

Biomass Yield and Stand Characteristics of Switchgrass in South Central U.S. Environments

K. A. Cassida,* J. P. Muir, M. A. Hussey, J. C. Read, B. C. Venuto, and W. R. Ocumpaugh

ABSTRACT

Optimizing feedstock production from switchgrass (*Panicum virgatum* L.) requires careful matching of genotype to environment, especially for southern U.S. regions. Nine genotypes from four combinations of ecotype and morphological type were harvested once yearly in autumn for 3 or 4 yr at five locations across Texas, Arkansas, and Louisiana that varied in latitude and precipitation. Genotypes were evaluated for dry matter yield (DMY), plant density, tiller density, lodging, and rust (caused by *Puccinia* spp.) infection. Genotype \times environment (G \times E) interactions were identified for most traits. Biomass yield of all genotypes tended to increase with latitude, but lowland morphological types may have been more sensitive than upland morphological types to differences in moisture availability. Yield (5.82 vs. 14.97 Mg ha⁻¹, respectively) and persistence (final stand density, 3.99 vs. 5.96 plants m⁻²) were lower for upland than for lowland genotypes, particularly at higher rainfall and more southern sites. Lowland genotypes were often able to compensate for stand thinning by increasing individual plant size, but upland genotypes were not. Lodging and rust scores were higher for upland than for lowland genotypes. Yield (13.65 vs. 9.75 Mg ha⁻¹) and final plant density (5.58 vs. 4.95 plants m⁻²) were higher for southern than northern ecotypes. The southern-lowland combination exhibited the best yield and persistence over the study region, and genotypes within this group exhibited variability in yield among sites. Therefore, development of switchgrass cultivars for biomass production in the southern USA should focus on the southern-lowland genotypes.

SWITCHGRASS has attracted considerable interest as a biofuel crop for cofiring in southern coal plants (Sanderson et al., 1996). Yields of most currently available cultivars are lower in this region than in the Great Plains, midwestern, or eastern regions of the USA (Bransby et al., 1989; Sanderson et al., 1996, 1999b; Lemus et al., 2002). The south central region of the USA is characterized by mild to moderate winters, hot and often dry summers, low native soil fertility, and rainfall patterns that vary from dry and bimodal in the western end of the region to evenly wet and humid in the east. None of these conditions of themselves suggest potential cultivation problems with switchgrass, a plant

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that is widely adapted across the USA (Moser and Vogel, 1995) with specific genotypes evolved to fit a variety of local conditions.

Ecotype and morphological type differences among switchgrass genotypes play a large role in adaptation to specific environments. Photoperiod and precipitation and humidity are reported as the most important environmental factors influencing adaptation to a region (Moser and Vogel, 1995). Switchgrass is a short-day plant and ecotypes are differentiated primarily by response to photoperiod (Moser and Vogel, 1995). Northern ecotypes flower earlier, are shorter, yield less, and have a longer winter dormant period with better winter survival than southern ecotypes when grown at the same latitude. Precipitation of the region of origin is a factor because ecotypes from the relatively dry Great Plains often have good drought tolerance, but poor tolerance to foliar pathogens when grown in higher rainfall environments. Switchgrass morphology is typified as lowland or upland (Moser and Vogel, 1995). Compared with upland types, lowland types are taller, coarser, more rust resistant, grow faster, have a stronger bunch-grass growth habit, and are found naturally on floodplains and areas with temporary poor drainage.

The difficulty in growing switchgrass in southern regions may be related to adaptation of ecotypes and morphological types to particular regions. Improved genotypes of switchgrass may be developed from a single collection or incorporate traits from several ecotypes or morphological types in an effort to meet agronomic needs for uses such as animal feed, conservation plantings, or biofuel feedstock production. As a result, varieties may exhibit a great degree of G \times E variation, particularly for dry matter yield (DMY) (Hopkins et al., 1995a, 1995b; Vogel and Jung, 2001; Casler and Boe, 2003). Managing this through proper matching of variety to environment and intended use may be critical to successful utilization. Most released varieties are of the upland morphological type (Moser and Vogel, 1995) and the northern ecotype (USDA, 1995). However, lowland types often have higher yields in a given environment (Lemus et al., 2002; Sanderson et al., 1996, 1999b; Christian et al., 2002), and Vogel and Jung (2001) proposed that southern ecotypes had higher potential biomass productivity, albeit with a higher risk of winterkill. Casler et al. (2004) reported that showed that yield potential of lowland genotypes decreased and that of upland genotypes increased from 36 to 46° latitude, and that morphological type had greater impact on potential yield than ecotype. The winterkill problem has probably

Abbreviations: DMY, dry matter yield; G \times E, genotype \times environment interaction; L, lowland morphological type; N, northern ecotype; S, southern ecotype; U, upland morphological type.

discouraged widespread use of southern germplasm in development of switchgrass cultivars, but winterkill is unlikely to be a critical factor for switchgrass intended for use south of 36° latitude. The consistent success of the southern lowland cultivar Alamo in southern U.S. trials (Sanderson et al., 1996; 1999b) underscores the possibility that development of cultivars specifically for the south may alleviate switchgrass productivity problems in this region.

We compared switchgrass genotypes that differed in ecotype and morphological type in a 4-yr trial conducted at five locations of the south central USA. Our objective was to determine how genotypes responded to environments. Locations were selected to differ in latitude and the amount and distribution of precipitation, and genotypes represented four combinations of ecotype and morphological type. Dry matter yield, persistence, and stand characteristics are reported herein, with biomass chemical composition and yield of fuel components reported elsewhere.

