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Perennial Biomass Grasses and the Mason–Dixon Line: Comparative Productivity across Latitudes in the Southern Great Plains

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Perennial Biomass Grasses and the Mason–Dixon Line: Comparative Productivity across Latitudes in the Southern Great Plains

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Abstract Understanding latitudinal adaptation of switchgrass (*Panicum virgatum* L.) and *Miscanthus* (*Miscanthus*× *giganteus* J. M. Greef & Deuter ex Hodk. & Renvoize) to the southern Great Plains is key to maximizing productivity by matching each grass variety to its optimal production environment. The objectives of this study were: (1) to quantify latitudinal variation in production of representative upland switchgrass ecotypes (Blackwell, Cave-in-Rock, and Shawnee), lowland switchgrass ecotypes (Alamo, Kanlow), and *Miscanthus* in the southern half of the US Great Plains and (2) to investigate the environmental factors affecting yield variation. Leaf area and yield were measured on plots at 10 locations in Missouri, Arkansas, Oklahoma, and Texas. More cold winter days led to decreased subsequent Alamo switchgrass yields and increased subsequent upland switchgrass yields. More hot-growing season days led to decreased Kanlow and *Miscanthus* yields. Increased drought intensity also contributed to decreased *Miscanthus* yields. Alamo

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switchgrass had the greatest radiation use efficiency (RUE) with a mean of 4.3 g per megajoule intercepted PAR and water use efficiency (WUE) with a mean of 4.5 mg of dry weight per gram of water transpired. The representative RUE values for other varieties ranged from 67 to 80 % of Alamo's RUE value and 67 to 87 % of Alamo's WUE. These results will provide valuable inputs to process-based models to realistically simulate these important perennial grasses in this region and to assess the environmental impacts of production on water use and nutrient demands. In addition, it will also be useful for landowners and companies choosing the most productive perennial grasses for biofuel production.

Keywords Biofuel grasses · Switchgrass · *Miscanthus* · Simulation modeling

Introduction

Switchgrass (*Panicum virgatum* L.) and *Miscanthus*×*giganteus* J. M. Greef & Deuter ex Hodk. & Renvoize (hereafter referred to as *Miscanthus*) represent two primary plant species of interest for bioenergy production in the USA. Both have repeatedly shown promise as being highly productive perennial grasses adapted to either marginal or prime agricultural soils. Switchgrass, with its high variation in ecotypes, can be grown as far south as northern Mexico and as far north as southern Canada. The sustainability and yield stability of switchgrass biomass production will depend on understanding the adaptation of representative ecotypes to different environments. Widespread reports of *Miscanthus* grown in the Midwest have spurred interest in it as an alternative to switchgrass. However, no *Miscanthus* yields have been reported for the southern Great Plains. It is therefore imperative to quantify productivity of these biofuel grasses in this region of the USA. If biofuel production is targeted for "marginal" soils, identifying the species and ecotypes adapted to these conditions also is extremely important.

There are many environmental gradients that transverse the southern two thirds of the US Great Plains. In the often-cited biofuel crop regional adaptation map [30] (Electronic supplementary material (ESM) Fig. S1), there is a break in adaptation regions running east to west through eastern Oklahoma and western Arkansas. There are north-to-south gradients in the average daily temperature of the coldest quarter (ESM Fig. S2a) and in average daily temperature of the warmest quarter (ESM Fig. S2b) and east-to-west gradients annual precipitation (ESM Fig. S2c). Casler et al. [3–5] described latitudinal and longitudinal variation in switchgrass in the northern Great Plains. The major abiotic factors that regulate adaptation of switchgrass populations are photoperiodism, heat tolerance, cold or freezing tolerance, and precipitation [5, 25]. Furthermore, Vogel et al. [34] used climate and ecoregions to develop plant adaptation regions for switchgrass ecotypes.

Previous switchgrass studies have shown variable responses to photoperiod manipulation depending on the ecotype. In the central Great Plains, switchgrass ecotypes from the Dakotas (upland ecotypes) flower and mature early and are short in stature, whereas those from Texas and Oklahoma (lowland ecotypes) flower late and are tall [9, 24]. When upland (northern) ecotypes (i.e., Blackwell, Cave-in-Rock, and Shawnee) are grown in the south, they remain shorter and flower earlier thus decreasing their dry matter yields. However, when lowland (southern) ecotypes (i.e., Alamo) are planted further north, they flower later and are taller, thus having more stable yields than upland ecotypes. The photoperiod response has also been reported to be responsible for winter survival. Southern types moved too far north mature too late and do not survive late season winter freezes [34].

Switchgrass water use efficiency (WUE), the balance of carbon assimilated per unit of water transpired, has been linked to higher yields. While transpiration and photosynthesis are closely related to yield, WUE is most closely linked to higher biomass yield [37]. Measurements of WUE on single leaves indicate that switchgrass, as expected, uses relatively low levels of water, and that the highest yielding switchgrass varieties have the highest water use efficiencies [23].

In this study, five switchgrass ecotypes and *Miscanthus* were planted in replicated field trials at 10 locations in Texas, Arkansas, Oklahoma, and Missouri. The main objectives were to: (1) describe and identify the most productive (highest biomass and leaf area) perennial species and ecotype at each location; (2) determine the impact of photoperiod, precipitation, high temperature stress during the growing season, and low temperature stress during the preceding winter on yield; (3) determine the radiation use efficiency (RUE) and WUE of these perennial grasses in these representative sites in the central and southern Great Plains to allow realistic simulation of their production with process-based simulation models. Process-based models such as Agricultural Land Management Alternatives with Numerical Assessment Criteria (ALMANAC) [17], Environmental Policy Integrated Climate (SWAT) [35, 36], and Soil and Water Assessment Tool (EPIC) [2] provide realistic simulation of biofuel plant species for assessing management practices that maximize

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production and minimize environmental impact. Process-based simulation of these perennial biofuel grasses requires realistic understanding of the important processes affecting adaptation and consequently biomass production.

Methods

In 2009, we selected nine locations (Table 1) across the south-central USA to capture a range of environmental conditions. In 2010, plots at an additional site, Booneville, AR, were also established. At each site, five switchgrass ecotypes, "Alamo", "Blackwell", "Cave-in-Rock", "Kanlow", and "Shawnee" (Table 2) were sown from seed from Turner Seed, Breckenridge, TX, 76424-8165. Seeding rate was 5.6 kg pure live seed per hectare. *Miscanthus* plants (originally purchased from Kurt Bluemel, www.kurtbluemel.com/Miscanthus_giganteus.html) in 4-l pots were transplanted into the plots. Genetic analysis of the *Miscanthus* material used indicated that the plant material was identical to the Illinois clone (Michael Casler, personal communication). In spring 2009, all ecotypes and species were planted in randomized complete block design with single row plots, 1 m apart and 5 m long, with four replicate rows per plant variety. Harvest dates were chosen to establish plant growth during the active growing portion of spring and summer, with logistical constraints due to travel distances between plots. In 2010, plants were harvested once in June or July at each location and again in October. In 2011, plants were harvested three times at each location. These were in May or June, July and August, September, or October. At each location, weeds were controlled by use of pre- and postemergence herbicides [Prowl H20 (pendimethalin: (*N*-(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzenamine)) and 2,4-D-2,4-dichlorophenoxyacetic acid], hoeing, and hand weeding.

Destructive harvests were taken during the growing seasons in order to characterize plant growth. These harvests were all taken from areas not previously harvested during the growing season. "Final yield" was the biomass at the final harvest each year. At each harvest, plant height, fresh and dry weights, fraction intercepted photosynthetically active radiation (FIPAR), and leaf area index (LAI) were also measured. For switchgrass ecotypes, 0.5 m of a row was harvested, while with *Miscanthus* 1.0 m of a row (one plant) was harvested. The samples were weighed for a total fresh weight. When the total sample exceeded 1,000 g, a grab sample of 200–500 g was separated. Samples were dried at 66 °C in a forced-air oven until the dry weight had stabilized. Measurements of FIPAR were taken using an AccuPAR LP-80 Ceptometer (Decagon Devices, Pullman, WA, USA) within 2 h of solar noon. These values of FIPAR consisted of multiple measurements with the light sensor moving parallel to the row, in the area from mid-row to mid-row. In this way, the pertinent ground area for each row was sampled. Care was taken to avoid shadows from neighboring rows. An external light source was used for concurrent above and below values that were averaged for the row. Leaf area of a subsample was measured with a LI-3100 Area Meter (LI-COR Biosciences, Lincoln, NE, USA).

WUE and RUE were calculated using output from the ALMANAC model [17]. The ALMANAC model was parameterized so that the actual LAI equaled the simulated LAI for the first harvest date each year. We used only this early growth interval for RUE and WUE calculations in an effort to minimize the prevalent drought impacts evident at several of the sites in these years. This avoided unrealistically low values of RUE and WUE due to growth decreasing drastically due to drought. Daily weather data at each site and (2009–2011) from National Oceanic and Atmospheric Administration were used in the model [29]. The RUE was calculated as the ratio of measured dry matter over cumulative simulated intercepted PAR. The WUE was calculated in terms of measured dry matter produced per unit simulated water transpired [28]. Plant dry weight was the total above-ground dry weight (cutting height, 0.1 m). Water use was determined using the ALMANAC model to simulate the amount of water transpired by plants during the growth period.

