Received: 14 November 2022 | Accepted: 19 January 2023

DOI: 10.1111/gcbb.13046

GCB-BIOENERGY BIOPRODUCTS FOR A SUSTAINABLE BIOECONOMY Open Access

WILEY

RESEARCH ARTICLE

Local adaptation of switchgrass drives trait relations to yield and differential responses to climate and soil environments

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Funding information
Office of Science, Grant/Award Number: DE-SC0014156, DE-SC0021126 and DEAC02-06CH11357

Abstract

Switchgrass, a potential biofuel crop, is a genetically diverse species with phenotypic plasticity enabling it to grow in a range of environments. Two primary divergent ecotypes, uplands and lowlands, exhibit trait combinations representative of acquisitive and conservative growth allocation strategies, respectively. Whether these ecotypes respond differently to various types of environmental drivers remains unclear but is crucial to understanding how switchgrass varieties will respond to climate change. We grew two upland, two lowland, and two intermediate/hybrid cultivars of switchgrass at three sites along a latitudinal gradient in the central United States. Over a 4-year period, we measured plant functional traits and biomass yields and evaluated genotype-by-environment (G × E) interaction effects by analyzing switchgrass responses to soil and climate variables. We found substantial evidence of G × E interactions on biomass yield, primarily due to deviations in the response of the southern lowland cultivar Alamo, which produced more biomass in hotter and drier environments relative to other cultivars. While lowland cultivars had the highest potential for yield, their yields were more variable year-to-year compared to other cultivars, suggesting greater sensitivity to environmental perturbations. Models comparing soil and climate principal components as explanatory variables revealed soil properties, especially nutrients, to be most effective at predicting switchgrass biomass yield. Also, positive correlations between biomass yield and conservative plant traits, such as high stem mass and tiller height, became stronger at lower latitudes where the climate is hotter and drier, regardless of ecotype. Lowland cultivars, however, showed a greater predisposition to exhibit these conservative traits. These results suggest switchgrass trait allocation trade-offs that prioritize aboveground biomass production are more tightly associated in hot, dry environments and that lowland cultivars

may exhibit a more specialized strategy relative to other cultivars. Altogether, this research provides essential knowledge for improving the viability of switchgrass as a biofuel crop.

KEYWORDS

bioenergy crops, genotype-by-environment, *Panicum virgatum*, plant economics spectrum, plant trait allocation, sustainable agriculture

1 | INTRODUCTION

As atmospheric carbon dioxide levels continue to climb and climate variability increases, the development of sustainable, carbon-neutral, and climate-adapted bioenergy production systems has become imperative (Creutzig et al., 2015). Perennial grasses native to North American grasslands possess many characteristics needed in a climate-adapted bioenergy crop. Many species are highly productive, deep-rooted, tolerant of drought and limited nutrient availability, and contribute to multiple ecosystem services, including carbon sequestration, water retention, and protection against erosion. The most widespread North American perennial grasses occur across a broad range of climates and soils, and display extensive genetic variability in productivity and other traits (Fernando et al., 2018; Foley et al., 2011; Galliart et al., 2019, 2020; Kiniry et al., 2013; Lovell et al., 2021). Consequently, these grasses often possess locally adapted populations, which exhibit greater fitness in their home environments. While the large-scale expansion of perennial bioenergy crops may offer many benefits, it is limited by our current understanding of how environmental drivers, like soil and climate, contribute to local adaptation. Identifying these contributions is crucial for predicting crop responses to changing climates, improving yield, and maximizing the benefits of ecosystem services provided by perennial grasses in bioenergy crop production (Foley et al., 2011).

Local adaptation occurs when populations have higher fitness in their home environments than populations that originated in a different environment (Blanquart et al., 2013; Kawecki & Ebert, 2004). For species with wide geographic and environmental distributions, this process can result in locally adapted ecotypes that may be genetically divergent. However, the environmental drivers of local adaptation are not always clear. Many studies have combined all local environmental factors into a single "site" effect (Anderson et al., 2011). However, site effects can obscure the impacts of specific environmental variables and can hinder prediction beyond the sites studied (De Leon et al., 2016). As such, recent work has examined the impacts of specific environmental variables on local adaptation (e.g., Mu et al., 2022; Onogi et al., 2021). Two commonly proposed environmental drivers of local adaptation in plants are soil and climate (Macel et al., 2007). To unravel the separate roles that these drivers play in the local adaptation patterns of perennial grass systems, one must first understand the genotypic variation within a species and its subsequent ability to adjust to new or changing environments through phenotypic responses (i.e., phenotypic plasticity).

Genotypes within a species may differ in their ability to respond phenotypically to environmental stimuli (Saltz et al., 2018; Van Kleunen & Fischer, 2005), particularly if they originate from genetically divergent ecotypes. These genotype-by-environment (G×E) interactions may reveal the presence of different degrees of environmental specialization among genotypes. For instance, some genotypes may possess a generalist strategy that maintains similar productivity and fitness across a range of environments, while others may be specialists that perform well in their home environment, but poorly in others (Napier et al., 2022). These strategies are derived from phenotypic variation in plant functional traits, which can be important determinants of local adaptation and affect a variety of broader ecosystem functions, including net primary production and carbon and water cycle regulation (Reichstein et al., 2014). In widespread species like perennial grasses, functional traits often covary in predictable ways to produce functional syndromes hypothesized to vary with climate, soils, and other environmental drivers (Agrawal, 2020; Reichstein et al., 2014). These functional syndromes may capture whole-plant trade-offs between the cost of tissue production and resource acquisition, resulting in 'conservative' or 'acquisitive' functional strategies known as the plant economics spectrum (Reich, 2014). A conservative plant strategy of long-lived, low-nutrient tissue is often beneficial in environments where limited resource availability slows growth and thereby increases the time required for tissue to recoup its construction cost (i.e., slow-return on investment strategy). In resource-rich environments, an acquisitive plant strategy of short-lived, high-nutrient tissue may be beneficial (i.e., quick-return on investment strategy; Laughlin, 2014; Wright et al., 2004). Other key functional traits, like plant size, may vary independently of the plant economics spectrum (Díaz et al., 2016). Thus, quantifying linkages between functional traits and productivity across

genetically divergent genotypes and environmental gradients will be key to the development and establishment of locally adapted perennial grass bioenergy varieties within a given region.

One of the most studied perennial grass candidates for bioenergy production is switchgrass (*Panicum virgatum* L.). Switchgrass is native to North America and is a common species in tallgrass prairies (Samson & Knopf, 1996), occurring east of the Rocky Mountains from central Canada into Mexico. Switchgrass populations exhibit a high degree of local adaptation (Casler et al., 2007; Lovell et al., 2021; Lowry et al., 2014) and can be broadly classified into upland, lowland, and coastal ecotypes, although the upland and lowland ecotypes are the most divergent (Grabowski et al., 2014; Lovell et al., 2021). Lowland plants are often taller with wider leaves, have thicker stems with lower nitrogen concentrations, and produce fewer tillers—consistent with "conservative" resource allocation strategies. Upland plants shift toward higher tiller numbers, with shorter, thinner stems and leaves that have higher nitrogen concentrations, which are traits consistent with an acquisitive strategy (Aspinwall et al., 2013; Casler et al., 2011; Heckman et al., 2020). There are also many intermediate and hybrid forms which possess a mixture of traits that may either be expressed along a spectrum of conservative versus acquisitive extremes, possess conservative traits in some aspects but acquisitive traits in others, or both. In switchgrass, tillering traits are also highly variable, and the contribution of tiller numbers, mass, and height among switchgrass genotypes to trait syndromes and biomass production remains unclear. Although functional strategies in switchgrass have been studied extensively (Aspinwall et al., 2013; Chen et al., 2021; Heckman et al., 2020; Lovell et al., 2021), relative functional trait responses of genetically divergent and locally adapted switchgrass genotypes to soil versus climate environmental stimuli remain poorly understood. Yet, such knowledge will be essential for informing management decisions needed to sustain successful bioenergy crop production in the coming century.