MATERIALS AND METHODS

Switchgrass germplasm was evaluated at five locations with differing latitudes and annual rainfall: College Station, Dallas, and Stephenville, TX; Hope, AR; and Clinton, LA (Table 1). Soil types were: College Station—Weswood silty clay loam (fine silty, mixed thermic Fluventic Ustochrept); Dallas—Houston black clay (fine, montmorillonitic thermic Udic Pel-lusters); Stephenville—Windthorst fine sandy loam (fine, mixed thermic Udic Paleustalfs); Arkansas—Bowie fine sandy loam (fine-loamy, siliceous, thermic Fragic Paleudult); and Louisiana—Dexter silt loam (fine-silty, mixed thermic Ultic Hapludalf). Switchgrass genotypes were classified as upland or lowland by morphological type and as northern or southern according to latitude of origin within the south central region. They included the following: Alamo—a southern lowland variety from south Texas; Caddo, a northern upland variety from Stillwater, OK; SL931, SL932, SL941—southern lowland synthetic lines from central and southern Texas; NL931, NL942—northern lowland synthetic lines from Oklahoma and southern Kansas; NU942—a northern upland synthetic line from Oklahoma and southern Kansas; and SU942—a southern upland synthetic line from central and southern Texas. All synthetic lines were developed at Oklahoma State University by C. Tali-ferro.

Greenhouse-grown seedlings were transplanted into prepared seedbeds between 16 July and 7 Aug. 1997. All seedlings were grown at one site to minimize variability. Seedlings were planted in 51-cm rows on 30-cm centers to give an initial plant density of 6.45 plants m⁻². There were six rows per plot (plot size 3.0 × 6.1 m) at all sites except Dallas, where seven rows were used (plot size 3.6 × 6.1 m). Stands in College Station and Dallas were irrigated once in late June of the 1998 harvest year because severe drought threatened loss of stands. Other sites were not irrigated after the establishment year. At the Arkansas site, plots were treated with 0.56 kg a.i. ha⁻¹ of 2,4-dichlorophenoxyacetic acid plus 0.15 kg a.i. ha⁻¹ of picloram (4-amino-3,5,6-trichloropicolinic acid) on 6 March 1998 and with 0.0043 kg a.i. ha⁻¹ of metsulfuron [2-(4-methoxy-6-methyl-1,3,5-triazin-2-ylcarbonylsulfamoyl)benzoic acid] on 6 April 1999 and 24 April 2000 to control broadleaf weeds. Plots were treated with 2,4-dichlorophenoxyacetic acid at 1.06 kg a.i. ha⁻¹ on 21 August 1999 at Louisiana and on 6 June 1998 at Dallas. No weed control was necessary at College Station or Stephenville.

All stands were fertilized once per year within 4 to 6 wk of initiation of spring growth. Phosphorus and potassium were applied annually according to local soil recommendations in Arkansas and Louisiana but were not required at the other sites. Nitrogen was applied at 150 kg ha⁻¹ to all stands except at Arkansas, where 168 kg ha⁻¹ was applied. The center two (6-row plots) or three (7-row plots) rows of each plot were harvested once per year at a 10-cm stubble height. A single annual harvest was targeted to occur in late summer or autumn when the standing crop stopped initiating new tillers and leaves were no longer green. In Louisiana, upland entries were not harvested in 2001 because stands had declined to negligible yields, and yields were recorded as zero for these entries. Harvested material was weighed, dry matter content determined from subsamples collected from each plot, and DMY calculated. Precipitation and air temperature data were summarized for each location (Table 1).

Additional measurements were obtained in some site-years. At harvest, tillers were counted from three plants per plot at Dallas and Louisiana in 1998 to 2000 and at Stephenville in 1998 and 2001. At Arkansas, Dallas, and Louisiana, stand density at harvest was determined every year by counting the number of crowns in each harvest strip. At College Station and Stephenville, stand density at harvest was determined only in the final year of the trial. Lodging as a percentage of plot area was estimated visually at Arkansas in 1999 and 2000, at Dallas in 2000, at Louisiana and Stephenville in 2001, and at College Station in 1999 and 2001. Leaf rust (caused by

Table 1. Environmental characteristics at Stephenville, Dallas, and College Station, TX; Hope, AR; and Clinton, LA, from 1998 through 2000.

| | Location | | | | | SE† |
|--|--------------|--------------|-----------------|------------|------------|------|
| | Stephenville | Dallas | College Station | Arkansas | Louisiana | |
| April–September growth period | | | | | | |
| Precipitation, total (normal), mm period ⁻¹ | 304 (474) | 351 (519)‡ | 280 (545) | 490 (691) | 539 (803) | 57.6 |
| Mean maximum daily air temperature, °C | 31.9 | 31.7 | 33.3 | 30.7 | 31.1 | 0.4 |
| Mean minimum daily air temperature, °C | 17.6 | 19.6 | 17.3 | 17.3 | 19.7 | 0.3 |
| Harvest dates§ | | | | | | |
| 1998 | 22 September | 22 September | 8 October | 28 October | 14 October | – |
| 1999 | 14 October | 6 October | 8 October | 8 November | 15 October | – |
| 2000 | 20 September | 26 October | 27 October | 28 October | 20 October | – |
| Mean day of year at harvest | 271 | 280 | 286 | 304 | 288 | 6.1 |
| Latitude | 32°13' N | 32°58' N | 30°36' N | 33°40' N | 30°51' N | – |
| Longitude | 98°12' W | 97°16' W | 96°21' W | 93°35' W | 90°3' W | – |
| Elevation, m | 400 | 207 | 107 | 107 | 70 | – |

† SE reflects variation among sites and years.

‡ Stands in College Station and Dallas were irrigated once in late June of the 1998 harvest year because severe drought threatened loss of stands.

§ Harvest dates for each site-year were determined as the earliest dates where active plant growth had ceased and weather was favorable for harvest.

Puccinia spp.) scores were estimated visually as percentage of leaf area affected at Arkansas in 2000.