Final dry weights for each plant type as a function of latitude were analyzed by regression with Statistical Analysis System [32]. Firstly, within each year, the three upland types were analyzed for significant different slopes and intercepts using

Table 1 Soil type, latitude, and average annual precipitation for 10 locations

Location	Soil type	Latitude	Precipitation[a] (mm)
Elsberry, MO	Menfro silt loam	39.16	972
Columbia, MO	Mexico silt loam	38.89	1,025
Mt. Vernon, MO	Gerald silt loam	37.07	1,171
Stillwater, OK	Kirkland silt loam	36.12	932
Fayetteville, AR	Pickwick gravely loam	36.09	1,169
Booneville, AR	Leadvale silt loam	35.09	1,213
Nacogdoches, TX	Attoyac fine sandy loam	31.50	1,229
Temple, TX	Houston black clay	31.04	910
Kingsville, TX	Cranell sandy clay loam	27.54	736
Weslaco, TX	Hidalgo sandy clay loam	26.22	645

[a]Obtained from US Climate Data [29]

Table 2 County, state, and latitude of origin for each switchgrass type

Types	Site of origin		
	County	State	Latitude
Alamo	Live Oak	Texas	28
Blackwell	Kay	Oklahoma	37
Cave-in-Rock	Hardin	Illinois	38
Kanlow	Hughes	Oklahoma	35
Shawnee	Hardin	Illinois	38

indicator variables [27], comparing both Cave-in-Rock and Blackwell to Sunburst. Subsequently, after pooling these three upland types, Alamo, Kanlow, and *Miscanthus* were compared to the pooled upland responses using indicator variables for slope and intercept. All differences were compared using a 95 % confidence level.

Photoperiod was calculated at 30 days after the estimated green-up date using standard equations based on latitude and day of the year, as described in the CERES-Maize book [15]. The green-up date was estimated using the model, based on measured temperatures and the base temperature of 12 °C. This corresponds to the approximate timing of photoperiod sensitivity as described for short day C_4 plants such as maize (*Zea mays* L.) [16]. Cold temperature effects were estimated by determining the number of days with temperatures below 0 °C in the autumn and winter prior to the growing season of each year. High temperature effects were estimated by determining the number of days with temperatures exceeding 32 °C during each growing season. Above this temperature, maximum quantum yield of photosystem II and the activation state of Rubisco decreased for C_4 maize (*Z. mays* L.) plants [8]. First, linear regression and Pearson's product–moment correlations were used to analyze the relationship between each individual environmental variable or surrogate (latitude, photoperiod, precipitation, high temperature stress, and low temperature stress) on yearly biomass yield. A principal component analysis (PCA) was then used create orthogonal decompositions of the highly correlated environmental variables. Next, the new PCA variables were used in a multiple regression to analyze the ecotype, environment, and ecotype×environment interactions as predictors of yield. Lastly, stepwise linear regression was used to determine which sets of variables accounted for the largest amount of observed yield variation. Only variables with a 95 % confidence level were included in these regression models.

Results

Yearly Biomass Yield and Leaf Area

Overall, yearly biomass yield and LAI increased between the second and third year after establishment at all sites. We

Table 3 Yield in Mg per hectare±SD for the highest yielding harvest

	Alamo	Blackwell	Cave-in-Rock	Kanlow	Shawnee	*Miscanthus*
Year 2						
Weslaco	**19.5**±10.8	6.0±2.3	6.3±3.1	9.5±4.9	6.7±2.5	
Kingsville	**19.0**±2.4	4.6±2.4	5.2±2.6	**11.3**±7.3	5.7±1.4	5.7±5.7
Nacogdoches	12.5±5.2	6.2±3.5	6.3±3.8	7.2±4.2	4.3±1.3	5.1±3.6
Stillwater	12.1±4.2	**10.0**±1.3	**10.6**±2.3	9.6±3.1	7.8±1.4	3.4±2.9
Fayetteville	15.9±4.5	7.8±1.7	**10.3**±6.5	**12.4**±2.0	7.9±2.9	11.8±4.9
Booneville	9.5±3.4	8.0±1.5	5.5±1.8	**10.7**±12.6	**9.3**±5.3	4.5±2.6
Mt. Vernon	**17.3**±4.1	**8.8**±3.0	5.0±2.4	**11.0**±5.9	**11.0**±3.3	17.1±12.9
Columbia	11.8±3.3	4.4±0.8	7.4±3.9	**10.5**±3.7	5.1±1.0	**15.8**±8.9
Elsberry	**19.9**±3.9	**12.0**±2.6	**11.4**±1.7	**16.6**±2.4	**9.4**±1.4	**17.6**±3.9
Mean of RMV	18.9	10.3	10.8	12.1	9.9	16.8
Year 3						
Weslaco	**26.1**±19.3	1.7[a]	2.0±1.1	9.4±6.2	2.0±0.8	
Kingsville	**26.7**±16.4	2.2[a]	2.1±1.0	7.4±1.9	1.6±0.3	5.1±1.5
Temple	**30.6**±26.5	4.8±2.8	4.8±1.5	13.8±7.3	5.2±0.3	4.2±2.3
Nacogdoches	**33.3**±14.6	3.7±1.7	3.1±1.3	14.9±10.5	4.9±2.3	2.8±2.3
Stillwater	15.0±7.0	8.8±3.6	**12.5**±3.6	12.4±0.9	9.7±6.0	2.5±0.6
Fayetteville	13.8±5.2	**9.5**±3.8	9.8±3.5	13.7±4.2	**10.0**±3.9	9.1±3.8
Mt. Vernon	15.1±7.0	**11.6**±1.9	**14.8**±3.5	**21.2**±9.7	**12.6**±4.0	10.7±1.0
Columbia	20.9±8.9	6.7±1.4	8.9±1.3	**21.2**±7.0	7.6±2.6	**27.3**±6.3
Elsberry	21.6±7.0	**12.0**±4.5	**15.8**±3.9	**28.0**±6.6	**14.2**±5.1	**49.7**±5.7
Mean of RMV	29.1	11.0	13.6	23.5	12.3	38.5

The bold values were selected as representative maximum values (RMV) for the year to define realistic potential values for each grass for each year

[a] Only one rep harvested, so no value for SD

Table 4 First harvest date values for Leaf Area Index±SD

	Alamo	Blackwell	Cave-in-Rock	Kanlow	Shawnee	*Miscanthus*
Year 2						
Weslaco	**4.7**±2.3	1.0±0.7	0.9±1.0	1.5±0.9	1.0±0.9	–
Kingsville	**5.6**±3.9	**3.2**±1.7	2.7±0.8	**5.9**±6.4	**4.2**±1.5	0.4
Nacogdoches	2.7±1.0	1.9±0.8	1.6±0.4	2.3±0.8	2.1±0.7	0.7±0.6 (1.1)
Stillwater	**4.7**±0.5	**3.3**±1.3	**4.2**±1.4	1.6±0.9 (2.2)	**3.6**±0.9	0.6±0.3 (1.2)
Fayetteville	2.2±0.3 (**4.37**)	2.9±0.4	2.9±0.3	1.9±0.8 (2.5)	2.7±0.4	1.1±0.5 (3,3)
Booneville[a]	1.7±0.5	1.7±0.6	1.7±1.0	1.4±0.7	2.9±0.8	0.6±0.2
Mt. Vernon	**5.4**±0.9	**3.8**±1.9	1.8±1.5	**3.1**±0.7	**4.5**±2.6	2.5±0.4 (**4.45**)
Columbia	**4.7**±1.7	2.8±0.6	**4.1**±1.3	2.6±1.2	2.6±0.6	**4.5**±1.7
Elsberry	**4.3**±0.4	2.2±1.5	2.9±1.6	**3.5**±0.3	1.2±0.4	**3.6**±1.2
Mean of RMV	4.8	3.4	4.2	4.2	4.1	4.2
Year 3						
Weslaco	1.8±0.4 (**8.2**)	(0.23)	(0.45)	0.7±0.6 (2.1)	(1.7)	
Kingsville	**9.5**±6.1	0.5±0.2 (0.9)	0.6±0.5	2.4±2.8	0.3±0.1	0.92 (1.9)
Temple	**10.9**±5.1	2.4±2.2	1.9±0.8 (2.0)	2.0±0.8	2.6±0.2	2.9±1.8
Nacogdoches	4.4±0.9 (5.4)	1.3±0.4 (1.34)	1.2±0.9	2.4±0.8	1.2±0.4 (1.5)	1.0±0.8
Stillwater	4.8±1.6	**4.2**±0.4	**4.3**±0.9	3.5±1.3	**4.3**±1.2	1.0±0.4
Fayetteville	5.5±2.2	**4.8**±1.8	**4.0**±1.5	**5.2**±2.1	3.5±2.0	5.9±2.1
Mt. Vernon	5.6±1.1	**5.4**±3.8	3.7±1.3 (**4.9**)	3.7±0.7	**4.0**±3.0	2.8±0.7
Columbia	5.2±1.1	**4.3**±1.4	**4.7**±0.6	3.1±1.8 (**6.5**)	**4.3**±1.2	6.5±2.1 (**7.6**)
Elsberry	**8.0**±0.8	**5.9**±1.8	**6.6**±1.2	**8.0**±2.1	**8.8**±2.3	**7.6**±3.3
Mean of RMV	9.2	4.9	4.9	6.6	5.4	7.6