Here we examine the relationships among climate, soils, plant functional traits, and biomass yield for six switchgrass cultivars grown in replicated plots at three locations along a 10.8° latitudinal gradient in the United States. The locations spanned much of the climatic range of switchgrass and varied in mean annual precipitation (MAP), mean annual temperature (MAT), and soil physical and chemical properties. The six switchgrass cultivars represent a range of genotypic diversity, latitudes of origin, and leaf and tiller functional traits. We measured these traits and aboveground biomass yield for 4 years (2017–2020) following an initial establishment year (2016). Our primary objectives were: (1) to identify how biomass yield varied with climate and soil properties across sites and among cultivars; and (2) to quantify the contributions of conservative versus acquisitive plant traits on biomass yield in different environments. We asked the following research questions: First, does switchgrass biomass yield exhibit significant G × E interactions? If so, are the effects of G × E interactions on biomass yield driven more by variations in climate or soil environments? Lastly, do cultivars with more conservative traits produce more biomass than cultivars with acquisitive traits where climate and soil properties are more stressful, and vice versa?

2 | MATERIALS AND METHODS

2.1 | Site descriptions

In 2016, switchgrass field sites were established in three locations; Temple, Texas (TX) at the Agricultural Research Service (ARS) Grassland, Water and Soil Research Laboratory, United States Department of Agriculture (USDA; 31.045109°, −97.348135°); Columbia, Missouri (MO) at the Bradford Research Center, University of Missouri (38.899708°, −92.213984°); and Batavia, Illinois (IL) at the Fermi National Accelerator Laboratory (Fermilab) National Environmental Research Park, United States Department of Energy (41.836701°, −88.239708°). Before establishment, each site had varying long-term, land-use histories, including periods of cultivation, fallow, or pasture. The soil types and characteristics differ substantially among sites (Figure S1 and Table S1). Briefly, the Houston Black clay at the TX site is a moderately well-drained, very slowly permeable vertisol that was formed in clayey residuum weathered from calcareous mudstone of Upper Cretaceous age and exhibits notable cracking during dry periods; the Mexico silt loam at the MO site is a poorly drained alfisol (with a relatively shallow claypan) that formed in deep loess over pre-Illinoian till; and the Mundelein silt loam at the IL site is a somewhat poorly drained mollisol formed in loess deposited over stratified calcareous loamy Wisconsinan glacial outwash (https://soilseries.sc.egov.usda.gov/).

Similarly, the three sites differed considerably in climatic conditions (Figure S2 and Table S2). We used the National Oceanic and Atmospheric Administration (NOAA) website (https://www.ncei.noaa.gov/products/land-based-station/us-climate-normals) to identify meteorological (MET) stations that were close to each site and had 30-year (1991–2020) MAP (mm) and MAT (°C) norms (Table S2). We also collected daily total precipitation (PRCP; mm), average maximum air temperature (T_{max}; °C), average minimum air temperature (T_{min}; °C), and average daily wind speed (ADWS; m s^{-1}) from MET stations

specific to each field site from December 1, 2016 through November 30, 2020. Lastly, we obtained average daily solar radiation (SOLRAD; MJ m^{-2}), and dew point temperatures (T_{dew}; °C) for the same time period from the National Solar Radiation Database (NSRDB) using the U.S. & Americas dataset with 60-minute temporal resolution and 4 km spatial resolution (https://nsrdb.nrel.gov/data-sets/us-data; Sengupta et al., 2018). The collected data were then used to calculate the average daily potential evapotranspiration (PET; mm $month^{-1}$) using the Penman–Monteith equation (R package SPEI) using T_{min}, T_{max}, ADWS, SOLRAD, T_{dew}, elevation and latitude for each site, with the crop argument set to "tall" to account for growth taller than 0.5 m (Allen et al., 1994; Beguería & Vicente-Serrano, 2017; Walter et al., 2002).

2.2 | Pre-planting soil measurements

Prior to planting in spring 2016, soil samples were collected from six pre-selected locations to capture and characterize the range of variability in soil physical and chemical properties at each site (Figure S1 and Table S1). Soil cores (3.8-cm diameter) were taken with a hydraulic coring machine to a depth of 1.5–2 m, depending on soil conditions. The cores were split into 25-cm depth increments, and the surface 25-cm increment was divided further into 0–5 cm, 5–15 cm, and 15–25 cm increments. After removing roots and large pieces of organic debris, samples were oven dried at 65°C, and homogenized through a 2-mm sieve. A subsample of the sieved soil was oven dried at 105°C to obtain a moisture correction factor for estimating the oven-dry soil mass of each sample. Bulk density (BD; kg m^{-3}) was determined for each sample from its oven-dry mass and volume (calculated from core diameter and depth interval). To facilitate comparisons of soil resources among sites, we used BD to express other soil properties on a volumetric basis, where applicable. Subsamples from each soil core and depth increment were finely ground in a high-energy ball mill (8000D Mixer/Mill, SPEX SamplePrep LLC), and then analyzed at Argonne National Laboratory for total organic carbon and total nitrogen (TOC and TN, respectively; kg m^{-3}) by dry combustion in an elemental analyzer (vario MAX cube, Elementar Americas, Inc.) at 900°C for TN and 650°C for TOC (Provin, 2014). Additional subsamples from three of the six cores from each site were analyzed for pH (1:1 soil:water), total phosphorus (TP; salicylic–sulfuric acid digestion; kg m^{-3}), Mehlich-3 extractable phosphorus (M3-P; kg m^{-3}), ammonium and nitrate nitrogen (NH_4^+-N and NO_3^--N; 2 M potassium chloride extraction; kg m^{-3}), electrical conductivity (EC; saturated paste; dS m^{-1}), cation exchange capacity (CEC; summation of neutral 1 M ammonium acetate exchangeable cations plus neutralizable acidity; meq cm^{-3}), and texture (sand, silt, and clay; hydrometer method; %) at the Kansas State University Soil Testing Laboratory.

2.3 | Experimental design and plant establishment

We established switchgrass field experiments at each site that consisted of 30 plots (6 m × 6 m each) separated by 3 m mowed alleys (Figure 1). The experiment was arranged in a randomized complete block design, where plots within each block were randomly assigned to one of six cultivars (5 blocks × 6 cultivars = 30 plots). The cultivars spanned the ecotypic diversity of switchgrass, with the lowland ecotype represented by Alamo and Kanlow cultivars, the upland ecotype represented by Blackwell and Cave-in Rock (CIR) cultivars, and the intermediate ecotypes represented by Carthage (a coastal ecotype) and Liberty (a hybrid of upland and lowland ecotypes) cultivars.

To ensure rapid and consistent establishment of experimental plots across all sites and cultivars, the plots were planted using switchgrass seedlings and standardized field management practices were applied across all sites. Seedlings of each cultivar were grown in pots (3.8 cm × 21.0 cm SC10 Conetainers™, Stuewe & Sons) filled with a soil mixture (6:2:1; Pro-Mix BX, Premier Tech; Turface MVP, Profile Products LLC; and Profile Field & Fairway, Profile Products LLC). Seeds from commercial seed sources (except Liberty, which was provided by the UDSA-ARS) were spread on the surface of the dampened soil mixture in each pot, covered with moist vermiculite, stratified in the dark at 4°C for 7 days, and subsequently placed in a greenhouse at the University of Texas at Austin (30°C/22°C, 14-h photoperiod). During early growth, pots were thinned to one seedling, then watered as needed and allowed to grow for ~7 weeks. The experimental fields were thoroughly and homogenously tilled to ~15 cm depth before each 6 m × 6 m plot was planted with 169 individual seedlings spaced 0.5 m apart in a 13 × 13 grid. To ensure consistent establishment, all plots were irrigated with broadcast sprinklers immediately after planting and then throughout the first 2 months, as needed, depending on precipitation, evaporative demand, and soil moisture conditions at each site. Seedling mortality was extremely limited during the establishment year (occurring within 2 weeks of planting), and those few individuals were replaced with extra seedlings of the same cultivar that were maintained in "nursery" plots at each site. After the initial establishment period, all cultivar responses were subject to natural climatic and soil variations. Additionally, pre-emergent and broadleaf herbicides (e.g., Prowl H_2O,