Within sites, experimental design was a randomized complete block with four replications. All statistical analyses were conducted by SAS (SAS Inst., 2001). The trial was analyzed as a multi-site, multi-year trial with appropriate error terms to test year and site effects in the analysis of variance. Sites were selected to cover a specific range of environments so were analyzed as a fixed variable. Year was analyzed as a fixed variable because the perennial nature of the crop caused performance in any given year to be related to the previous year's survival. When year \times genotype interactions were significant within sites, means were compared within years. Means for locations and years were separated by Fisher's protected LSD ($P < 0.05$). Comparisons among genotype groups were made by orthogonal contrasts as follows: (i) upland vs. lowland morphological type (UM vs. LM) and (ii) northern vs. southern ecotype (NE vs. SE). Individual genotypes and years were also compared by Fisher's protected LSD 0.05. A correlation analysis was performed within morphological type groups to evaluate relationships between DMY and water availability throughout the growing season, among lodging scores, stand DMY, and density; and among stand tillering characteristics. All mention of statistical significance refers to $P < 0.05$ unless otherwise specified.

RESULTS AND DISCUSSION

Dry Matter Yield

There was a year \times genotype interaction at every site except Arkansas (Table 2), but consistent effects of ecotype and morphological type (Fig. 1) allowed for general comparison. Genotypes in the lowland morpho-

logical type group had greater DMY than those in the upland group in every site-year (average over all site-years, 14.97 vs. 5.82 Mg ha⁻¹, respectively). Genotypes in the southern ecotype group had greater DMY than those in the northern group in all but two site-years (average over all site-years, 13.65 vs. 9.75 Mg ha⁻¹, respectively). Interaction was most likely attributable to variation in the magnitude of differences among years and to a general trend at most sites toward stable or increasing DMY over time for lowland genotypes and decreasing DMY over time for upland genotypes.

Average annual DMY for genotype groups was plotted versus latitude to examine potential relationships (Fig. 2). Yields showed a generally linear relationship with latitude across most sites, with most deviations explainable from differences in moisture availability. Unexpectedly high DMY for College Station may be an artifact caused by irrigation at that site in 1998. Dallas stands were also irrigated in 1998, but yields were only slightly elevated relative to other sites for lowland genotypes. The dry environment at Stephenville may account for relatively low lowland DMY at that location. If College Station data was excluded, yields increased 3.22 ($r^2 = 0.81$, $P < 0.11$), 2.86 ($r^2 = 0.99$, $P < 0.001$), 2.90 ($r^2 = 0.96$, $P < 0.05$, and 3.15 ($r^2 = 0.89$, $P < 0.06$) Mg ha⁻¹ yr⁻¹ for each degree of latitude for lowland, upland, northern, and southern genotype groups, respectively. Van Esbroeck et al. (2004) reported that Caddo yields increased with photoperiod length, but that Alamo yields did not. Conversely, Casler et al. (2004) reported declining lowland genotype DMY as latitude (and there-

Table 2. Average annual dry matter yield of switchgrass genotypes over three or four harvest years in Stephenville, Dallas, and College Station, TX; Hope, AR; and Clinton, LA.

| Genotype or year | Dry matter yield, Mg ha ⁻¹ | | | | |
|------------------------|---------------------------------------|-----------|--------------|----------|----------|
| | College Station | Louisiana | Stephenville | Dallas | Arkansas |
| Alamo | 19.74 ab† | 10.70 ab | 10.88 b | 19.48 a | 16.75 bc |
| SL931 | 21.40 a | 10.79 ab | 11.28 b | 19.04 ab | 19.96 a |
| SL932 | 19.02 abc | 10.42 b | 13.65 a | 18.72 ab | 18.17 ab |
| SL941 | 17.30 bcd | 11.59 a | 12.74 ab | 17.29 b | 17.38 bc |
| NL931 | 14.18 d | 9.30 c | 10.67 b | 17.69 ab | 15.12 c |
| NL942 | 16.15 cd | 10.65 b | 12.19 ab | 18.82 ab | 17.27 bc |
| Caddo | 5.42 e | 1.12 e | 5.00 c | 6.05 d | 7.41 e |
| NU942 | 5.82 e | 2.45 d | 7.08 c | 7.90 cd | 10.36 d |
| SU941 | 6.59 e | 1.81 de | 5.82 c | 9.28 c | 9.00 de |
| LSD 0.05 (genotype) | 3.33 | 0.93 | 2.14 | 1.99 | 2.40 |
| 1998 | 16.09 b | 4.79 c | 9.05 c | 14.55 b | 14.11 |
| 1999 | 19.66 a | 7.28 b | 10.95 a | 16.13 a | 14.06 |
| 2000 | 8.40 d | 8.19 b | 10.33 ab | 14.08 b | 15.52 |
| 2001 | 11.70 c | 10.32 a | 9.34 bc | — | — |
| LSD 0.05 (year) | 1.94 | 0.92 | 2.13 | 1.01 | ns |
| site mean | 13.96 | 7.65 | 9.92 | 14.92 | 14.56 |
| CV | 29.03 | 18.34 | 19.04 | 9.90 | 22.69 |
| Source | <i>P</i> < — | | | | |
| year | 0.001 | 0.001 | 0.01 | 0.01 | 0.17 |
| genotype | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 |
| U vs. L ‡ | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 |
| N vs. S | 0.001 | 0.001 | 0.001 | 0.001 | 0.001 |
| NL vs. SL | 0.001 | 0.01 | 0.28 | 0.53 | 0.05 |
| NU vs. SU | 0.50 | 0.43 | 0.84 | 0.05 | 0.91 |
| Caddo vs. NU942 | 0.81 | 0.05 | 0.07 | 0.08 | 0.05 |
| Alamo vs. SL931 | 0.32 | 0.86 | 0.70 | 0.66 | 0.05 |
| Alamo vs. SL932 | 0.69 | 0.54 | 0.05 | 0.44 | 0.24 |
| Alamo vs. SL941 | 0.15 | 0.10 | 0.10 | 0.05 | 0.59 |
| year \times genotype | 0.001 | 0.001 | 0.05 | 0.001 | 0.001 |

† Within sites, genotype means followed by the same letter are not significantly different (Fisher's protected LSD 0.05); within sites, year means followed by the same letter are not significantly different (Fisher's protected LSD 0.05).