Harvest dates were June and July in 2010 and May and June in 2011. Values in parenthesis are means from a later harvest if that LAI was greater than the first one. These were for October in 2010 and in July in 2011. In this table and subsequent tables and figures, year 2 was the second year after the establishment year, which was 2010 everywhere but Booneville. In Booneville, year 2 was 2011. Correspondingly, year 3 was 2011 and there was no year 3 for Booneville. The bold values were selected as representative maximum values (RMV) for the year, chosen in an attempt to define realistic potential values for each grass for each year

[a] The Booneville LAI values did not correspond to the date of maximum dry matter shown below. LAI was not measured on the date of maximum dry matter at that site

Table 5 Photoperiod of 30 days after green-up, number of days with mean temperature less than 0 °C during previous winter, number of days with mean temperature greater than 32 °C during the growing season, and precipitation (Jan–Aug) for 10 locations

	Elsberry	Columbia	Mt. Vernon	Stillwater	Fayetteville	Booneville	Nacogdoches	Temple	Kingsville	Weslaco
Photoperiod	15.78	15.75	15.54	14.55	14.48	14.54	13.27	13.26	13.18	13.15
No. of days <0 (°C)										
Year 2	88	84	80	74	84	76	43	18	6	4
Year 3	107	99	82	85	93	–	46	18	14	9
No. of days >32 (°C)										
Year 2	42	35	38	69	46	66	115	107	100	128
Year 3	29	40	57	100	68	–	106	111	128	133
Precipitation (mm)[a]										
Year 2	739	1,189	655	843	782	826	412	597	757	437
Year 3	625	673	564	358	871	–	513	289	193	203

The numbers of cold days were calculated in the previous winter for 1 September through 3 April (estimated green-up date) for the three Missouri locations for 1 October through 31 March for Fayetteville and Stillwater, and for 1 September through 28 February for the four Texas locations. The numbers of hot days during the growing season were calculated for 1 May through 31 August for the three Missouri locations, for 1 April through 31 September for Fayetteville and Stillwater, and for 1 March through 31 August for the Texas locations. Year 3 data for Booneville is missing, since it was planted a year later than the other locations

[a] Precipitation total from January through August

selected representative high values of final biomass of each species and ecotype, in an attempt to define the potential yields for each species and ecotype within this group of locations for these years. These values were chosen to show the potential values for modeling the species and ecotypes in the areas for which they are optimally adapted. These will serve as guides for simulating the species and ecotypes in the regions of adaptation. For these selected biomass values (Table 3), Alamo had the highest yield in the second year, while *Miscanthus* had the highest yield in the third year. Alamo's yield the second year was 19 $Mgha^{-1}$, and this increased to 29 $Mgha^{-1}$ by the third year. The biomass yield of *Miscanthus* increased from 17 to 38 $Mgha^{-1}$ over the 2 years. Blackwell, Cave-in-Rock, and Shawnee had similar yields near 10 $Mgha^{-1}$ in the second year and Kanlow was near 12 $Mgha^{-1}$. Blackwell, Cave-in-Rock, and Shawnee showed increases between the second and third year, up to 11–14 $Mgha^{-1}$. Kanlow showed more of an increase to over 23 $Mgha^{-1}$.

The mean LAI values of the selected representative high values increased between the second and third year after establishment, with Alamo switchgrass having the greatest LAI values and *Miscanthus* the second greatest LAI by year 3 (Table 4). Leaf areas of Alamo and *Miscanthus* nearly doubled in year 3 as compared to year 2. Other switchgrass ecotypes showed increases, but not as dramatic. For the second year, based on these selected high values, a LAI value of about 4.2 would be reasonable for Cave-in-Rock, Kanlow, Shawnee, and *Miscanthus*, with Alamo larger near 5 and Blackwell smaller near 3.5. By the third year, Alamo's LAI value was greater than 9 and *Miscanthus*' nearly 8. A LAI value of 5 would be reasonable for Blackwell, Cave-in-Rock, and Shawnee, with Kanlow nearly 7.

Latitudinal Differences

The photoperiods, number of cold days in the previous winter, number of hot days during the growing season, and

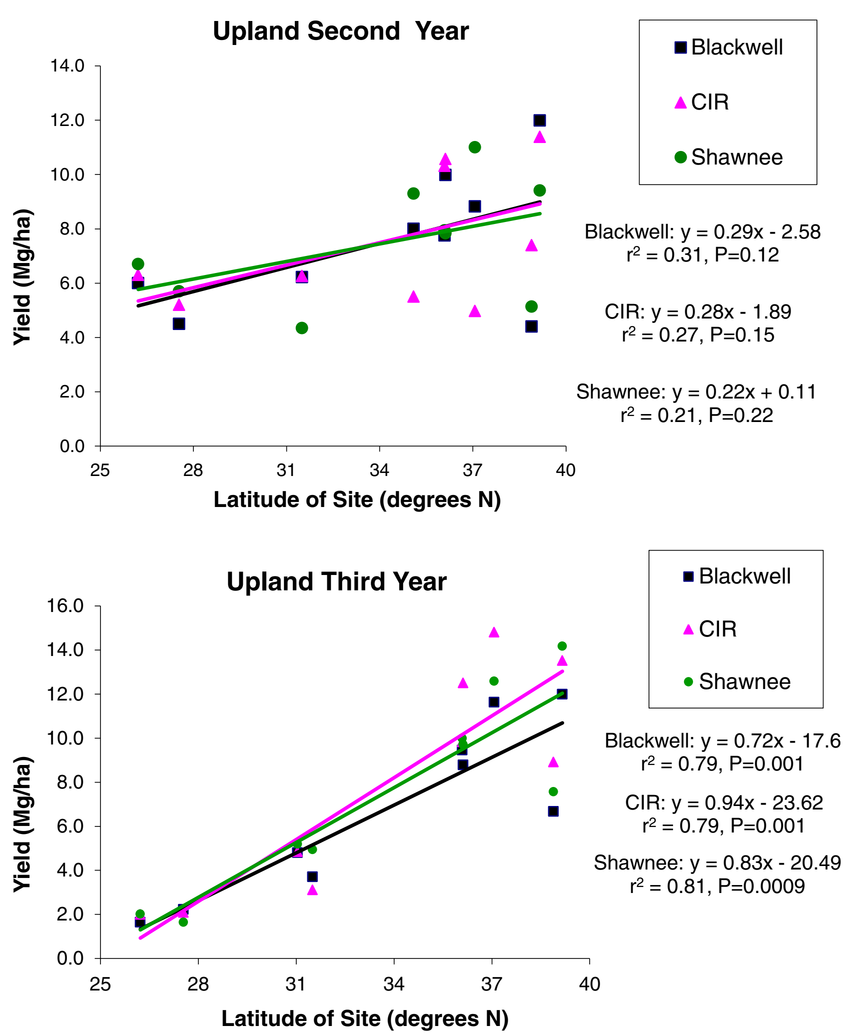


Fig. 1 Final dry matter yields as related to latitude for three upland switchgrass ecotypes at 10 locations for the second and third years after plot establishment. *P* values are the significance levels for the slopes

precipitation amounts showed expected trends with latitude (Table 5). Photoperiod of 30 days after green-up was only about 13 h in the southernmost locations and nearly 16 h in the northernmost. There were fewer days of temperatures below freezing and more days of hot temperatures at the more southern locations. Likewise, precipitation was least in the southern locations.

The three upland ecotypes of switchgrass (Blackwell, Cave-in-Rock, and Shawnee) showed similar responses to latitude, with increasing yields at the higher latitudes (Fig. 1). The slopes were not significant in the second year, but were all significant the third year, as shown by the *P* values. Regression analysis showed that Blackwell and Cave-in-Rock did not have significantly different intercepts or slopes for their regressions relative to Shawnee in either year. Thus, for the following analyses, these three were pooled and called "Upland". Correspondingly, relative to this Upland data, Alamo had a significantly different slope and intercept in each year. Kanlow and *Miscanthus* did not differ significantly from Upland in slope or intercept in 2010, while both had significantly different slopes than Upland in 2011. Kanlow and *Miscanthus* also showed increases in yield at higher latitudes, especially in the third year, while the Alamo ecotype with the most southern latitude of origin, showed no significant yield response to latitude in either year (Fig. 2). *Miscanthus* showed the greatest change with latitude both years, as shown by the steepest slope each year. Kanlow showed a greater responsiveness than the pooled upland ecotypes but not as great as the *Miscanthus* slopes each year. Maximum yields occurred near the latitude of origin for all species in all years (Fig. 3). Because of the closeness of the latitudes of origin of the three upland ecotypes, the mean value for latitude of origin was used for the pooled analysis. Moving northward (for Alamo) or moving southward (for all others) resulted in reduced yield, especially in the third year.