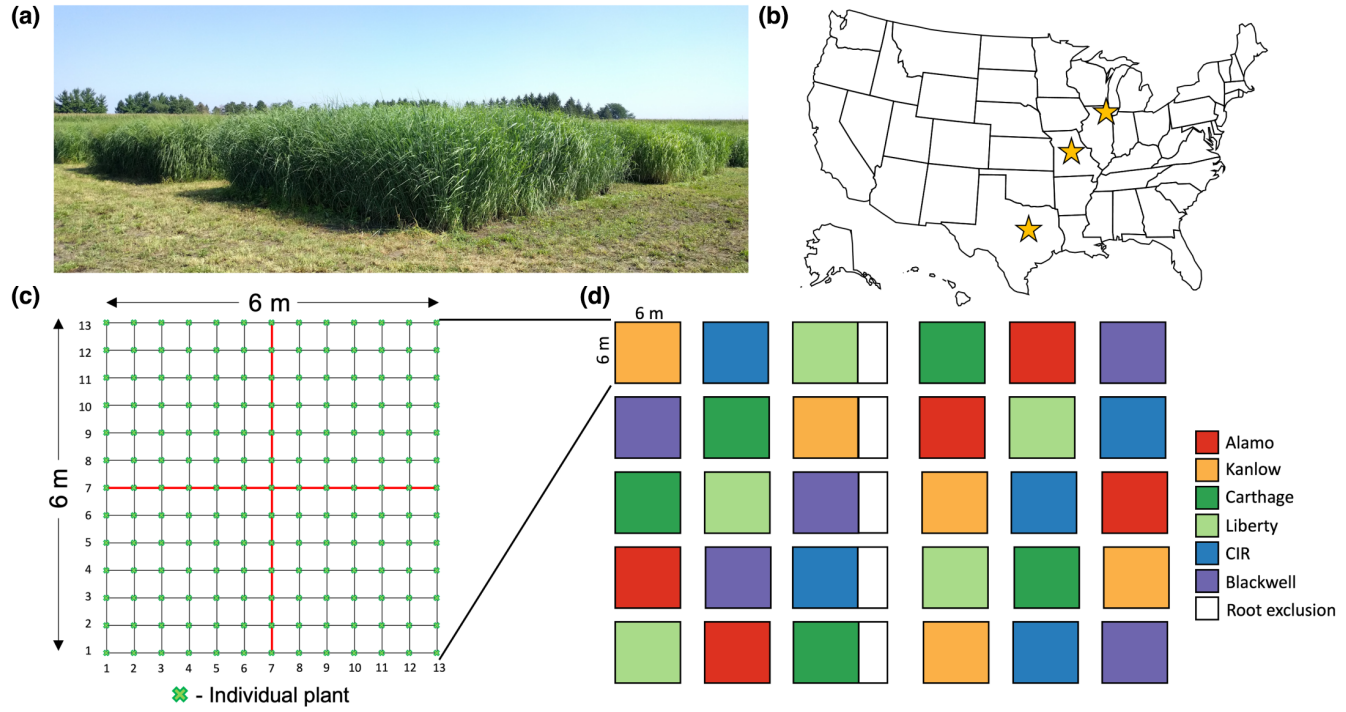

FIGURE 1 Illustration of experimental design and site layout. (a) Photograph showing several switchgrass plots at the IL site in early July 2018 (Photo credit: Scott Hofmann). (b) Map of site locations within the United States (Fermilab, IL; Columbia, MO; and Temple, TX). (c) Diagram of a single 6 m × 6 m plot consisting of 169 individually planted seedlings of a single cultivar. (d) Layout of the 30 plots at one of the sites. Plots at each site were similarly arranged in a randomized complete block design. Each row is a block and colors represent the randomly located position of the six different cultivar plots within each block. White areas next to plots in the third column represent root-exclusion zones which were kept clear of all vegetation.

Simazine, 2,4-D) were applied before planting and at the beginning of each growing season to minimize potential site variations due to interspecific competition related to site differences in the soil seed bank or nearby windblown seed sources. During the growing season, plots were also maintained by supplemental hand weeding within, and regular mowing between plots, as necessary.

2.4 | Cultivar trait measurements

We measured leaf, stem, whole tiller, whole plant, and plot-level traits during the calculated "peak biomass" of each plot throughout the 2017–2020 growing seasons. We recorded plant height and number of tillers from five preselected plants in each plot and harvested five tillers from each of three additional plants per plot. We separated leaves from stems and measured their areas using leaf area meters (LI-3100C Area Meter in TX and MO, LI-3000C Portable Area Meter with LI-3050C Transparent Belt Conveyer in IL, LI-COR Biosciences), then dried the samples at 65°C for at least 72 h before determining dry weights. Mid-season biomass production ($Mg\,ha^{-1}$) was calculated by multiplying the average tiller dry mass (leaf + stem) by the average number of tillers per plant and the number of plants ($n = 169$) per plot. Specific leaf area (SLA; $cm^2\ g^{-1}$) was calculated as the ratio of leaf area to dry leaf biomass. Lastly, leaves and stems were combined and ground in a Wiley mill, and then subsamples of the homogenized tissue were finely ground with a cyclone mill for analysis of tiller C and N concentrations (%) by dry combustion at 900°C in the elemental analyzer as described above.

Annual aboveground biomass yield (i.e., total annual yield; $Mg\,ha^{-1}$) for each cultivar was measured by collecting and weighing aboveground biomass at the end of each growing season, typically mid-to-late November at all sites. Biomass was collected from two 2 m × 2 m quadrats (16 plants each) within each plot, which were left undisturbed throughout each year of the study. Plants were cut at roughly 10–15 cm above the soil surface, loaded onto a tarp, and weighed immediately using a hanging scale (OP-926, Optima Scale Inc.). Harvested wet weights were converted to dry weights by weighing subsamples before and after drying at 65°C and computing a moisture correction factor. The remaining aboveground biomass in each plot was cut at the same height above the surface and removed to simulate agricultural harvest practices. To provide further context to switchgrass biomass yields, all individual plants at each site were examined during the

early growing season of 2020 to determine survival rates after 4 years of growth.

2.5 | Data processing and statistical analysis

All data were consolidated into single, averaged values per plot for statistical analyses (R version 4.1.0; R Core Team, 2021) and all data files and R code are openly available in the Dryad open data publishing platform (datadryad.org) at https://doi.org/10.5061/dryad.7sqv9s4w9. Because our data were not normally distributed, we used non-parametric tests (i.e., Kruskal–Wallis and Wilcox posthoc tests with Benjamini and Hochberg *p*-value corrections) to compare biomass yields among cultivars and ecotypes at each site regardless of year, among sites within each cultivar, and year-to-year changes in yield. We tested variation in yield across sites and years using a modified signed-likelihood ratio test (SLRT) for equality of coefficients of variation (c_v; R package *cvequality* Version 0.2.0; Krishnamoorthy & Lee, 2014; Marwick & Krishnamoorthy, 2019).

To characterize the soil and climates of these sites, we performed principal component analyses (PCAs) separately on soil and climate data. Our soil PCA included the following variables measured in the topsoil (0–25 cm depth) before planting in 2016: BD, TOC, TN, TOC:TN, NH_4^+-N, NO_3^--N, TP, M3-P, pH, EC, CEC, % Sand, % Silt, and % Clay. For each site, topsoil values were determined by calculating the weighted average of measured values for the 0–5 cm, 5–15 cm, and 15–25 cm depth increments from each of the three soil cores with sufficient soil to analyze all variables (Table S1). Our climate PCA included the four following site-level variables: T_{max}, T_{min}, PRCP, and PET. Averages (and sums in the case of PRCP) were calculated for the 270 days preceding the collection of switchgrass biomass yield to represent the yearly climate data for each growing season.

