significant effect on biomass yield: decreased lignification of the cell wall and decreased dry matter were associated with high biomass yield. At Mead, both lignin and dry matter were strongly and positively associated with maturity (r = 0.77 and 0.82, respectively; $P < 0.01$) and plant height ($r = -0.74$ and -0.83, respectively; $P < 0.01$). Thus, the effects of lignin and dry matter on biomass yield at Mead were likely due to associations of late maturity ($r = -0.74$; $P < 0.01$) and taller plants ($r = 0.69$; $P < 0.01$) with high biomass yield. The regression coefficients for maturity and plant height, being partial regression coefficients, are small because (i) lignin, dry matter, maturity, and plant height are highly collinear and (ii) lignin and dry matter had the highest correlations with biomass yield. This resulted in an association of high biomass yield at Mead with a cadre of collinear traits, including plant height and maturity. Therefore, it is likely that the centrality of the Mead location to Stillwater and the two Wisconsin locations caused multiple factors (variation in plant height due to the extended growing season, observed at Stillwater, and variable stand loss due to variation in cold tolerance, observed in Wisconsin) to induce variability for biomass yield at this location. The principal factor or combination of factors regulating biomass yield among these 20 populations appears to vary strongly with latitude of the evaluation environment.

The first two principal components resulted in complete separation of lowland and upland cytotypes at four of five locations, and nearly complete separation at Manhattan (Fig. 5). Northern-Upland and Southern-Upland populations had partially overlapping distributions at each of the five locations. Thus, neither the long growing season at Stillwater nor the extreme cold temperatures of the Wisconsin locations was sufficient to segregate northern vs. southern populations within the upland cytotype.

Table 6. Standardized linear regression coefficients from path analysis of seven switchgrass traits (direct effects on biomass yield) measured at four locations.

Trait	Stillwater, OK (36° N)	Mead, NE (41° N)	Arlington, WI (43° N)	Spooner, WI (46° N)
Survival	−0.16	0.50**	1.23**	1.00*
Maturity	0.05	−0.04	0.08	−0.06
Plant height	0.86*	0.24	0.07	0.07
Lodging	0.19	0.24	−0.19	−0.02
Dry matter concentration	−0.07	−0.51*	−0.18	0.05
Holocellulose concentration	0.22	−0.01	−0.17	0.06
Lignin concentration	0.10	−0.41*	−0.30	0.18
Residual†	0.45	0.25	0.37	0.55

* Regression coefficient significant at $P = 0.05$.
** Regression coefficient significant at $P = 0.01$.
† The residual was computed as $(1 - R^2)^{1/2}$.

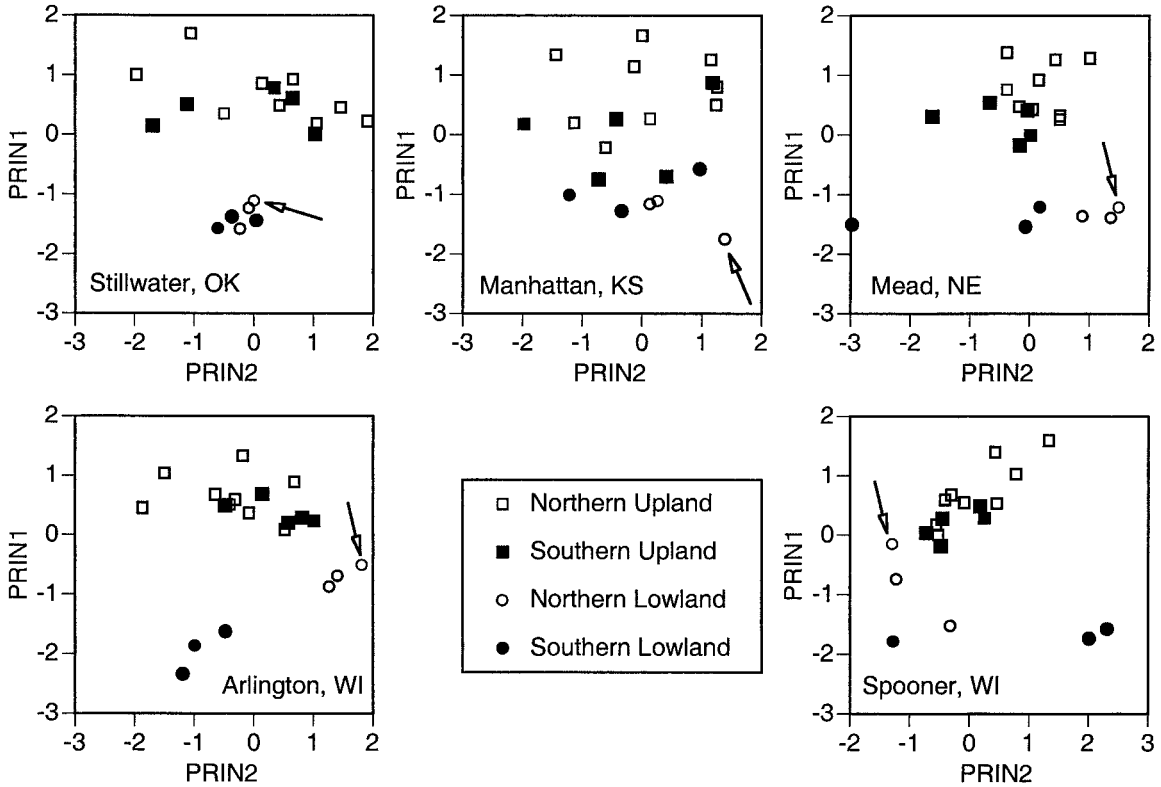

Fig. 5. Scatterplot of the first two principal components for 10 traits of 20 switchgrass population evaluated at five locations. Kanlow is indicated by the arrow on each graph. The percentage of variation described by the first two principal components was 66% for Stillwater, 69% for Manhattan, 74% for Mead, 82% for Arlington, and 77% for Spooner.