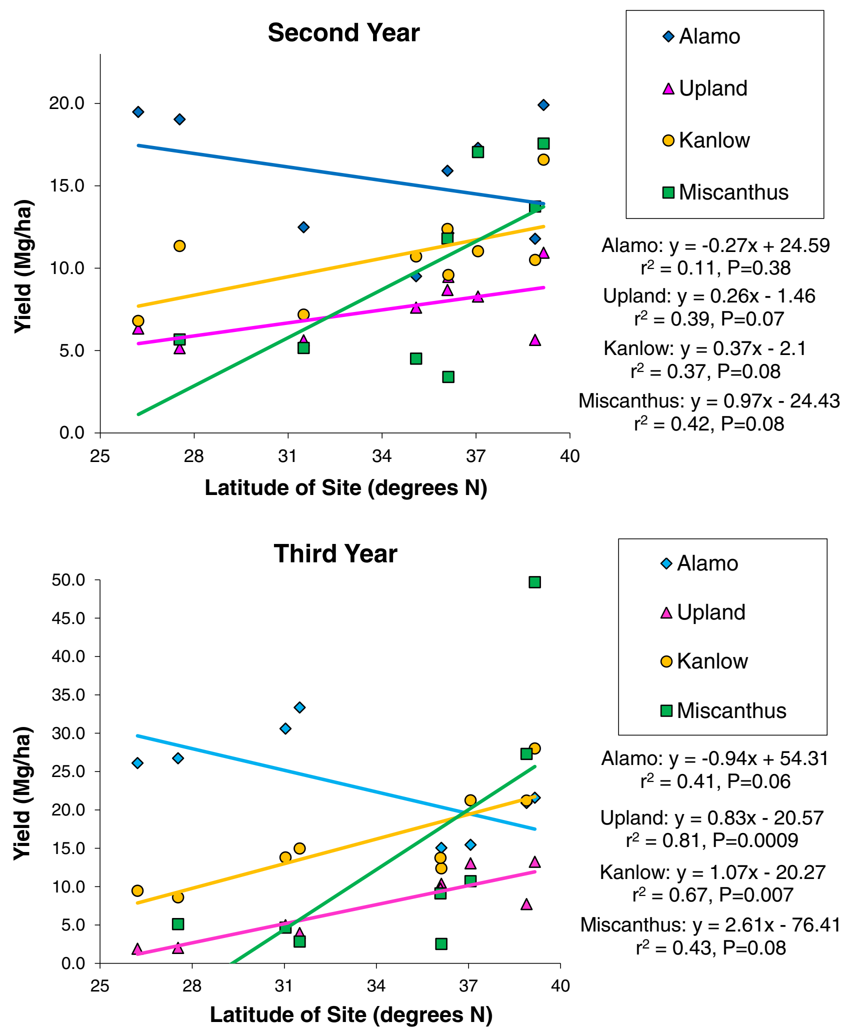


Fig. 2 Final dry matter yields as related to latitude for pooled upland switchgrass ecotypes, Alamo and Kanlow switchgrass, and *Miscanthus* at 10 locations for the second and third years after plot establishment. *P* values are the significance levels for the slopes

Potential causes for Yield Differences

The correlation between each environmental variable and the total yield harvested the third year after establishment varied among switchgrass ecotypes and *Miscanthus* (Table 6). There was a significant positive relationship between photoperiod and yields of *Miscanthus* in the second year, and of all the switchgrass ecotypes and *Miscanthus* in the third year (Fig. 4). For Alamo, there was a significant negative relationship for the third year. There was a significant positive correlation between precipitation during the growing seasons and yield in the third year for Kanlow and *Miscanthus* (Table 6 and Fig. 5). The correlation between Alamo and upland yields and growing season rainfall were not significant in either year. It appeared that even the drier sites had sufficient rainfall to meet demands for at least Alamo growth both years.

High-growing season temperatures and cold winter temperatures had differing effects on the plants according to

Table 6 Pearson's correlation coefficients for final biomass yield after the third year of establishment as a function of four environmental variables

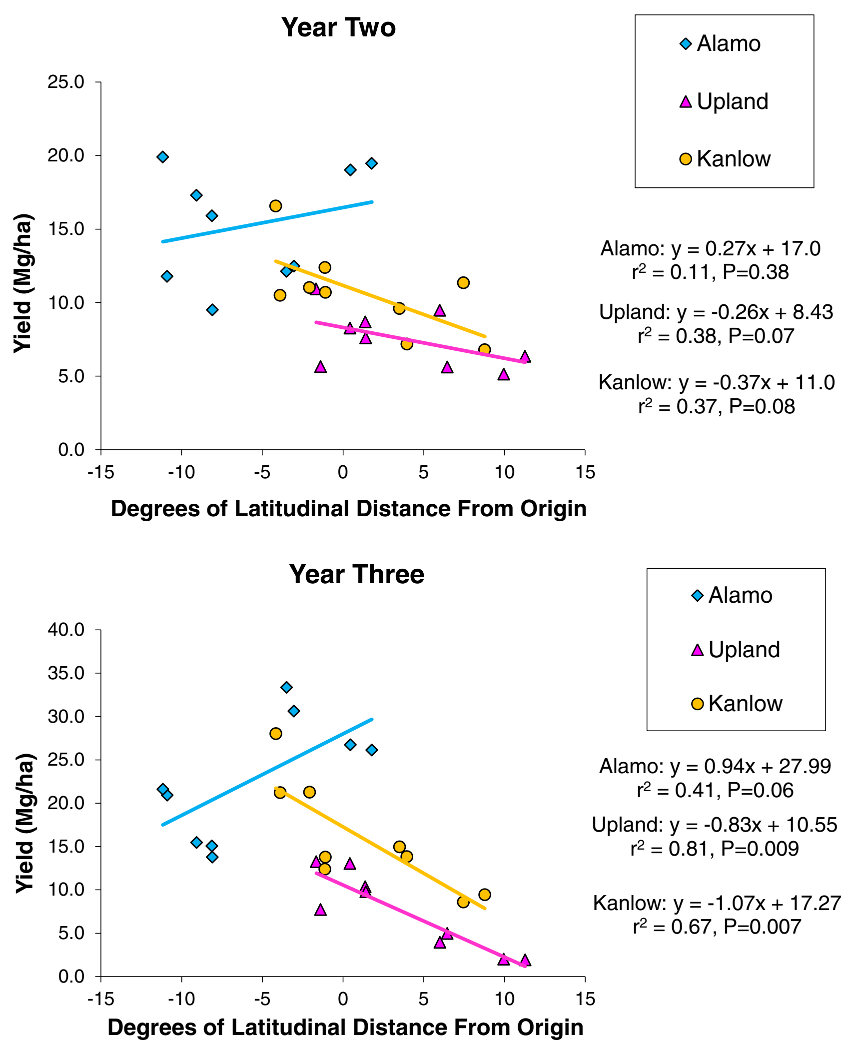
Pearson's correlation coefficient (*r*)

	Alamo	Kanlow	*Miscanthus*	Upland
Photoperiod	*−0.69*[a]	0.85[a]	0.72[a]	0.88[a]
Cold stress	*−0.72*[a]	0.75[a]	0.62	0.88[a]
Heat stress	0.53	*−0.92*[a]	*−0.83*[a]	*−0.83*[a]
Precipitation	*−0.32*	0.83[a]	0.83[a]	0.55

Photoperiod is the day length at 30 days after green-up. Cold stress is the number of days with daily minimum temperature less than 0 °C in the previous winter (October through February). Heat stress is the number of days with maximum temperature greater than 32 °C. Precipitation is from January through August.

[a] Significant correlation, α=0.05

Fig. 3 Final dry matter yields for pooled upland switchgrass ecotypes, Alamo and Kanlow switchgrass, at 10 locations for the second and third years after plot establishment as a function of degrees from latitude of origin. *P* values are the significance levels for the slopes



latitude of origin, as expected. Winter injury was a factor only for the most southern adapted switchgrass. Cold temperatures during the previous winter were positively correlated with yields in the third year for Kanlow and the Upland ecotypes (Table 6 and Fig. 6). Alamo's third year yields had a significant negative correlation with cold temperatures during the previous winter while *Miscanthus* failed to show a significant relationship in either year. In contrast, there was a significant negative relationship between heat stress and the yields of Kanlow and *Miscanthus* in both years and of the pooled upland ecotypes in the third year. Hot temperatures during the growing season did not significantly affect Alamo in either year (Fig. 4 and Table 6). *Miscanthus* was especially sensitive to hot growing season temperatures, having the steepest negative slope each year.

Comparing the correlation coefficient for each ecotype and environmental variable revealed some interesting trends for the latitudinal clines in yield (Table 6). The factor that explained the most variation in Alamo's yield was cold temperatures in the preceding winter, probably due to cold injury affecting the subsequent growing season's productivity. For the pooled upland ecotypes, cold temperatures during the preceding winters and photoperiod rainfall explained the most variation in yield differences. However for the upland ecotypes, cold temperatures actually led to higher yields in subsequent growing seasons. For the other lowland type, Kanlow, hot temperatures during the growing season appeared to drive latitudinal differences by decreasing yields. Finally, for *Miscanthus* yields, heat stress and decreased precipitation during the growing season were the most important explanatory variables.