To determine the effects of G×E interactions on switchgrass biomass yield, we developed mixed effects models (R package *lme4*; Bates et al., 2015). The models included fixed effects of cultivar and either soil, climate, or soil and climate PC scores, as well as their interactions with cultivar. Block and year of harvest were fitted as random effects. All models were evaluated for best fit, predictive power, and overall quality using marginal R^2 ($_mR^2$; Nakagawa & Schielzeth, 2013) and Akaike information criterion (AIC). To determine the relative importance of soils and climate on switchgrass biomass yield, and whether G×E interactions occurred, we used a two-step approach. First, we fit a full model containing main effects and all interactions of cultivar with the first two soil and climate PC axes. Interactions involving PC axes from the same PCA (e.g., soil PC1 and soil PC2), which are by definition orthogonal, were excluded from the model. The various time scales of averaged climate data were evaluated to find the time scale which achieved the best fit. We then fit four reduced models: (1) soil PCs and their interactions with cultivar, (2) climate PCs and their interactions with cultivar, (3) soil PCs and cultivar without interactions, and (4) climate PCs and cultivar without interactions. These reduced models were compared to the full model using $_mR^2$ and delta-AIC ($\triangle AIC = AIC_{Reduced\ model} - AIC_{Full\ model}$). All models are presented in the supplementary materials (Equations S1–S5).

To evaluate the contributions of plant leaf and tiller traits to switchgrass biomass yield, we calculated simple linear regressions between biomass yield and each plant trait. Data were analyzed by combining site and ecotype regardless of year. Plant traits included stem mass (g), specific leaf area ($cm^2\ g^{-1}$), whole tiller C:N, and tiller height (cm).

3 | RESULTS

3.1 | Switchgrass biomass yields

The most productive cultivar when averaged across all years (2017–2020) was Kanlow which yielded consistently high biomass across all sites. Kanlow was most productive in IL where it yielded an average of 14.1 ± 0.5 Mg ha^{-1} (mean ± standard error [se]; $n = 20$; Figure 2a). Carthage also yielded high biomass when grown in IL, producing 12.7 ± 0.3 Mg ha^{-1}. The least productive cultivar in both IL and MO was Alamo, likely due to its high mortality rates at those sites (24.0 ± 2.3% and 35.4 ± 5.9%, respectively). However, in TX, Alamo was the highest producing cultivar averaging 12.0 ± 0.9 Mg ha^{-1} over the 4-year period. Alamo also produced the highest biomass yield of any cultivar recorded during the study in 2017 in TX (17.8 ± 1.1 Mg ha^{-1}; $n = 5$; Figure 2b). Kanlow produced the second- and third-highest single-year yields; 16.6 ± 0.5 Mg ha^{-1} in IL in 2018, and 16.4 ± 0.7 Mg ha^{-1} in MO in 2017. Although Alamo occasionally had very high biomass yield, it was also the most variable cultivar across years and sites (*M-SLRT statistic* = 20.6, $p < 0.001$). In general, biomass yield of the lowland cultivars (especially in MO) significantly declined over the 4-year study period ($p < 0.05$), while upland and intermediate cultivars remained reasonably stable (Figure 2b).

3.2 | Climate and soil ordinations

Principal component analyses resolved the predominant combinations of climate and soil characteristics

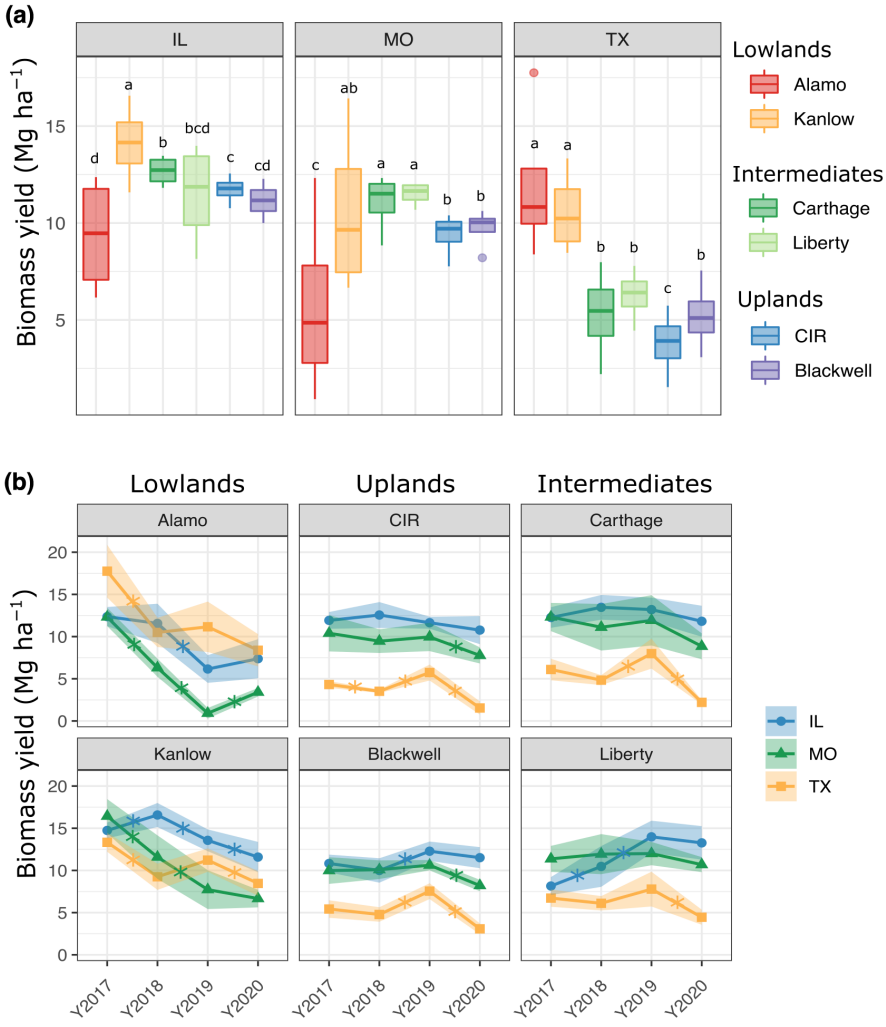

FIGURE 2 (a) End-of-season total switchgrass biomass yield for each cultivar averaged over the 4 years of the study. Colors indicate the different cultivars and letters indicate significant differences between cultivar biomass yields within each site found using Wilcox posthoc tests ($p < 0.05$; $n = 5$ replicates × 4 years = 20). Boxplot lines represent the median, first and third quartiles, and whiskers represent the minimum and maximum values, except for outliers which are represented by circles. (b) Average annual end of season total switchgrass biomass yield for each cultivar during the 4-year study period. Colors indicate the site where switchgrass was grown, shaded areas indicate 95% confidence intervals ($n = 5$), and asterisks over lines indicate significant changes between years ($p < 0.05$). Columns are labeled by ecotype.

that varied across sites. We retained the first two axes of each PCA, which explained 78.5% of the variation in soils and 98.2% of the variation in climate (Figure 3). In the soil PCA (Figure 3a), PC1 explained 47.1% of variation and was primarily driven by soil texture (Silt = 14.6%, Clay = 13.8%) and CEC (13.7%). Soil PC1 scores were positively correlated with Clay and CEC, but negatively correlated with Silt. Soil PC2 explained 31.4% of variation and was driven by positive correlations with soil nutrients (TP = 21.5%, TN = 20.3%) and TOC (18.9%). In the climate PCA (Figure 3b), PC1 explained 85.4% of variation and was primarily driven by positive correlations with temperature (T_{max} = 28.2% and T_{min} = 28.0%) and PET (27.0%) but was also, to a lesser degree, driven by negative correlations with PRCP (16.8%). Climate PC2 explained only 12.8% of variation and was driven almost entirely by a positive correlation with PRCP (83.2%). The soil and climate PC scores and clustering indicated that the environments at our sites differed substantially. The soil PC1 values for IL and MO were similar to one another, but distinct from TX. Soil PC2 values for IL and MO were separated much more distinctly, with TX in between. These patterns show that the soil textures in IL and MO are somewhat similar and highlight the high clay content in the TX soil. They also reveal the differences in soil nutrient and organic C content among sites, especially between IL and MO. Likewise, the separation of sites along the climate PC1 axis shows clear differences in temperature and PET between TX and IL, with MO in the middle. While climate PC2 values (representing PRCP) were similar among the sites, it should be noted that the explanatory power for climate PC2 (12.8%) is relatively low compared to climate PC1 (85.4%), and that PRCP contributions were not only the primary driver of climate PC2, but also contributed a fair amount of influence on climate PC1. This suggests that PRCP does substantially contribute to site separation within the PCA state space. Thus, the PC axes effectively quantified the predominant soil texture, nutrient content, temperature, precipitation, and PET differences among the locations, to which the cultivars could differentially respond (Figure 3 and Tables S1 and S2).