‡ Contrast codes: U, upland; L, lowland; N, northern; S, southern.

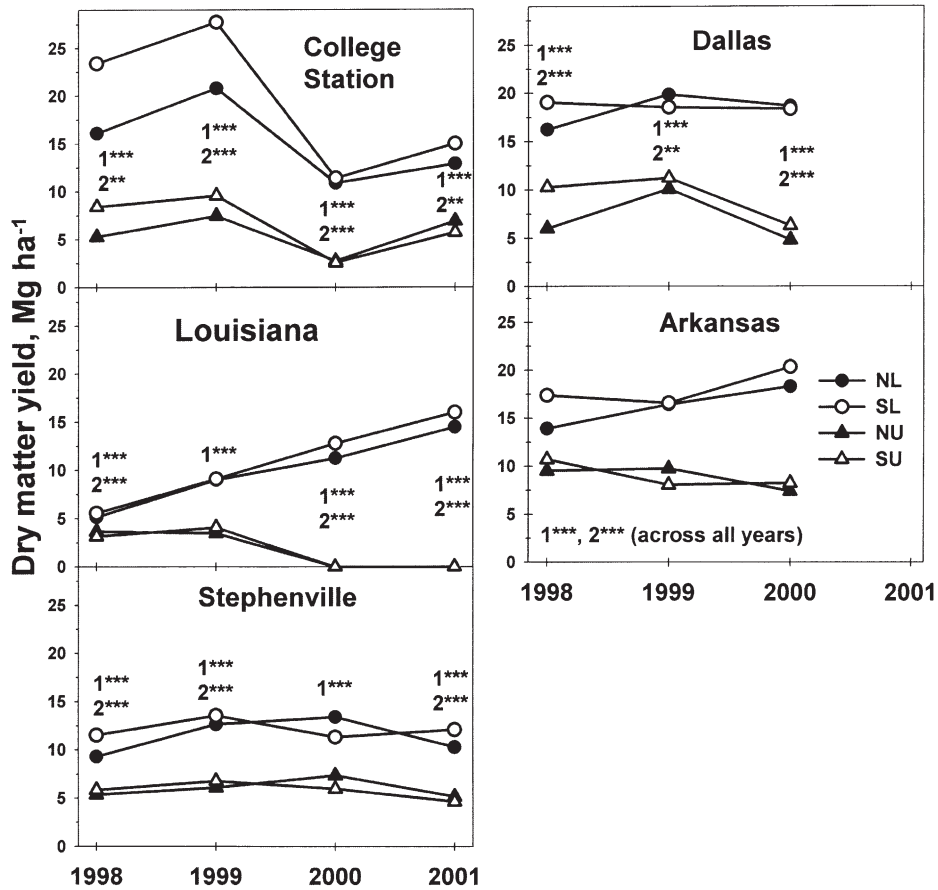


Fig. 1. Dry matter yield of northern lowland (NL), southern lowland (SL), northern upland (NU), and southern upland (SU) groups of switchgrass entries harvested once yearly at Clinton, LA, Hope, AR, and Dallas, Stephenville and College Station, TX. Within years, numbers followed by *, **, *** indicate differences at the 0.05, 0.01, and 0.001 levels, respectively, for orthogonal contrasts of (1) upland vs. lowland and (2) northern vs. southern.

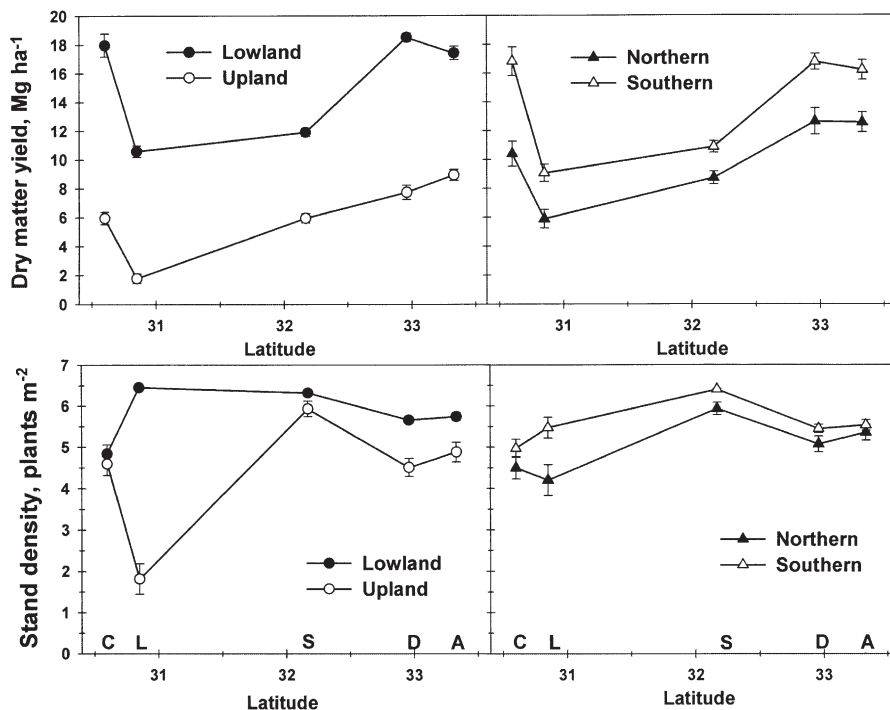


Fig. 2. Average annual dry matter yield and stand density at final harvest for lowland versus upland morphological types and northern and southern ecotypes of switchgrass grown at five sites (A–Hope, AR; C–College Station, TX; D–Dallas, TX; L–Clinton, LA; and S–Stephenville, TX) varying in latitude.

fore photoperiod) increased from 36 to 46°. Greater variability in lowland compared to upland DMY across latitudes indicates the former may be more sensitive to differences in moisture availability among sites. In addition, southern ecotypes appear to have a stronger response to latitude changes across these locations than do northern ecotypes.