Measures of temperature, precipitation, and photoperiod are known to be highly correlated. The first two PCA components explained 99.97 % of the variance in the four environmental variables (ESM Table S1). The first component corresponded to average precipitation (hereafter termed pca1 precip), and the second component (hereafter, termed pca2 temp stress) was a composite of heat and cold stress. Four different models were analyzed to determine the strength of ecotype, environment, and ecotype × environment interactions. The first model

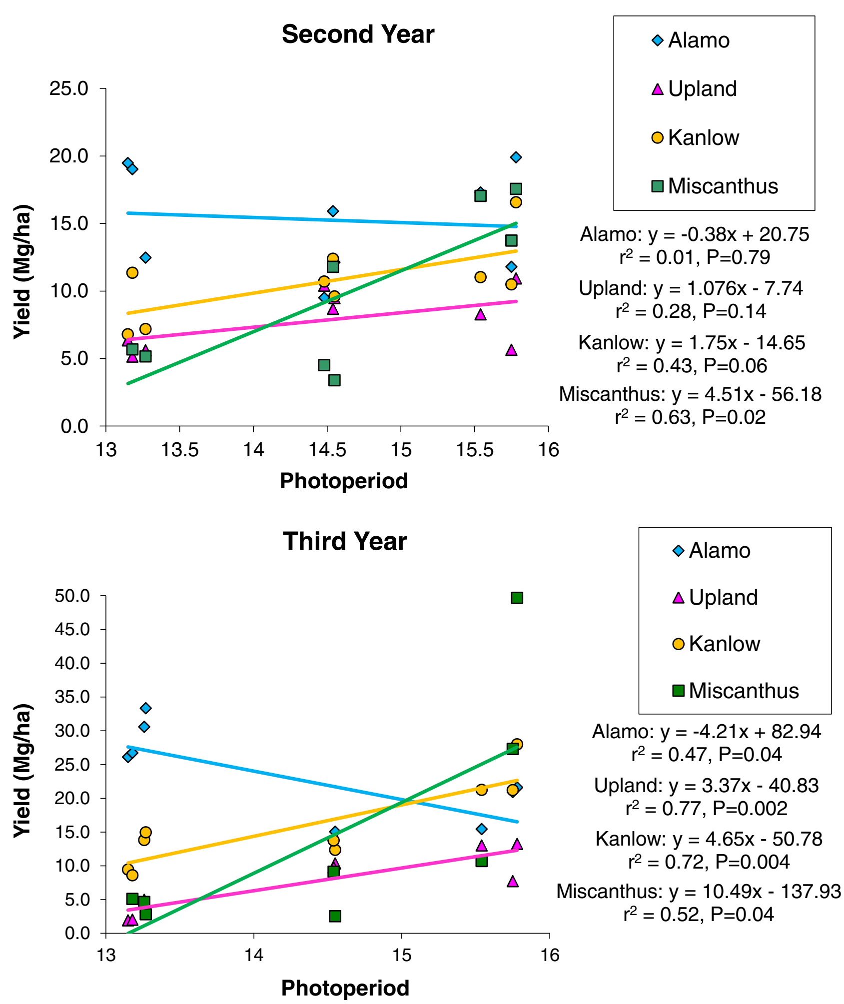


Fig. 4 Final dry matter yields as related to photoperiod of 30 days after green-up for pooled upland switchgrass ecotypes, Alamo and Kanlow switchgrass, and *Miscanthus* at 10 locations for the second and third years after plot establishment. *P* values are the significance levels for the slopes

comprised of only four ecotypes (Alamo, Kanlow, Upland, and *Miscanthus*) had an R^2 value of 0.35 (p=0.003). The second which contained the two environmental pca axes (pca1 precip and pca2 temp stress), had an R^2 value of 0.10 (p=0.16). The third model included all ecotype by environment interactions and had an R^2 of 0.45 (p=0.031). The last model with all ecotypes, environmental variables, and ecotype × environment interactions had an R^2 of 0.80 (p<0.001). The parameter estimates for all ecotypes were highly significant (ESM Table S2). In addition, pca2 temp stress, Kanlow × pca1 precip, *Miscanthus* × pca1 precip, Upland × pca2 temp stress, and Kanlow × pca2 temp stress were significant. An increase in precipitation caused the largest increase in yields for *Miscanthus*. Temperature stress had the largest influence on the Upland ecotypes.

Stepwise regression showed varying results among the species and ecotypes and between years. For Alamo switchgrass, minimum temperature during the winter accounted for the greatest amount of variability in observed yields, but it was only significant in 2011. In 2010, none of the variables had a significant effect. In 2011, only minimum temperature was significant. For Kanlow switchgrass, photoperiod was the variable accounting for the most variability in 2010 while maximum temperature accounted for the most in 2011. Again, none of the other variables were significant in either year. For the pooled upland switchgrass ecotypes, in 2010 photoperiod and precipitation were the two variables accounting for the greatest amount of variability in observed yields, while in 2010 maximum temperatures, minimum temperatures, and precipitation accounted for the most. For both years, these were the only significant variables. Finally, for *Miscanthus*, in 2010, photoperiod was the most descriptive variable and the only significant one, while in 2011 the most descriptive variables were maximum and minimum temperatures. In the latter case, no other variables were significant.

Water use efficiency and radiation use efficiency

Radiation use efficiency showed two distinct sets of values (in bold and normal font in Table 7), high and low, for each

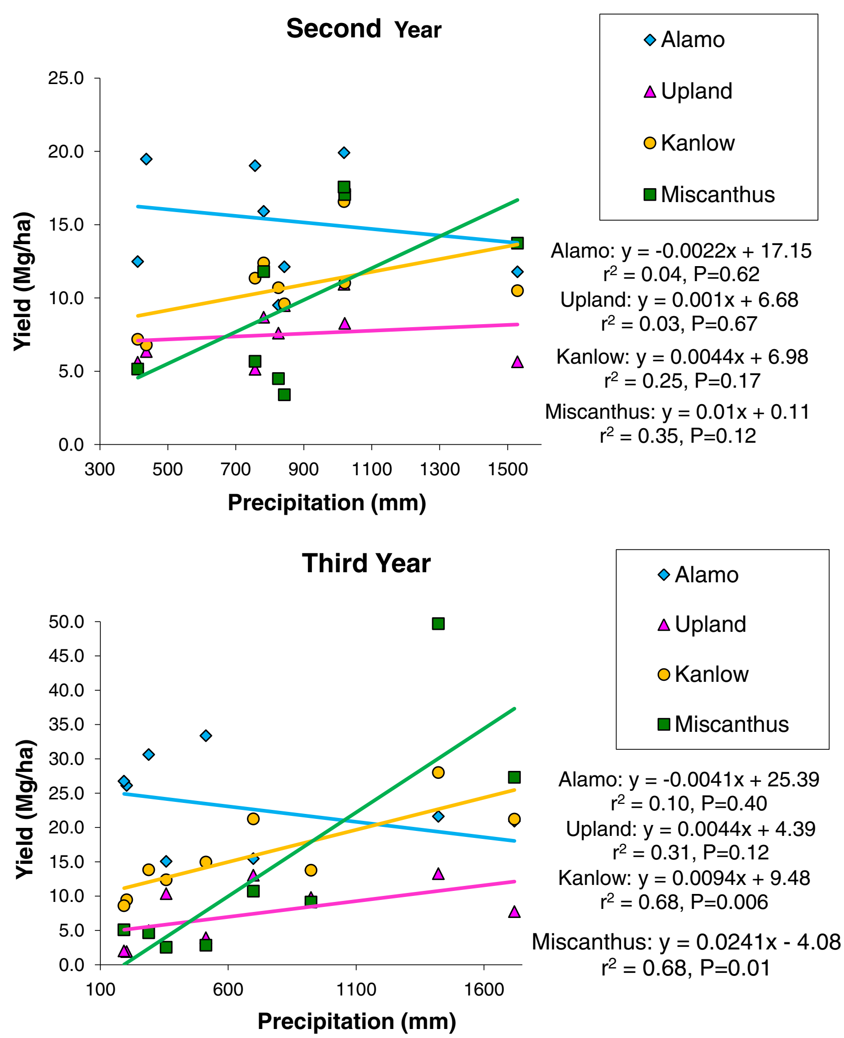


Fig. 5 Final dry matter yields as related to precipitation (for January through August) for pooled upland switchgrass ecotypes, Alamo and Kanlow switchgrass, and *Miscanthus* at 10 locations for the second and third years after plot establishment. *P* values are the significance levels for the slopes