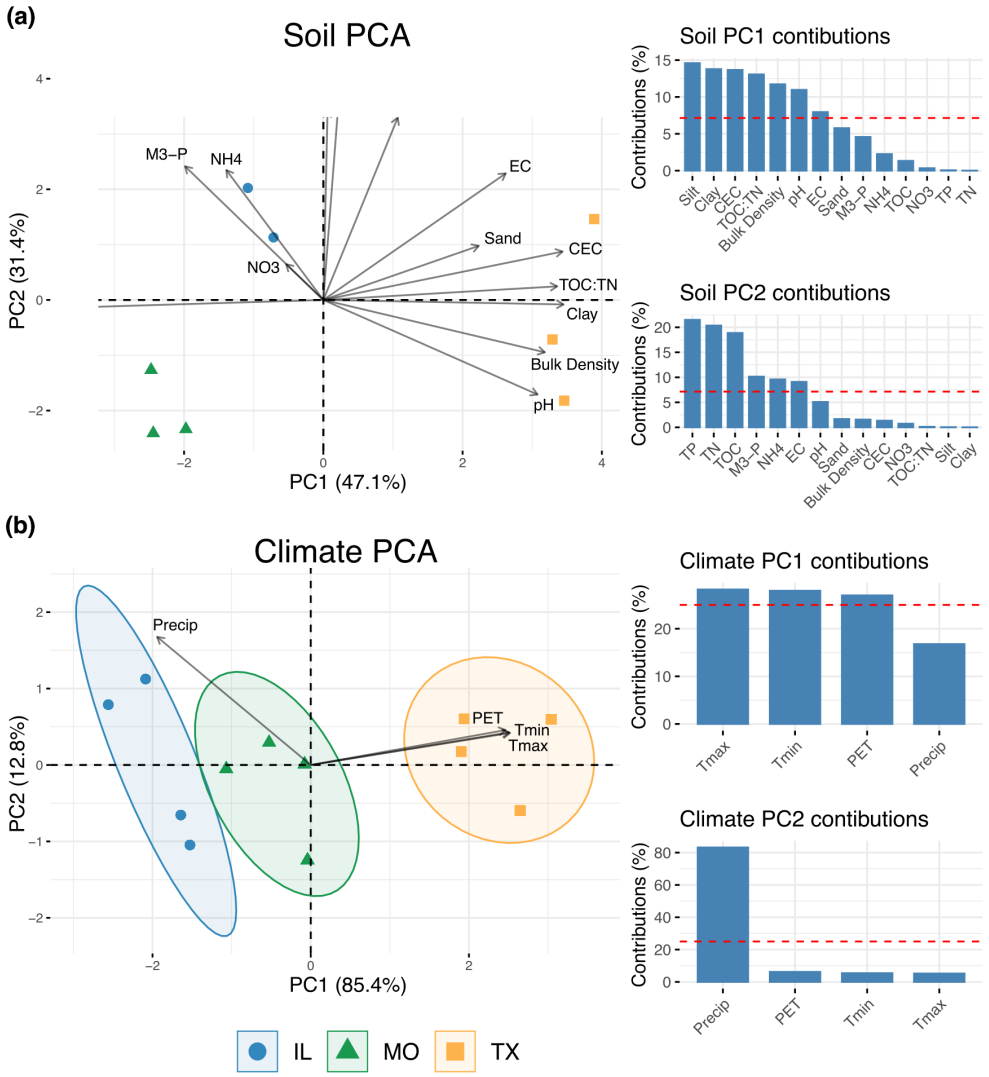

FIGURE 3 Principal component analyses (PCAs) of soil (a) and climate (b) data. In the soil PCA, the points represent the surface 25-cm depth increment of the three fully analyzed soil cores from each site. In the climate PCA, the points represent each year of the study (4 years per site). Climate data included in the PCA were values averaged over 270 days preceding the harvest date for each year (except for precipitation which was summed over the same time periods).

3.3 | G × E interactions and model comparisons

The analysis of mixed effects models used to evaluate G × E responses in switchgrass biomass yield supported the presence of G × E interactions among the cultivars in our study and in both soil and climate variables (Tables 1 and S3, and Figure S3). These significant interactions likely result from the opposite directionality of slope lines in Alamo relative to the other cultivars (Figure 4). Additionally, the site-specific responses of cultivars (dashed lines in Figure 4), particularly for soil PC2, show how yield responses differ from the overall linear trend and contribute to significant G × E interactions. The full model with the lowest AIC value (1347.6) and most predictive power ($_mR^2 = 0.76$) contained cultivar and its interactions with soil PC1 and PC2 and climate PC1 and PC2 (Equation S1). Although all two-way interaction terms with cultivar were significant ($p < 0.001$; Table 1), climate PC1 was the most significant ($F = 52.2$) followed by soil PC2 ($F = 20.4$), climate PC2 ($F = 5.7$), and soil PC1 ($F = 5.2$). These interactions indicated that the high biomass yields of the lowland cultivars Kanlow and Alamo in TX compared to other cultivars were associated with high T_{max}, T_{min}, and PET (climate PC1), intermediate soil nutrient content (soil PC2), low PRCP (climate PC2), and clayey soil texture (soil PC1; Figure 4). In IL, the high biomass yields of Kanlow and Carthage were associated with relatively lower T_{max}, T_{min}, and PET (climate PC1) and higher soil nutrient content (soil PC2).

While the reduced models that contained either soil or climate PCs alone did not fit the data as well as the full model ($\triangle$AIC ≥269; Table 2), they do provide information

TABLE 1 ANOVA table of the full mixed effect model (see Equation S1) with switchgrass biomass yield as the response variable. Random effects are Block and Year. "Soil" fixed effects include PC1 and PC2 from the soil PCA and "Climate" fixed effects include PC1 and PC2 from the climate PCA. Cultivar is included as a fixed effect.

Model terms	Sum Sq	NumDF	DenDF	*F* value	*p*-value
Soil PC1	15.2	1	297.7	9.4	0.0023
Soil PC2	5.4	1	316.8	3.3	0.0688
Climate PC1	12.4	1	271.9	7.7	0.0060
Climate PC2	5.7	1	321.9	3.5	0.0610
Cultivar	177.6	5	341.8	22.0	<0.0001
Soil PC1 × Climate PC1	40.3	1	332.5	25.0	<0.0001
Soil PC1 × Climate PC2	5.3	1	288.9	3.3	0.0701
Soil PC2 × Climate PC1	10.4	1	343.2	6.5	0.0115
Soil PC2 × Climate PC2	15.5	1	345.2	9.6	0.0021
Soil PC1 × Cultivar	42.2	5	341.8	5.2	0.0001
Soil PC2 × Cultivar	164.2	5	341.8	20.4	<0.0001
Climate PC1 × Cultivar	420.2	5	341.8	52.2	<0.0001
Climate PC2 × Cultivar	45.8	5	341.8	5.7	<0.0001
Soil PC1 × Climate PC1 × Cultivar	198.0	5	341.8	24.6	<0.0001
Soil PC1 × Climate PC2 × Cultivar	251.1	5	341.8	31.2	<0.0001
Soil PC2 × Climate PC1 × Cultivar	55.1	5	341.8	6.9	<0.0001
Soil PC2 × Climate PC2 × Cultivar	73.1	5	341.8	9.1	<0.0001

regarding the relative environmental contributions of soil and climate variables on switchgrass biomass yield. The model including only soil PCs (soil model) was a much better overall predictor of biomass yield than the model including only climate PCs (climate model; $\triangle$AIC = 27.6) and explained slightly more variation in our dataset (soil $_{m}R^2 = 0.59$ vs. climate $_{m}R^2 = 0.56$). This comparison suggests the G × E interactions in our study depended more on location differences in soil characteristics than in climate variability across our field sites. Additionally, removal of the G × E interaction terms from each of these models resulted in a loss of predictive power and model quality (soil model $\triangle$AIC = 195.3 and climate model $\triangle$AIC = 162.3; Table 2), reaffirming that G × E interactions substantially affect aboveground biomass yield.