Rainfall during the primary growing period for switchgrass, April to September, was 17 to 73% below normal in all site-years (Table 1). When examined across all site-years, monthly or cumulative moisture (rainfall plus irrigation) (Fig. 3) was not correlated with DMY for any genotype group. When compared within sites, high June or July moisture was associated ($r > 0.97$) with greater lowland DMY at Arkansas and Louisiana, but with less lowland DMY at Dallas. High April rainfall was associated ($r = 0.95$) with better upland DMY at Stephenville. High rainfall near harvest was negatively associated with DMY ($r > 0.97$) for upland genotypes in Stephenville and for northern ecotypes in Stephenville, Dallas, and Arkansas.

In Texas, Sanderson et al. (1999b) suggested that precipitation received during the primary growing period for switchgrass is most critical in determining yields. Soil water holding capacity is a major factor affecting switchgrass yield when precipitation is low or unevenly distributed (Stout et al., 1988; Reynolds et al., 1996). Stands that are damaged by drought may be unable to respond to subsequent moisture, and this may account for the lack of overall relationship between moisture availability and DMY across our sites. Our data indicate that water availability from April to July was most likely to impact switchgrass yields, that the most critical month differed among sites, and that genotype groups differed in their response to moisture availability. Moisture availability in June and July was most important for lowland genotypes, while upland genotypes showed no positive response to moisture availability except at the driest site (Stephenville). High moisture availability near harvest was likely to reduce DMY for upland and northern genotypes, probably as a result of increased decay of senesced biomass. Negative correlations between DMY and early season moisture availability at some locations were possibly related to increased leaf or root diseases or increased lodging of stems in hard rains.

Individual genotype DMY averaged across years is shown in Table 2. Alamo was used as the standard of comparison for the experimental southern lowland genotypes. No experimental genotype was consistently superior to Alamo across sites, but Alamo was first-ranked only in Dallas. Genotype SL931 was first-ranked for DMY in Arkansas and College Station and second-ranked in Louisiana, but only yielded statistically more than Alamo in Arkansas. Genotype SL941 was first-ranked in Louisiana but not statistically different from Alamo. Among the southern lowland group, both Alamo and SL941 displayed great variability in ranking among sites, ranging from first-ranked to last-ranked. Alamo yields in this trial were comparable to those reported for single harvest biomass yields in Texas (Sanderson et al., 1999a, 1999b; Muir et al., 2001). At Louisiana and Stephenville, aver-

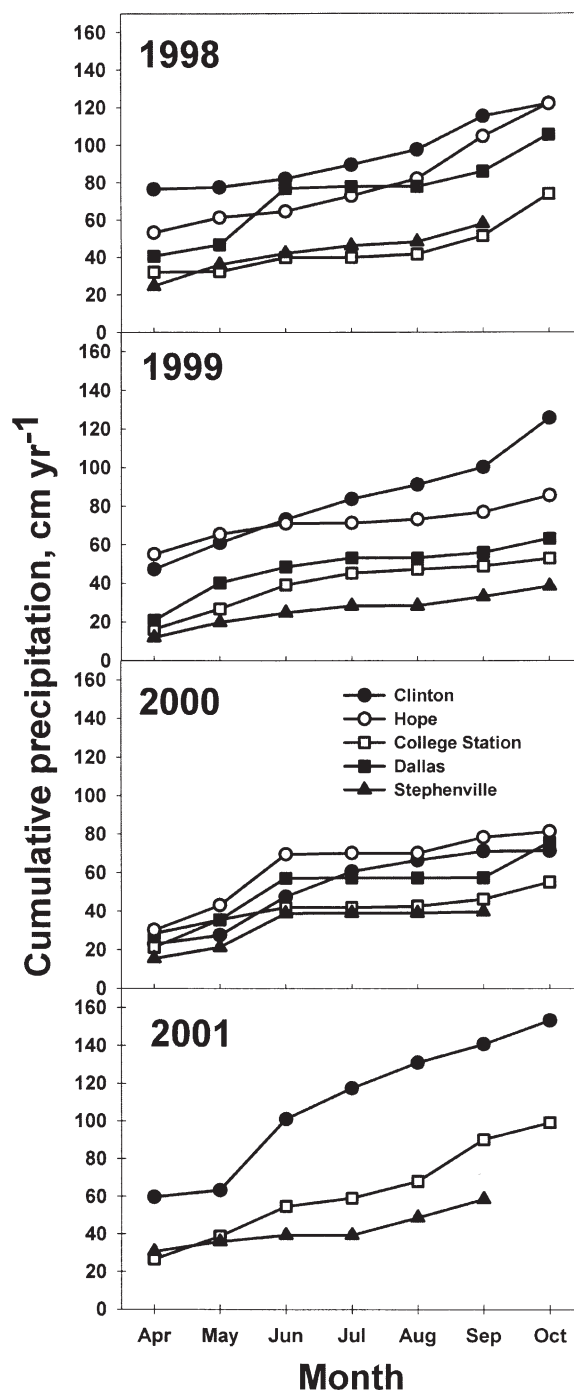


Fig. 3. Cumulative precipitation over the growing season (April to harvest) during harvest years in Clinton, LA, Hope, AR, and Dallas, Stephenville and College Station, TX. Values reported for April are cumulative for January through April. Normal cumulative rainfall at harvest for the five sites is 131.0, 110.8, 80.6, 61.3, and 84.2 cm, respectively.