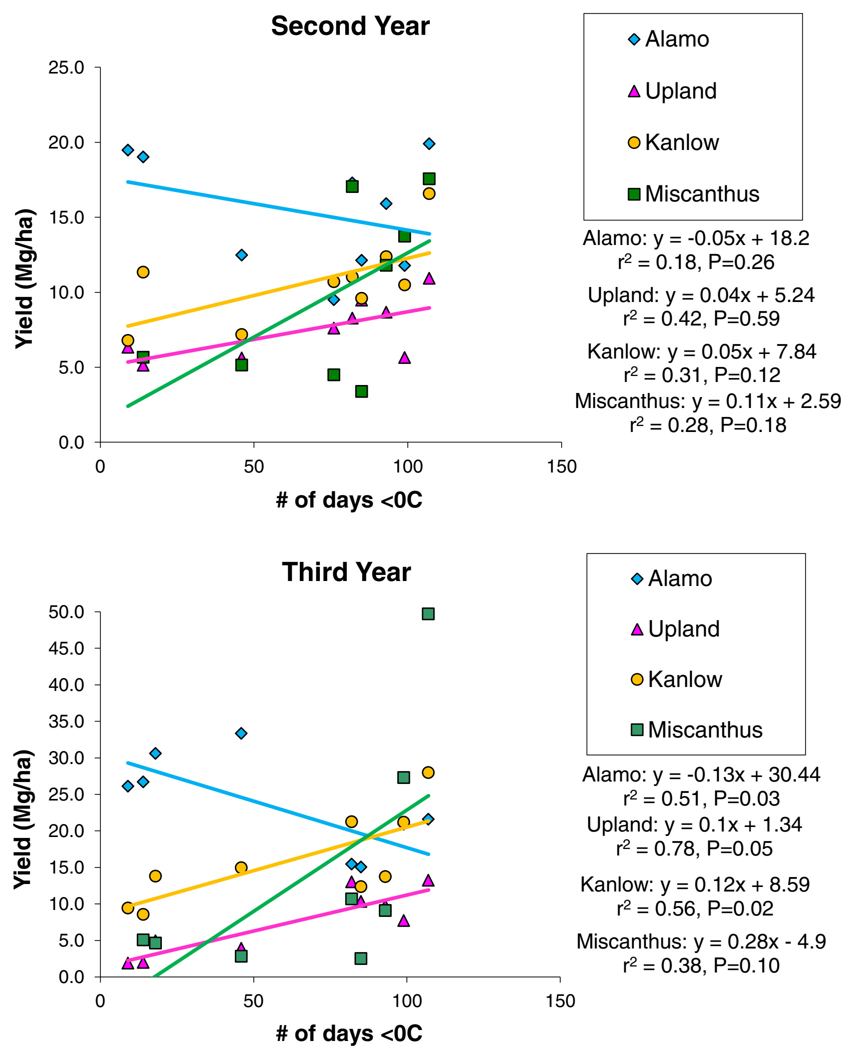


Fig. 6 Final dry matter yields as related to number of cold days in the previous winter for pooled upland switchgrass ecotypes, Alamo and Kanlow switchgrass, and *Miscanthus* at 10 locations for the second and third years after plot establishment. *P* values are the significance levels for the slopes

switchgrass ecotype and *Miscanthus*. The overall mean RUE for Alamo for the higher groups of values was 4.35 (Table 8), with values of the upland types and Kanlow being 72–78 % of Alamo's value and the mean for *Miscanthus* being 68 % of Alamo's value (Table 8). The overall mean for the lower group for Alamo (also in Table 8) was 2.08, with values of the upland ecotypes being 75–82 % as great, for Kanlow being 81 % as great, and *Miscanthus* being 62 % as great. For the following discussion, we will only concentrate on the higher groups of values of each ecotype and *Miscanthus*, since these illustrate the potential values of each and thus are most valuable for simulating potential growth of each.

For WUE, we compared the actual means for all the values of each species and ecotype within each year. Again, Alamo showed the largest mean each year (Table 9). Alamo's values increased from 3.5 mg dry weight per gram of water transpired in years 2 to 5.6 in year 3. Blackwell and Cave-in-Rock had the lowest values for WUE of all the switchgrass ecotypes each year. Kanlow had the highest WUE value each year, for species and ecotypes other than Alamo. Shawnee was intermediate between Kanlow and Blackwell/Cave-in-Rock. *Miscanthus* had the lowest WUE in year 2 but one of the highest in year 3.

Mean temperatures and duration of the growing season (from green-up to harvest) for the calculations of RUE and WUE had similar values among locations (Table 10). Temperatures ranged from approximately 20 to 22 °C in the second year across all sites and from 17 to 20 °C across all sites in the third year. The duration of the time period from green-up to first harvest (when RUE and WUE were calculated) ranged from 81 to 112 days in year 2 and from 57 to 100 days in year 3. We used the means of the high RUE values, as an attempt to identify the most optimum values within each species and ecotype and compared means of these among the grass types. Alamo had the greatest mean RUE in these cases for both years, with a mean of 4.05 g per megajoule (MJ) intercepted PAR in year 2 and 4.65 g per MJ intercepted PAR in year 3. In year 2, all the other switchgrass

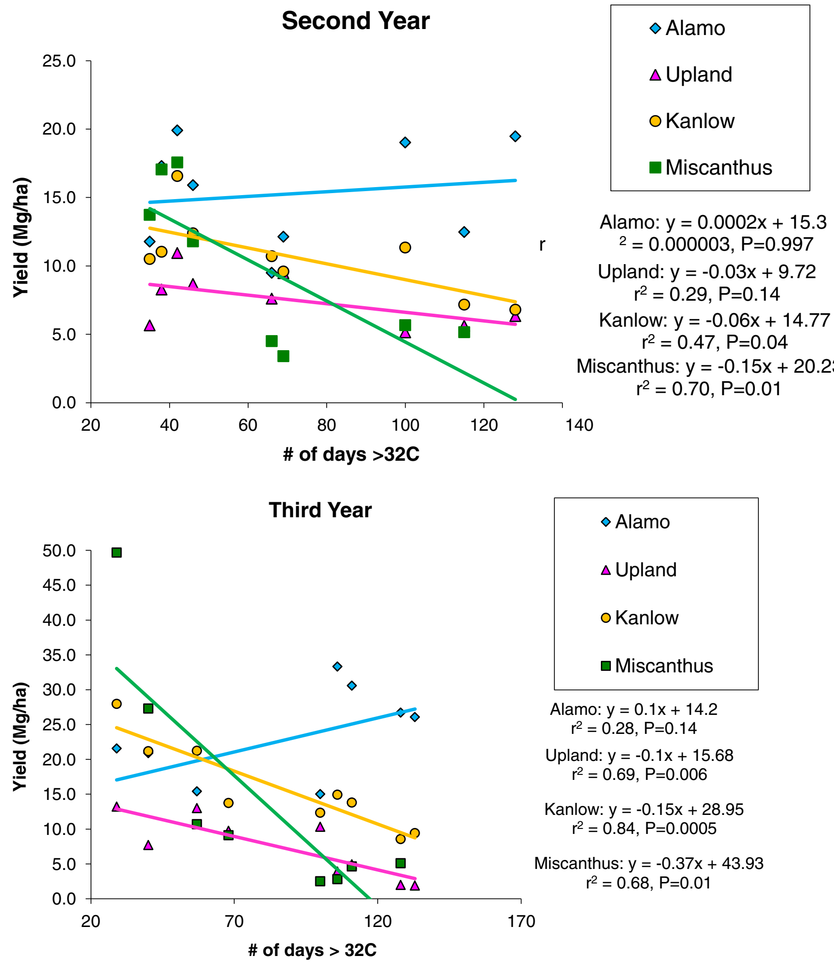


Fig. 7 Final dry matter yields as related to number of hot days during the growing season for pooled upland switchgrass ecotypes, Alamo and Kanlow switchgrass, and *Miscanthus* at 10 locations for the second and third years after plot establishment. *P* values are the significance levels for the slopes

ecotypes had similar means for this with values ranging from 3.65 to 4.0 g per MJ intercepted PAR. *Miscanthus*, in contrast, in year 2 had only 2.4 g per MJ intercepted PAR for RUE. In year 3, the four other ecotypes of switchgrass had lower values for RUE, with means varying from 2.4 to 2.9 g per MJ intercepted PAR. *Miscanthus* in year 3, on the other hand, had a larger value of 3.45 g per MJ intercepted PAR, which was still below the value for Alamo.

Discussion

There appeared to be a breakpoint in adaptation regions of these species and ecotypes, roughly corresponding to the Missouri Compromise Line, an extension of the Mason–Dixon line, that forms the border between Missouri and Arkansas. Our results demonstrate that the regions of maximum productivity of these plant ecotypes had boundaries somewhere near the northern edge of Texas or through southern or central Missouri. For the three upland switchgrass types, the boundary was between Texas on the south and Oklahoma and Arkansas on the north. For Alamo, there was no distinct border in year 2, but it appeared to have a boundary in year 3 between Missouri on the north and Oklahoma and Arkansas on the south. For Kanlow, there appeared to be no distinct breakpoint in year 2, while in year 3 the breakpoint was between Missouri on the north and Okahoma and Arkansas on the south. For *Miscanthus* in year 2, the boundary was the same as Kanlow in year 3, with Missouri being distinctly high yielding. However, for *Miscanthus* in year 3, only the two most northern Missouri sites were high yielding.