3.4 | Functional trait relationships with yield

Analysis of the relationships between switchgrass biomass yield and several plant functional traits revealed that tiller height and stem mass generally had stronger relationships to yield than did SLA or tiller C:N, and that the strength of these relationships varied among ecotypes and sites (Figure 5). The strongest and tightest relationships occurred in TX where stem mass and tiller heights were positively associated with biomass yield ($p < 0.001$) regardless of ecotype. Significant yield relationships with tiller height and stem mass also occurred in MO for lowland cultivars but became much weaker in upland and intermediate cultivars; whereas, they were non-existent in IL. These trends reveal a potential pattern among stem mass and tiller height functional traits, the ecotypic predisposition to express these traits, and the geographic location of the sites represented in this study. Conversely, the relationships of biomass yield to SLA and tiller C:N were inconsistent and showed no clear geographic or ecotypic patterns. However, the biomass yields of intermediate cultivars were significantly related to SLA in IL ($p < 0.001$), and somewhat significant relationships were found between the biomass yields of lowland cultivars and tiller C:N in MO and TX ($p < 0.01$).

4 | DISCUSSION

Studies examining the effects of G × E interactions on traits in switchgrass common gardens have been important in establishing how locally adapted switchgrass responds to being grown in alternate climates (Zhang et al., 2021). Here we established replicated experimental plots at three locations across the United States containing closed canopies of six common switchgrass cultivars and characterized

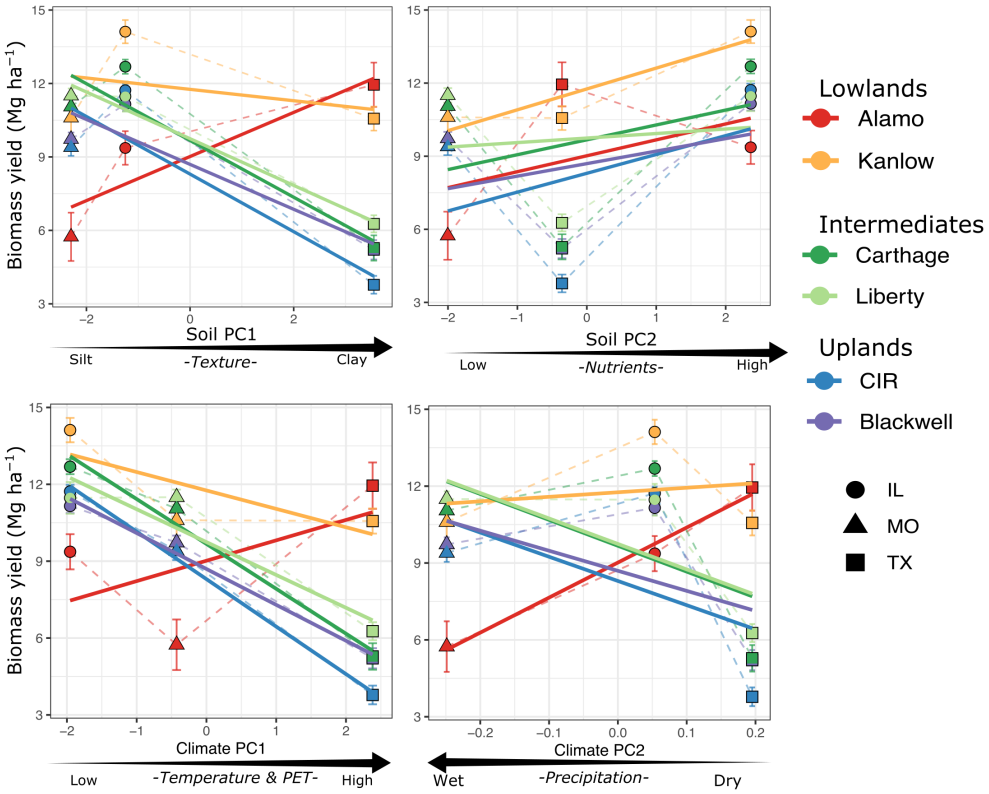

FIGURE 4 G×E interactions on switchgrass biomass yield (means ± standard errors for each genotype at each site; $n = 5$ replicates × 4 years = 20), where the site-specific environment is represented by PC's 1 and 2 from both the soil (top row) and climate (bottom row) PCA. Arrows at the bottom of each panel represent the prevailing environmental gradient for that individual PC. Solid lines represent the overall linear trend across all sites for each genotype and each PC. Dashed lines show patterns between sites.

TABLE 2 Mixed effect model comparisons of reduced models to the full model. In all models, biomass yield is the response variable and random effects are Block and Year. "Soil" fixed effects include PC1 and PC2 from the soil PCA and "Climate" fixed effects include PC1 and PC2 from the climate PCA. Cultivar is included as a fixed effect in all models. △AIC were calculated as the difference between each reduced model and the full model. Model structures can be found in Equations S1–S5.

Model	Cultivar interactions	Marginal R^2	AIC	△AIC
Full (Soil and Climate)	Yes	0.759	1347.6	–
Soil	Yes	0.594	1616.9	269.3
Soil w/o G×E	No	0.367	1812.2	464.6
Climate	Yes	0.559	1644.5	296.9
Climate w/o G×E	No	0.345	1806.8	459.2

the G×E interactions over 4 years (Figure 1). We observed strong G×E interactive effects on biomass yield, primarily due to substantial differences in the response of Alamo relative to the other cultivars (Figure 4). These G×E interactive effects were most significantly driven by variations in cultivar responses to climate (Table 1). However, the best overall predictor of switchgrass biomass yield in this study was the soil environment (Table 2). Furthermore, conservative plant traits, such as high stem mass and plant height, became increasingly associated with biomass yield following the latitudinal trend from IL to MO to TX, regardless of cultivar or ecotype (Figure 5). Moreover, this pattern was especially evident in the lowland cultivars Alamo and Kanlow, which exhibited a more conservative functional strategy and produced the highest yields overall. While both Kanlow and Alamo grew successfully in TX, Alamo produced significantly lower yields in MO and IL relative to Kanlow. Altogether, this evidence suggests that while the soil environment may play a larger role than climate in determining the general patterns of switchgrass