age Alamo yields were similar to the 12.1 Mg ha⁻¹ reported in Iowa (Lemus et al., 2002), but Alamo DMY was higher than in Iowa at our remaining sites. In contrast, our Caddo yields were low at all locations relative to the 7.8 Mg ha⁻¹ reported in Iowa (Lemus et al., 2002). In agreement with our data, Muir et al. (2001) reported reduced first-year switchgrass yields in Stephenville com-

Table 3. Switchgrass plant density after three harvest years in Hope, AR, and Dallas, TX, and after four harvest years at Stephenville and College Station, TX†.

| | Arkansas | Dallas | Stephenville | College Station |
|------------------|------------------------|---------|--------------|-----------------|
| | plants m ⁻² | | | |
| Alamo | 4.88 abc‡ | 5.22 a | 6.30 a | 5.08 |
| SL931 | 4.92 abc | 5.35 a | 6.37 a | 4.60 |
| SL932 | 5.20 ab | 5.24 a | 6.45 a | 5.65 |
| SL941 | 3.75 d | 5.05 a | 6.45 a | 5.00 |
| NL931 | 5.89 a | 5.84 a | 5.84 abc | 4.60 |
| NL942 | 4.52 bcd | 4.78 ab | 5.76 abc | 4.11 |
| Caddo | 2.42 e | 2.74 c | 5.22 bc | 4.68 |
| NU942 | 3.95 cd | 2.61 c | 4.84 c | 4.60 |
| SU941 | 3.75 d | 3.63 bc | 6.15 ab | 4.52 |
| LSD 0.05 | 1.02 | 1.22 | 1.01 | ns |
| Site mean | 4.36 | 4.49 | 5.93 | 4.76 |
| CV | 16.00 | 18.66 | 11.68 | 22.35 |
| Contrasts | P < | | | |
| U vs. L | 0.001 | 0.001 | 0.001 | 0.53 |
| N vs. S | 0.21 | 0.01 | 0.001 | 0.20 |
| NL vs. SL | 0.11 | 0.83 | 0.10 | 0.13 |
| NU vs. SU | 0.21 | 0.10 | 0.05 | 0.86 |
| Caddo vs. NU942 | 0.01 | 0.82 | 0.44 | 0.92 |
| Alamo vs. SL931 | 0.94 | 0.83 | 0.88 | 0.53 |
| Alamo vs. SL932 | 0.52 | 0.97 | 0.76 | 0.46 |
| Alamo vs. SL941 | 0.05 | 0.79 | 0.76 | 0.92 |

† In Clinton, LA, final plant density was 6.45 and 0 plants m⁻² for all lowland and upland genotypes, respectively ($P < 0.001$).

‡ Within sites, genotype means followed by the same letter are not significantly different (Fisher's protected LSD 0.05).

pared with subsequent years. Gradual improvements in stand productivity underscore the importance of collecting enough years of data when evaluating slow-developing perennial crops.

Stand Characteristics

Stand density declined from the initial population for all genotype groups except lowland morphology in Louisiana and Stephenville (Table 3). Final stand density was higher for lowland than for upland morphological type at Louisiana (6.45 vs. 0 plants m⁻², respectively), Stephenville (6.32 vs. 5.93 plants m⁻², respectively), Dallas (5.66 vs. 4.51 plants m⁻², respectively), and Arkansas (5.74 vs. 4.88 plants m⁻², respectively). Final stand density was higher for southern than for northern ecotypes at Dallas (5.44 vs. 5.07 plants m⁻², respectively) and Stephenville (6.40 vs. 5.93 plants m⁻², respectively). Final stand density (Fig. 2) was not related to latitude ($P > 0.05$) for any genotype group, in contrast to results of Casler et al. (2004) who found that lowland survival decreased while upland genotype survival increased with latitude.

Stand loss over time was monitored at three sites: Dallas, Arkansas, and Louisiana (Fig. 4). At Dallas, stand density was higher for lowland than for upland morphological type in every harvest year. Lowland stands maintained a slow but constant loss throughout the trial, but upland genotypes showed a sharp decline in stand density in 2000. In Arkansas, upland stands again thinned faster than lowland stands and were only 52% of initial density by the third year, compared to 75% for lowland genotypes. In Louisiana, upland stands declined rapidly and were completely lost by the third year, while lowland stands spread to such extent that individual crowns were no longer distinguishable.

The number of tillers per plant at harvest was monitored for three consecutive years in Dallas and Louisi-

ana (Fig. 5). In Dallas, lowland genotypes had higher tiller counts than upland genotypes in 1999 and 2000, with the magnitude of the difference increasing each year. By 2000, upland tiller counts were less than one-fourth of those in 1998. In 1998, southern ecotypes had higher tiller counts than northern ecotypes within the upland group of genotypes, but this difference did not appear in subsequent years or among lowland genotypes. In Louisiana, lowland genotypes had greater tiller counts than upland in each year, and northern upland genotypes had greater tiller counts than southern upland genotypes in 1998. Tiller density was measured in the first and last harvest years at Stephenville (data not shown) and did not differ among entries within either year. However, across all genotypes, tiller density at Stephenville declined from 1998 to 2001 (from 74 to 51 tillers plant⁻¹ or 475 to 306 tillers m⁻², respectively,) while mean tiller weight increased (from 2.0 to 3.5 g DM tiller⁻¹, respectively). Lowland tillers (2.4 and 4.2 g DM tiller⁻¹ for 1998 and 2001, respectively) were twice as large as upland tillers (1.2 and 2.1 g DM tiller⁻¹, respectively) in both years. Across all sites, plant density was positively correlated with tillers per plant ($r = 0.32$, $P < 0.001$) and with tiller density ($r = 0.53$, $P < 0.001$). Tillers per plant were negatively correlated with tiller weight within the lowland morphological genotype ($r = -0.42$, $P < 0.001$), but not within upland genotypes. Tiller density was negatively correlated with tiller weight within both lowland ($r = -0.52$, $P < 0.001$) and upland groups ($r = -0.27$, $P < 0.01$). Others have also reported that switchgrass tiller density is negatively related to plant spacing (Kassel et al., 1985; Sanderson and Reed, 2000; Muir et al., 2001).