These results add clarification and better details to the often-shown regional adaptation map showing regions for *Miscanthus* and switchgrass (ESM Fig. S1). It is important to note that our measurements were largely made during abnormally low precipitation years in most of the central and southern sites (Table 5). This emphasizes the importance of yield stability across years, showing that some of the centrally located sites can have drastically reduced yields of *Miscanthus* and Kanlow when drought occurs. Likewise, these results are consistent with previous studies

Table 7 Mean±SD of radiation use efficiency (gram per megajoules IPAR)

	Alamo	Blackwell	Cave-in-Rock	Kanlow	Shawnee	*Miscanthus*
Year 2						
Weslaco	**3.9**±1.4	**3.7**±1.5	**3.9**±1.0	**4.1**±1.8	**4.2**±1.4	–
Kingsville	**4.2**±3.2	1.0±0.5	1.1±0.4	**3.2**±1.5	1.2±0.2	0.32
Nacogdoches	2.7±1.5	2.7±0.4	2.4±0.6	2.0±0.2	2.7±0.3	1.0±0.7
Stillwater	1.6±0.3	1.3±0.3	1.8±0.6	0.7±0.4	1.4±0.3	0.6±0.3
Fayetteville	2.8±0.5	2.3±0.1	2.4±0.2	1.5±0.2	2.3±0.4	**2.4**±0.6
Booneville	2.1±0.4	2.1±0.7	1.9±1.2	2.1±1.1	**3.8**±0.8	0.9±0.5
Mount Vernon	1.7±0.5	1.6±0.7	0.4±0.3	1.5±1.0	1.6±0.7	1.5±0.3
Columbia	0.9±0.3	0.5±0.3	1.4±0.4	2.7±0.9	1.3±0.1	**2.7**±1.5
Elsberry	2.0±0.5	2.5±0.5	1.8±1.1	3.5±0.4	1.9±0.3	**2.2**±0.7
Year 3						
Weslaco	–	–	–	–	–	–
Kingsville	**5.1**±3.1	**2.6**±0.4	**2.9**±1.3	1.1±1.2	**2.3**±0.4	0.7
Temple	**4.2**±3.6	1.3±0.7	1.1±0.7	1.8±0.4	1.4±0.1	1.1±0.5
Nacogdoches	2.8±0.8	1.4±0.4	1.0±0.6	**2.7**±0.9	1.5±0.6	1.1±0.7
Stillwater	1.4±0.4	1.3±0.2	1.5±0.5	1.5±0.4	1.3±0.5	1.2±0.6
Fayetteville	2.7±1.1	2.3±0.6	1.9±0.8	**2.6**±1.1	**2.5**±1.1	**3.9**±1.6
Mount Vernon	1.8±1.2	1.4±1.6	1.5±0.4	2.1±0.4	2.2±0.5	1.9±1.1
Columbia	2.0±0.3	1.6±0.4	1.7±0.2	1.6±0.5	1.7±0.5	2.7±0.9
Elsberry	2.4±0.3	1.7±0.5	1.6±0.9	**2.9**±0.8	**2.4**±0.4	**3.0**±0.8

Values were split into two groups; representative high values for the year (in bold font) or less than optimal (the normal font). These are summarized by the two groups in Table 8

showing that lowland ecotypes "Alamo" and "Kanlow" were higher yielding than various upland ecotypes ("Cave-in-Rock" and "Shelter") in Virginia, Tennessee, Iowa, West Virginia, Kentucky, North Carolina, Alabama, Georgia, and Texas [13, 21, 23, 33].

These trends in yield were found to be related to different environmental factors. More cold winter days led to decreased subsequent Alamo switchgrass yields and increased subsequent upland switchgrass yields, especially in the last year. More hot-growing season days led to decreased Kanlow yields in the last year. More hot- and dry-growing season days led to decreased *Miscanthus* yields in both years. For each abiotic factor analyzed, Alamo consistently had a response slopes with a different sign than those of the other switchgrass ecotypes and *Miscanthus*. These differences in responses are expected and can be attributed to Alamo's southern latitude of origin (Table 2). Our results are consistent with other studies of latitudinal adaptation performed in the Northern Great Plains that highlight that latitude of origin has a significant impact on productivity, survival, and adaptation traits of switchgrass [3, 5, 31].

Alamo switchgrass had the greatest mean RUE, with an overall mean of high values of 4.35 g per MJ intercepted PAR. Relative to the mean for Alamo, Blackwell's great RUE

Table 8 Means of radiation use efficiency (g per MJ IPAR) of the two groups in Table 7: the selected high values and the other, lower values that were not in bold in Table 7

	Alamo	Blackwell	Cave-in-Rock	Kanlow	Shawnee	*Miscanthus*
Year 1, mean of bold values	4.05	3.7	3.9	3.65	4.0	2.43
Fraction of Alamo		0.91	0.96	0.90	0.99	0.60
Year 2, mean of bold values	4.65	2.6	2.9	2.7	2.4	3.45
Fraction of Alamo		0.56	0.62	0.59	0.60	0.74
Means of bold value	4.35	0.72	0.78	0.73	0.74	0.68
Year 1, mean of other	1.97	1.75	1.65	1.75	1.77	1.00
Fraction of Alamo		0.89	0.84	0.89	0.90	0.51
Year 2, mean of other	2.18	1.57	1.47	1.62	1.62	1.58
Fraction of Alamo		0.72	0.68	0.59	0.74	0.72
Means of other		0.80	0.75	0.81	0.82	0.62

Table 9 Mean±SD of water use efficiency (mg dry weight per gram of water transpired)

	Alamo	Blackwell	Cave-in-Rock	Kanlow	Shawnee	*Miscanthus*
Year 2						
Weslaco	4.2±1.5	3.7±1.5	4.0±1.9	4.3±2.2	4.3±1.6	–
Kingsville	3.1±2.3	1.3±0.7	1.5±0.7	2.3±1.6	1.6±0.4	0.3
Nacogdoches	3.6±1.9	2.5±0.3	2.2±0.5	3.1±0.5	2.5±0.7	1.1±0.9
Stillwater	2.8±0.5	1.9±0.5	2.6±0.9	1.5±0.8	2.0±0.4	1.0±0.6
Fayetteville	4.3±0.7	3.9±0.3	4.3±0.4	4.0±0.9	4.0±0.8	3.9±1.2
Booneville	3.3±0.7	3.5±1.1	3.1±1.9	3.5±1.7	6.2±1.3	1.1±0.8
Mt. Vernon	5.4±1.5	5.9±2.5	2.9±1.4	6.5±0.8	5.4±3.2	4.5±0.9
Columbia	1.4±0.4	0.6±0.3	2.5±1.3	3.6±1.3	1.8±0.3	3.9±2.2
Elsberry	3.7±0.9	3.7±0.8	3.5±0.5	5.1±0.7	2.9±0.4	3.9±1.2
Year 2 means	3.5	3.0	3.0	3.9	3.8	2.5
Year 3						
Kingsville	7.4±4.5	3.9±0.6	4.4±2	3.8±4.1	3.5±0.7	2.0
Temple	11.3±4.1	3.5±2	2.9±1	4.9±1	3.7±0.2	3.3±1.6
Nacogdoches	4.7±1.3	1.9±0.6	1.4±0.9	4.1±1.4	2.1±0.9	1.4±0.9
Stillwater	3.3±1.1	3±0.6	3.5±1.2	2.9±0.8	3±1.1	1.8±0.9
Fayetteville	5.7±2.4	5.8±1.5	4.9±2.1	6.4±2.7	6.3±2.8	8.4±3.5
Mount Vernon	5.3±0.5	2.9±1.2	2.3±0.6	4.7±1	3.2±0.7	3.5±2.1
Columbia	3.1±0.5	2.5±0.5	2.7±0.4	2.5±0.8	2.7±0.8	4.2±1.3
Elsberry	3.6±0.4	2.7±0.7	2.6±1.4	-	3.7±0.6	4.7±1.3
Year 3 means	5.6	3.3	3.1	4.1	3.5	3.7
Means both years	4.5	3.1	3.0	3.9	3.5	3.2

averaged 74 %, Cave-in-Rock's averaged 79 %, Kanlow's averaged 75 %, Shawnee's averaged 80 %, and *Miscanthus*' averaged 67 %. Radiation use efficiency showed two distinct sets of values, high and low, for each switchgrass ecotype and *Miscanthus*. The group with high RUE were generally similar to high values published previously, with 4.5 for Alamo switchgrass in Texas [18], 4.3 for Alamo switchgrass in Elsberry, MO, USA [20], 3.7 for *Miscanthus* in Illinois [14], and 3.7 for *Miscanthus* in Elsberry, MO, USA [20]. The others had lower values for RUE, similar to the 2.38 for Cave-in-Rock in Canada [22], 1.2 for Cave-in-Rock in Illinois [10], 2.4 for *Miscanthus* in the UK [6], 2.19 for *Miscanthus* in Italy [7] and 2.3 and 3.0 for *Miscanthus* in Illinois [10]. The high RUE values for individual species and ecotypes in this study were comparable to previously published values from Elsberry, MO, USA [20], where the mean RUE was 4.30 for Alamo, with Cave-in-Rock's mean being 74 % as large, Kanlow's mean being 86 % as great, and *Miscanthus*' mean being 86 % as great.