Within the lowland cytotype, complete separation of northern vs. southern populations was achieved at Mead and Arlington, with partial separation at Manhattan and Spooner. The tight clustering of lowland cytotypes at Stillwater may have resulted from their uniformly favorable reaction to the long growing season and/or from the relatively mild winters at Stillwater. The intermediate phenotype of NL92-1 and NL94-1 between Kanlow and the Southern Lowland populations was observed at all five locations. Of the three Northern-Lowland populations, Kanlow was always the most distant from the Southern-Lowland populations, confirming previous observations that selection at Stillwater has apparently moved these populations away from the Kanlow phenotype and closer to the Southern-Lowland phenotype. Kanlow has much more genetic variability for biomass yield than other switchgrass populations (McLaughlin et al., 1999), suggesting that it may serve as a source of valuable germplasm for creating lowland populations better adapted to longer growing seasons of more southern latitudes or to cold-winter climates of more northern latitudes.

SUMMARY AND CONCLUSIONS

Switchgrass populations show considerable variation in adaptation across a geographic transect ranging from 36 to 46° N lat. Much of this variation can be attributed to adaptive differences among ecotypes related to climatic conditions. Increasingly later maturity and the more rapid stem elongation rate of more southern-origin ecotypes results in high biomass yield potential, reduced dry matter concentration, and longer retention of photosynthetically active tissue, traits that allow switchgrass to extend its growth rate, taking advantage of the longer growing season of more southern locations. Conversely, increasing cold tolerance of more northern-origin ecotypes results in higher survival, stand longevity, and sustained biomass yields, traits that allow switchgrass to thrive at cold, northern latitudes. Genetic variation for biomass yield of switchgrass is a complex quantitative trait, subject to huge genotype × environment interactions, and regulated by genetic variation for several more simply inherited traits. Uniform multiple-location collaboration is a necessary tool to dissect causal factors and components of complex interactions involving complex traits.

Within the Great Plains and Midwest states of the USA, most USDA plant hardiness zones (Cathey, 1990) are ≈2° latitude in width. This study spanned Hardiness Zones 3 through 7. The variability among linear regressions on latitude for biomass yield and survival indicated that switchgrass populations vary in their sensitivity to movement out of their hardiness zone of origin. Populations originating from the most extreme latitudes, either north or south, showed the greatest sensitivity to latitude. Moving Southern-Lowland populations north of their hardiness zone of origin resulted in a 9 to 17% reduction in both biomass yield and survival, relative to other populations, for each numerical shift in hardiness zone. Northern-Lowland populations were less sensitive

to latitude, but their biomass yield and survival increased by moving south or decreased by moving north by an average of 3% for survival and 9% for biomass yield for each numerical shift in hardiness zone. For upland populations, the distinction between northern and southern origins was less clear than for lowland populations. Nevertheless, moving upland populations south of their hardiness zone of origin resulted in decreases in biomass yield of 1 to 11% and decreases in survival of 1 to 9%, relative to other populations. Conversely, upland populations from more southern latitudes increased in biomass yield and survival as they were moved north, although there is likely an upper limit to the number of hardiness zones that can be crossed. Moving lowland populations slightly south and upland populations slightly north of their hardiness-zone-of-origin seem to be the safest moves for maintaining, or potentially increasing, biomass yield and survival. Upland populations should not be moved south of their origin by more than one hardiness zone and lowland populations should not be moved north of their origin by more than one hardiness zone without expecting severe losses in biomass yield and survival.

Finally, all 20 populations showed evidence of a latitudinal response for either biomass yield or survival, indicating that we are unlikely to find switchgrass germplasm sources that are uniformly adapted across numerous hardiness zones. However, selection and breeding can rapidly speed up the evolutionary process that has created such adaptive differences, allowing humans to rapidly change the adaptation characteristics of switchgrass populations. The genetic changes observed in the Kanlow-derived populations suggest that some switchgrass populations contain a large amount of genetic variability for adaptative traits. Much of this variability is locked away in the polyploid genome of switchgrass, hidden from detection by simple agronomic testing procedures. Simply moving switchgrass populations out of their hardiness zone of origin results in severe losses in biomass yield and survival because the majority of plants are not phenotypically adapted to the new hardiness zone. However, in a relatively short period of time, selection pressure in a new environment can unlock reserves of genetic variability that may be useful for phenotypic expression in the new environment. Selection and breeding increases the frequency of alleles for adaptive traits, which then increases the frequency of plants phenotypically adapted to the local environment, resulting in adaptive changes to a population. The perennial nature of switchgrass provides the potential for these adaptive changes to become fixed following successful establishment of a selected population.

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