Other researchers have reported on the effect of row spacing on switchgrass yields but not on the influence of stand thinning. Sladden et al. (1995) reported that DMY increased as row spacing increased from 20 to

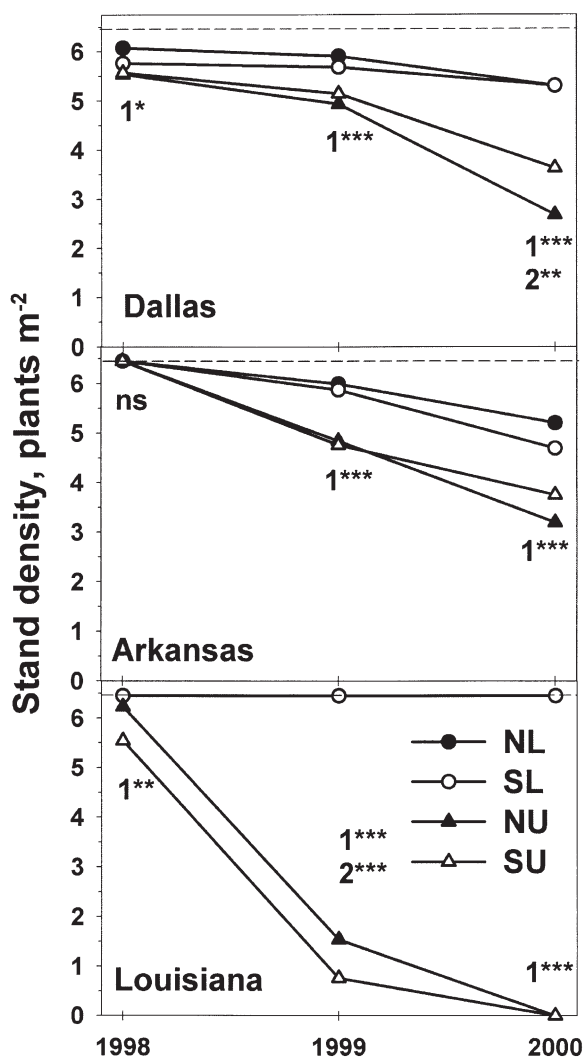


Fig. 4. Stand density of northern lowland (NL), southern lowland (SL), northern upland (NU), and southern upland (SU) groups of switchgrass entries over 3 yr in Hope, AR, Clinton, LA, and Dallas, TX. The dotted line represents stand density of 6.45 plants m⁻² at establishment. In Clinton, the NL and SL lines are superimposed. Within years, numbers followed by *, **, *** indicate differences at the 0.05, 0.01, and 0.001 levels, respectively, for orthogonal contrasts of (1) upland vs. lowland and (2) northern vs. southern.

81 cm in Alabama. Muir et al. (2001) reported that DMY was not consistently affected by row spacing in central Texas but tended to decrease linearly with row spacing in south Texas. In that trial, row spacing differences in DMY at the southern Texas site tended to diminish in each successive year, suggesting that plants at lower densities compensated by slowly increasing plant size over time. Yield components of a switchgrass biofuel crop include plant density and size, and the latter is determined by number of tillers per plant and tiller size. At Stephenville, differences in DMY among genotypes were mediated primarily through differences in tiller size. In Louisiana and Dallas, differences in DMY were mediated through changes in plant density or tillers per plant. The relationships among DMY, stand density, and plant size and tiller count suggest that switchgrass genotypes differed in ability to compensate for stand

thinning by increasing individual plant size. At most sites, DMY of lowland morphology entries remained relatively constant or increased over time despite stand thinning, while upland entries were not able to compensate to the same degree. This suggests that morphological type may cause critical stand density to differ across environments.

Lodging of switchgrass was reported at all sites except Stephenville (the site with the least rainfall) in some or all years (Table 4). Lodging was most severe at Arkansas, where high winds and heavy rain occurred by late May–early June each year. Lodging was greater for upland than for lowland genotypes in five of the six site–years. The exception was College Station in 1999, where the reverse occurred. Southern ecotype entries lodged more than northern entries in three of six site–years within the lowland morphological group, but ecotype did not affect lodging scores within the upland group. Within morphological type groups, lodging score at harvest was not correlated with DMY or plant density at harvest. For three site–years (Dallas 1999, Arkansas 1999 and 2000) where data for both lodging at harvest and plant density data the following year were collected, lodging was correlated with stand loss in the following year (calculated as plant density at harvest minus plant density in the following spring) among upland genotypes ($r = 0.60$, $P = 0.09$), but not among lowland genotypes. From this data it is impossible to conclude whether upland plants died because they lodged, or lodged because they died. Across all sites, larger tillers were less likely to lodge (tiller size and lodging score, $r = -0.95$, $P < 0.01$ and $r = -0.59$, $P < 0.05$, for upland and lowland genotypes, respectively).

Lodging can decrease yields by restricting access of harvest equipment to the crop or by decay of crop before harvest. Kätterer et al. (1998) cited lodging caused by stem weakness as a primary limiting factor in biofuel productivity of reed canarygrass (*Phalaris arundinacea* L.). Lemus et al. (2002) reported that lodging of switchgrass varied among growing seasons in Iowa, but not among varieties, while Casler et al. (2004) reported that lodging was more a function of genotype than environment. Christian et al. (2002) reported that upland morphological type varieties were more prone to lodging than lowland varieties in England. Cell wall components that give strength to stems, lignin and cellulose, are also the most desirable yield components of biomass crops intended for cofiring with coal (Hohenstein and Wright, 1994), so selection of plants for reduced lodging may be complementary to selection for increased cell wall content.