Our values for WUE also were in the range of published values for grasses. In this study, our values of WUE for Alamo had the highest mean value at 4.5 mg of plant dry weight per gram of water transpired, with Blackwell being 69 % of Alamo, Cave-in-Rock 67 %, Kanlow 87 %, Shawnee 76 %, and *Miscanthus* 67 %. Previously published values for grass WUE ranged from 1 to 5 mg dry matter production per g of water transpired. Blue grama (*Bouteloua gracilis* (H.B.K.)) in a greenhouse had a WUE value of 4.55 $mg\,g^{-1}$ [12]. In a greenhouse, grass seedlings (*Sporobolus arabicus* and *Leptochloa fusca*) had WUE values of 1.0–1.4 $mg\,g^{-1}$ [1]. In the field in Nebraska,

Table 10 Mean temperatures (degree Celcius) and days of duration from green-up to first harvest date

	Mean temp to harvest		Days since green-up	
	Year 2	Year 3	Year 2	Year 3
Elsberry	21.6	19.9	112	61
Columbia	21.8	19.5	108	67
Mt. Vernon	21.4	19.8	110	59
Stillwater	20.6	17.8	85	65
Fayetteville	20.2	16.5	81	57
Booneville	18.1	–[a]	70	–[a]
Nacogdoches	21.1	18.5	97	88
Temple	–[b]	19.5	–[b]	100
Kingsville	21.2	19.9	102	88
Weslaco	22.4	–[a]	109	–[a]

These were the intervals used for calculating RUE and WUE described below

[a] Not harvested in year 3

[b] Not harvested in year 2

switchgrass WUE values were 1.0–5.5 $mg\,g^{-1}$ [11], values similar to those demonstrated by switchgrass seedlings in a growth chamber (1.45–5.5 $mg\,g^{-1}$ [38]). In the shortgrass steppe of Colorado, a mixture of cool-season and warm-season grasses (including blue grama) had WUE values of 1.0–4.5 $mg\,g^{-1}$ [26]. Switchgrass simulated WUE had values of 2.8–5.3 $mg\,g^{-1}$ for various groups of upland and lowland types [19].

This study provided valuable results for various switchgrass ecotypes and *Miscanthus* related to understanding adaptation to various latitudes in the southern portion of the USA. In addition, these results will provide valuable inputs to process-based models (i.e., ALMANAC [17]) to realistically simulate these important perennial biofuel grasses in this productive region. This improved understanding will enable us to realistically simulate the production of different ecotypes of switchgrass and *Miscanthus*. Such improved simulations will allow rapid assessment of resource utilization (water and nutrients) under the diverse climatic conditions and soils in this and similar regions. Because of the nature of such process-based models, such simulations should be realistic on both prime agricultural soils and more marginal soils of the region. This will allow rapid assessment of land area and resource requirements as interest grows in the use of marginal soils for biofuel production.

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Table S1: Loadings of environmental variables to create the first two principal components.

Variable	PCA1	PCA2
Heat Stress Days	0	0.843
Cold Stress Days	0	0.537
Precipitation	-0.995	0
Photoperiod	0	0
Proportion of Variance	0.995	0.005

Table S2. Principal component analysis results with factors affecting final biomass yield each year.

Variable	Estimate	p
Intercept (Alamo)	19.59	< 0.001
Upland	-11.91	< 0.001
Kanlow	-6.31	< 0.01
Miscanthus	-7.97	< 0.001
Pca1 Precip	0.00	0.15
Pca2 Temp Stress	-0.11	0.03
Upland * Pca1 Precip	0.01	0.09
Kanlow * Pca1 Precip	0.01	0.01
Miscanthus * Pca1 Precip	0.03	< 0.001
Upland * Pca2 Temp Stress	0.20	0.01
Kanlow * Pca2 Temp Stress	0.16	0.03
Miscanthus * Pca2 Temp Stress	0.14	0.06

Figure S1. Regional adaptation zones of biofuel crops (Oak Ridge National Laboratory, cited in Porter et al., 2009).

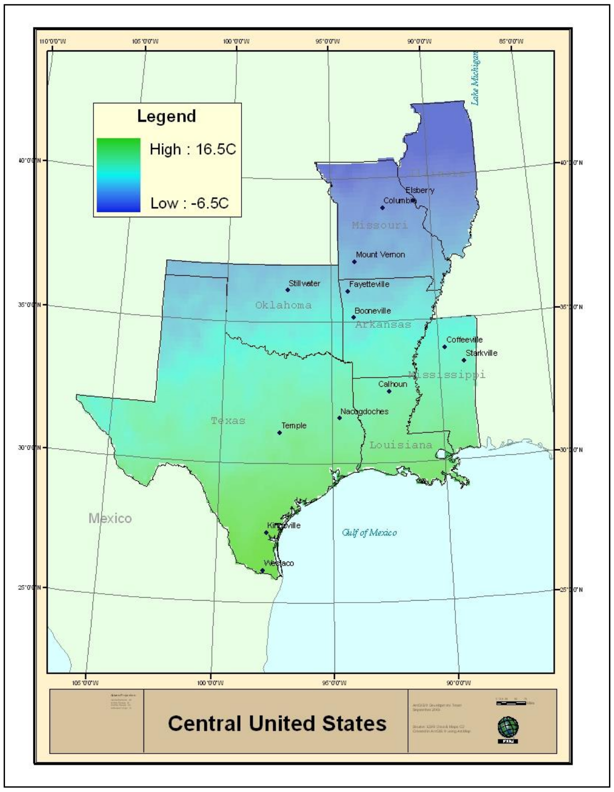

Figure S2a. Average day temperature of coldest quarter.

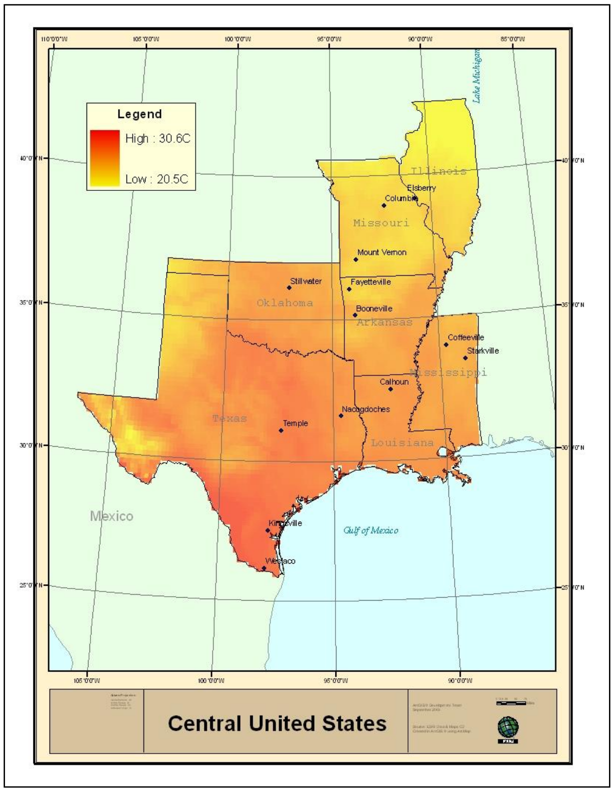

Figure S2b. Average day temperature of hottest quarter.

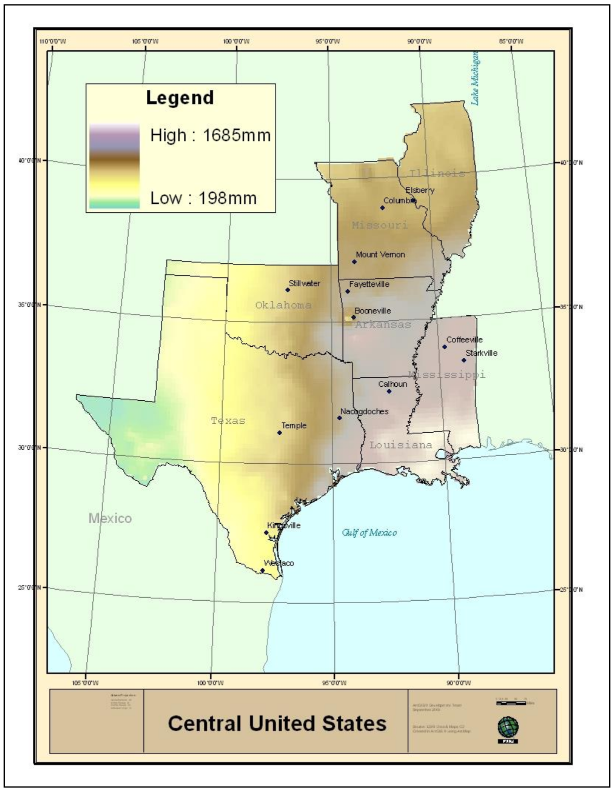

Figure S2c. Average annual precipitation.