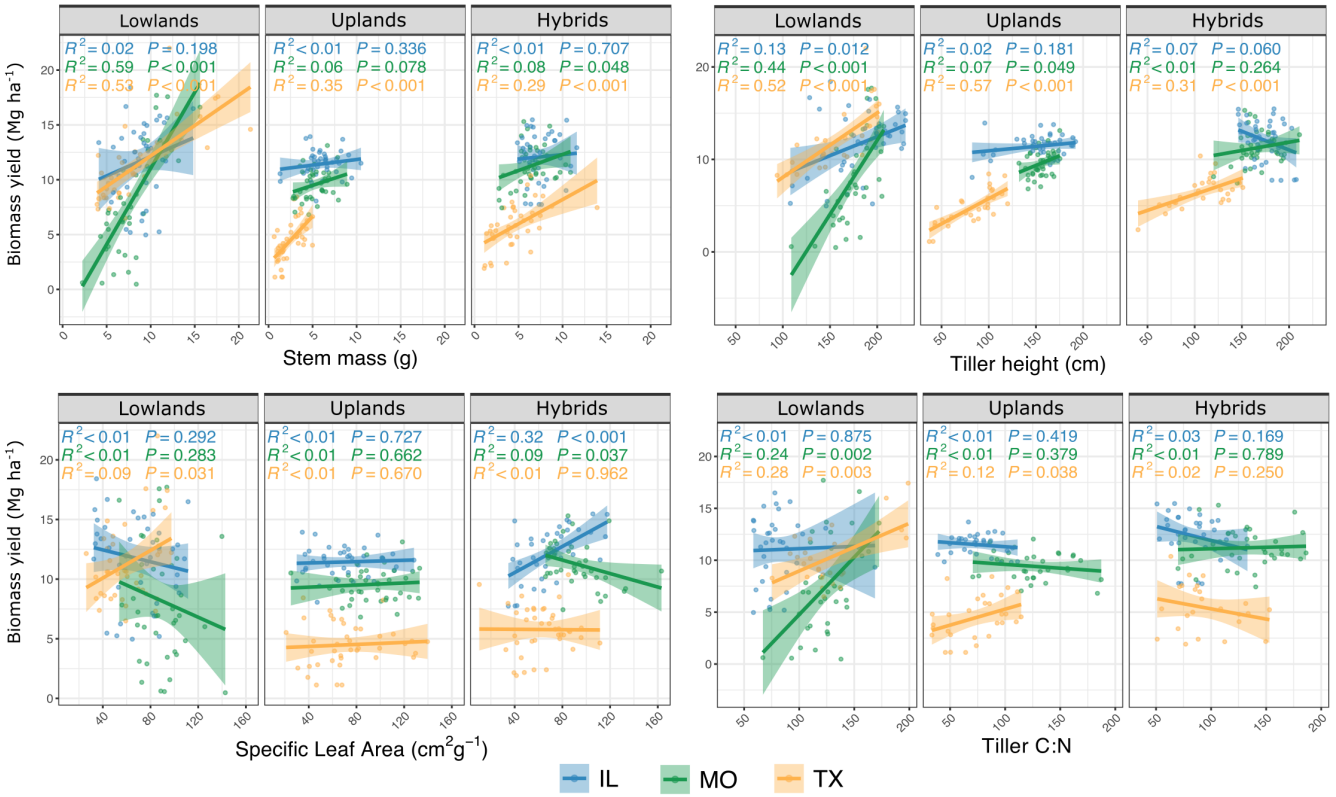

FIGURE 5 Linear relationships between end-of-year aboveground biomass yields and plant tiller and leaf trait components. Cultivars are grouped by ecotype for each trait and colors represent different sites. Shaded areas represent standard error. Adjusted R^2 and p-values of the linear models for each site and ecotype are provided at the top of each panel.

biomass yield, independent of cultivar or ecotype, site differences in climate may exert disproportionately more influence over the biomass yields of lowland cultivars examined in this study. Untangling how plant traits from different cultivars can affect yield and survival under varying environmental conditions will help inform future agronomic strategies in the production of switchgrass as a biofuel feedstock.

4.1 | Drivers of switchgrass G × E interactions

Several studies have examined the factors driving local adaptation in switchgrass across environmental gradients. Latitudinal variation in climate factors such as photoperiod, temperature, and precipitation has a pronounced effect on switchgrass productivity and survival when moved north or south from the latitude of origin (Aspinwall et al., 2013; Behrman et al., 2014; Casler et al., 2004, 2007; Lovell et al., 2021; Reichmann et al., 2018; Sanderson et al., 1999; Wullschleger et al., 2010; Zhang et al., 2019). This climatic response is supported by our results which show significant G × E interactions in biomass yield between cultivar and climate PC1 (Table 1) with lowlands having higher production in TX, and uplands having higher production in MO and IL (Figure 2a). These significant interactions were largely driven by biomass yield responses of the Alamo cultivar (Figure 4 and Table 1). Alamo had the highest yields in the hottest, driest environment (TX) and its lowest yields in the wettest environment (MO). This suggests that Alamo is locally adapted to a specialist strategy focused on surviving hot, dry environments, but its inconsistency in year-to-year yields relative to other cultivars (Figure 2a) may indicate sensitivity to short-term environmental anomalies, which are predicted to become more severe and frequent under climate change scenarios. This response differed substantially from the other cultivars, particularly the upland and intermediate cultivars, which showed decreasing biomass yields with increasing temperature and PET across sites (Figure 4) yet remained relatively stable over the 4-year period at each site (Figure 2b). The success of the Kanlow cultivar across sites is interesting because it provides an example of how a lowland cultivar that is locally adapted to relatively northern climates (Kanlow originates from Oklahoma) can maintain fitness and production across a broad latitudinal gradient. This ability to maximize biomass yield in such a wide variety of environments

indicates a more generalist strategy that may be useful in adapting to climate change. Climate, however, is only one piece of the story.

In addition to climate, the soil environment plays a critical role in determining plant productivity, distribution, and functional trait variation (Dubuis et al., 2013; Joswig et al., 2022). A recent meta-analysis has suggested that climate may be a better predictor of biomass yield than soil environments (Zhang et al., 2019). However, our model comparisons, which more directly compare the independent fixed effects of soil versus climate environmental variables, show that site soil characteristics play a more important role in switchgrass production than does climate at our sites (Tables 2). This disparity within our results is likely due to the removal of soil/climate interactions and aggregation of environmental variables within our reduced models, which does help to clarify and separate the environmental effects on biomass yield. The disparity with previous literature is likely due to the limited number of sites within our dataset relative to the meta-analysis and emphasizes the need for more studies that explicitly address this question. To our knowledge, few studies have specifically examined how variations in soil properties affect switchgrass production in unfertilized, non-irrigated systems, and fewer still have compared yields of multiple cultivars. In one field study, variations in both nutrient content (N and P) and soil texture (clay) had significant positive correlations with biomass yield in the Alamo cultivar (Di Virgilio et al., 2007). This supports our results which show the lowest Alamo yields occurred in MO where soil nutrient content was lowest, and the highest Alamo yields occurred in TX where soil clay content was highest (Figure 4). However, to fully understand switchgrass plasticity and functional trait responses to variations in the soil environment requires an understanding of the mechanisms underlying plant water and nutrient availability.

4.2 | Effects of water and nutrient availability on switchgrass biomass yield

Soil texture and soil organic matter (SOM) content both play a large role in determining plant water availability, but these dynamics are not straightforward. For example, soil with high clay content (i.e., small particle size), like our site in TX, have greater field capacity due to physical adsorptive properties allowing for greater water retention after a precipitation event; however, this same adsorption property also makes it more difficult for plants to access the water under drier conditions. The opposite is true in sandy soils which have much larger particle sizes. Similarly, while high SOM content can increase a soil's field capacity, particularly in sandy and silty soils, it can also reduce field capacity in some fine-textured, clayey soils (Rawls et al., 2003). Differences in SOM among our sites are reflected in the total organic carbon (TOC) concentration, which show TOC in the top 50 cm of the soil profile in IL to be more than double that in MO and significantly more than in TX (Figure S1). However, these site differences in soil characteristics affect more than just plant water availability. They also affect plant nutrient availability.

Soil organic matter provides a rich nutrient reserve and substrate for microbial decomposition leading to increased recycling of soil nutrients. Lower SOM content in MO and TX could lead to lower availability of soil nutrients needed to sustain plant productivity over long time periods and increase the need for fertilizer inputs. Furthermore, the removal of aboveground biomass harvested each year limits the amount of leaf litter and organic matter reentering the soil nutrient pool and may further exacerbate soil nutrient and SOM depletion. This could help explain the greater C:N values in switchgrass tissue from MO relative to IL (Figure S4), as plants grown in soils with lower nutrient availability may be forced to reallocate resources away from aboveground tissue, resulting in relatively lower aboveground N concentrations. Interestingly however, while all cultivars had relatively similar tiller C:N values in MO (Figure S4), it seemed to negatively affect the biomass yields of only the lowland cultivars over time (Figure 2b).

Biomass yields from the lowland cultivar Alamo may be particularly sensitive to soil environments with low nutrient availability. Zhang et al. (2019) reported N fertilization to be the third-best predictor of Alamo yield in random forest models behind temperature and precipitation. In contrast, for all other cultivars in the study (Kanlow, Cave-In Rock, and Shelter), N fertilization was not a main predictor. Likewise, Di Virgilio et al. (2007) found a significant positive correlation between variations in field soil N content and Alamo biomass yield. These findings align with our results which show significantly declining Alamo yields in MO where soil nutrient availability was lowest (Figure 2b) and may indicate that upland and intermediate cultivars are better adapted to environments with low-nutrient soils. Indeed, although lowland cultivars produce larger root systems in general, upland cultivars have been shown to have higher specific root lengths (i.e., finer roots) and develop greater root mass and length at depth that allows for greater nutrient uptake relative to lowland cultivars (De Graaff et al., 2014; Griffiths et al., 2022). This might help to maintain photosynthetic rates throughout the growing season and support long-term growth in low-nutrient soils.