Diseases of roots and shoots occurred. Rust outbreaks were seen in Arkansas in all years, but were not observed at other locations. In the most severe outbreak (2000), upland entries had higher peak rust scores than lowland entries (28.3 vs. 21.0% of leaf affected, respectively, $P < 0.05$), and there were no differences in rust scores between ecotypes. However, rust scores for genotypes within morphological type groups were not correlated with yield, stand density at harvest, or stand density the following spring, indicating that rust had no

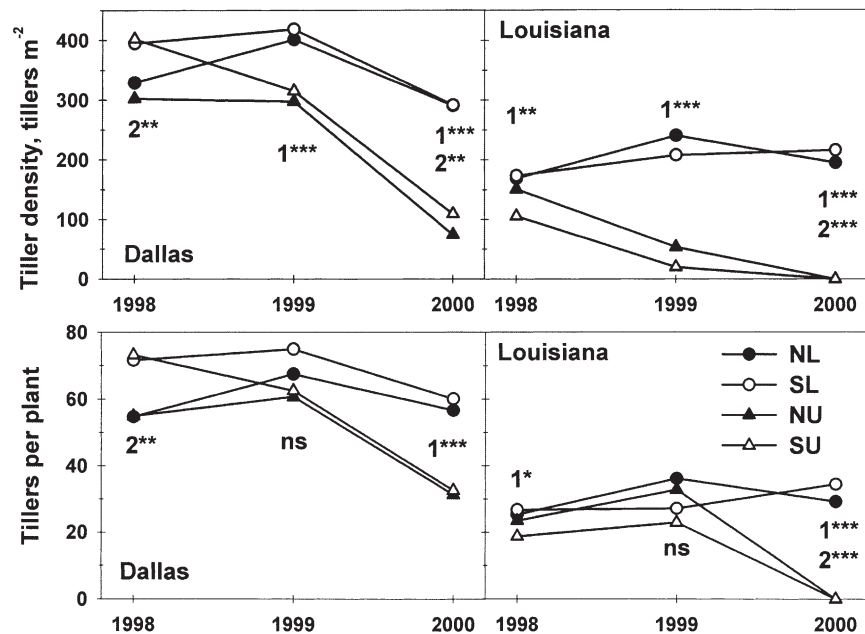


Fig. 5. Numbers of tillers per plant at harvest for northern lowland (NL), southern lowland (SL), northern upland (NU), and southern upland (SU) groups of switchgrass entries in Dallas, TX. Within years, numbers followed by *, **, *** indicate differences at the 0.05, 0.01, and 0.001 levels, respectively, for orthogonal contrasts of (1) upland vs. lowland and (2) northern vs. southern.

lasting impact on stand performance. In contrast, Hopkins et al. (1995b) found weak positive correlations between rust scores and yield and reported no differences in rust incidence between upland and lowland genotypes in the Midwest. Plant-parasitic nematodes from nine genera were identified in soil under the switchgrass plants at Louisiana, College Station, Arkansas, and Stephenville following harvest in 2001 (Cassida et al., 2002). In that report, lesion nematodes (*Pratylenchus* spp.) were associated with poor persistence of upland genotypes at the Arkansas and Louisiana sites, but the specific effect of parasitic nematodes on switchgrass remains unknown.

CONCLUSIONS

On average, genotypes in the lowland morphological type group yielded approximately three times more biomass and had greater persistence than upland genotypes. Differences in DMY and persistence between

lowland and upland morphological types tended to be greater at higher rainfall sites. Lowland genotypes showed a strong ability to compensate for stand thinning over time by increasing individual plant size, tillers per plant, or tiller size, while upland genotypes were not able to fully compensate for thinning in these environments. In addition, upland genotypes were more likely to lodge and had higher rust scores than lowland genotypes. On average, southern ecotypes yielded 40% more biomass than northern ecotypes, but there was little difference in persistence between ecotypes. Across sites, genotype SL931 was the most consistent of the experimental lines at equaling or bettering DMY of Alamo. All genotypes tended to yield more biomass as latitude increased, and lowland genotypes were more sensitive to differences in moisture availability than upland genotypes. We conclude that switchgrass feedstock production for the south central region of the USA should focus on southern lowland genotypes, and that upland genotypes have limited usefulness for biofuel production in the region be-

Table 4. Lodging score at harvest of northern lowland (NL), southern lowland (SL), northern upland (NU), and southern upland (SU) groups of switchgrass genotypes at Hope, AR, Clinton, LA, College Station, Texas, and Dallas, TX†.

| Site | Year | Switchgrass genotype group | | | | CV | Contrasts‡ |
|---------------------|------|----------------------------|------|------|------|------|------------|
| | | NL | SL | NU | SU | | |
| | | — % of plot area lodged — | | | | | |
| College Station, TX | 1999 | 47.5 | 63.4 | 15.6 | 33.8 | 33.2 | 1***, 2* |
| Clinton, LA | 2001 | 47.5 | 86.9 | § | § | 7.5 | 1***, 2*** |
| Dallas, TX | 1999 | 57.5 | 55.6 | 85.0 | 82.5 | 19.0 | 1**, 2* |
| | 2000 | 25.0 | 40.6 | 78.8 | 77.5 | 30.4 | 1***, 2*** |
| Hope, AR | 1999 | 50.0 | 59.1 | 77.5 | 70.0 | 38.3 | 1* |
| | 2000 | 60.6 | 64.4 | 83.3 | 90.0 | 26.3 | 1** |

* Significant at the 0.05 probability levels.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† No lodging was observed at Stephenville, TX, in any year.

‡ Orthogonal contrasts: (1) upland vs. lowland morphological type, (2) northern vs. southern ecotype.

§ Upland entries had all died by 2001 in Louisiana.

cause of low yields and poor persistence. Southern lowland genotypes exhibited small differences in yield across sites that suggest selection for particular environments may be beneficial.

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