4.3 | Other impacts on biomass yield

Several other possible contributing factors may explain patterns of variable or declining yields over time. For example, extreme weather events, or climate anomalies, may affect switchgrass survivability for some cultivars. Instances of extreme weather did occur during the study period, including in June and July of 2018 when TX and MO incurred a drought period with higher-than-normal temperatures (Figure S2) that could have affected switchgrass productivity. A similar event occurred in TX in 2019 where precipitation totals were lower than normal for four consecutive months (May–August), and temperatures were slightly higher than average. This extended period of drought stress likely reduced biomass yields in TX in the second year of the study. On the opposite extreme, both IL and MO experienced periods of abnormally cold temperatures during the winters of 2018 and 2019, with temperatures reaching as low as −31.8°C in IL, and −23.9°C in MO. Lowland cultivars (particularly Alamo) are not adapted to these extremely low temperatures (Lovell et al., 2021), and exposure to the cold air was exacerbated further by minimal snow cover. Consequently, Alamo experienced a fair amount of winter mortality in IL and MO (24.0 ± 2.3% and 35.4 ± 5.9%, respectively), which likely contributed to reduced biomass yields in subsequent years.

We may theorize many different reasons for the changing patterns we saw in switchgrass productivity over the course of our study, but ultimately these results are likely due to a combination of many interrelated factors that can affect not only biomass yield, but also survival. These include the climate and soil environmental factors discussed above, such as the relationships between precipitation, soil texture, and subsequent nutrient and water dynamics. The interrelated nature of these factors makes it difficult to separate soil versus climate effects, particularly against a background of differing responses from divergent cultivars. For instance, recent research has demonstrated the importance of accounting for multiple environmental factors in studies of population and community dynamics (e.g., abiotic stresses, biotic interactions, etc.; Komatsu et al., 2019; Zandalinas & Mittler, 2022). To that end, follow-up studies that factorially manipulate soil physical, chemical, or biological factors hypothesized to affect switchgrass biomass yield across cultivars would help clarify these plant/soil dynamics and offer insights into crop selection in different environments. Likewise, it is very difficult to link changes in long-term plant productivity to short-term extreme climatic events. Still, future manipulative experiments focusing on switchgrass responses to short-term climatic extremes would help determine switchgrass resilience and/or vulnerability to anomalies in weather patterns. Our PCA provided a way for us to begin untangling these environmental drivers (i.e., soil PC1 = texture; soil PC2 = nutrients; climate PC1 = temperature; climate PC2 = precipitation; Figure 3) and is an important first step toward identifying the most relevant environmental drivers of switchgrass productivity and G × E interactions that can be explored further in more targeted manipulative experiments (Napier et al., 2023).

4.4 | Contributions of conservative and acquisitive functional traits to yield

We found substantial variation in a variety of plant traits that could affect switchgrass yield. Based on the plant economics spectrum, functional strategies are driven by trade-offs in the acquisition and conservation of resources including light, nutrients, and water (Reich, 2014) and are affected by both soil and climate factors (Joswig et al., 2022). As such, plant resource allocation strategies can be helpful determinants of performance in different environments. For instance, in switchgrass, upland genotypes tend to have more acquisitive strategies, while lowland genotypes have more conservative strategies (Aspinwall et al., 2013; Chen et al., 2021; Heckman et al., 2020). Thus, if switchgrass exhibits local adaptation, then acquisitive phenotypes may be favored in the north, and conservative strategies may be favored in the south. This could manifest as changes in relative biomass production. Previous work shows some evidence for coordination in economics strategies across different organs in switchgrass (Chen et al., 2021; Heckman et al., 2020), suggesting that the plant economics spectrum holds within this species.

The concept of the plant economics spectrum can be extended to incorporate traits that are more relevant to biofuel production. For instance, high stem mass may be associated with a conservative strategy, if it is driven by higher stem specific density (Díaz et al., 2016). This may allow plants to resist cavitation and prevent lodging (Reich, 2014). These plant economics strategies may be driven by differences in growing season length—in the north, where shorter growing seasons limit leaf longevity, a quick-return on investment strategy of rapid growth should be advantageous, while in the south, where long growing seasons allow considerably longer leaf lifespan, a slower-return on investment strategy of slow-growing, tough leaves that can tolerate drought stress should prevail (Aspinwall et al., 2013; Chen et al., 2021). The success of this strategy can be seen in our results, which show stronger and tighter relationships of biomass yield with both stem mass and height in TX relative to more northern sites (Figure 5). This indicates that plants able to express these conservative traits adequately, regardless of

origin, produce more aboveground biomass when grown in a southern climate.

In addition to plant productivity, it is also important to consider how plant traits may affect survival in different environments. Because perennial cropping systems rely on interannual survivability, plants must be able to withstand regional climate extremes, as discussed above. In this context, the evolution of generalist strategies by upland cultivars makes sense: they are locally adapted to survive greater fluctuations in photoperiod and temperature typical at higher latitudes. For example, belowground resource allocation strategies in upland cultivars invest more in "inexpensive" acquisitive root structures compared to lowlands with more "expensive" conservative root structures, primarily due to differing strategies in overwintering root persistence and turnover dynamics (Chen et al., 2021). Likewise, survival in nutrient-deficient soil environments may require a tradeoff between above- and below-ground biomass production. Lowland cultivars with more conservative traits favoring aboveground biomass production may be forced to invest more resources belowground to obtain nutrients, resulting in stunted aboveground growth. This could help to explain the decline of aboveground biomass yields of the Alamo cultivar in the nutrient-deficient soils of MO (Figure 2b) and shows that conservative traits, optimized to survive in hot, dry environments, might result in reduced yields compared to ecotypes with more acquisitive traits when grown in low nutrient soils in "wet" climatic conditions (Figure 3).

5 | CONCLUSIONS

Over a 4-year period, switchgrass biomass yields of six commonly used cultivars from genetically divergent ecotypes revealed that Kanlow, a cultivar of the lowland ecotype, was on-average the highest producing switchgrass cultivar across all sites and years. Typically, the aboveground traits exhibited by lowland cultivars, such as thicker stems, wider leaves, and taller tillers, result in high biomass yields. However, consistent annual yields also depend on plant survival in the environment in which they are planted. The Kanlow cultivar exhibited traits which enabled both survival across broad environmental gradients as well as high productivity. The other lowland cultivar, Alamo, experienced mortality in the northern sites resulting in much lower biomass yields than the other cultivars. Ultimately, these environmental response differences between Alamo and the other cultivars led to significant G×E interaction effects across the latitudinal gradient from IL to TX and were primarily driven by climate. However, our models comparing the relative roles of soil and climate characteristics on biomass yield across all cultivars showed that the soil environment was a stronger determinant of biomass yield than climate. Furthermore, we found that with decreasing latitude, switchgrass biomass yield became more tightly associated with two of the four measured plant traits indicative of a conservative resource allocation strategy (i.e., stem mass and tiller height), regardless of cultivar or ecotype. This highlights how these traits become more important for switchgrass fitness and productivity in hotter and drier environments, and supports general patterns outlined in the plant economics spectrum. As climate patterns shift, the need to understand these dynamics which govern the fitness and plasticity of switchgrass, as well as other bioenergy crop species, will become increasingly necessary if they are to be sustainably produced at large scales.

Ultimately, by continuing research that compares the genotypic plasticity within a wide range of genetically diverse switchgrass genotypes, researchers and stakeholders will gain a better understanding of the genotype-by-environment interactions (G×E) that are key to the successful production of switchgrass within a given climate. This understanding is crucial for improving ecosystem services provisioning in switchgrass and predicting switchgrass survivability in rapidly changing climates as well as patterns of adaptation in native perennial grasses more generally.

ACKNOWLEDGMENTS

This work is based upon research supported by the U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research, Genomic Science Program under Award Numbers DE-SC0014156 and DE-SC0021126 (to T.E.J.). Argonne National Laboratory's work was supported by the U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research, Genomic Science Program under Contract DEAC02-06CH11357. Work in Temple, TX was conducted under USDA-ARS cooperative agreement 58-3098-2-003-N with the University of Texas at Austin. The findings and conclusions of this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. A special thank you to all the postdoctoral appointees, technicians, and students who helped gather field data and processed samples for analysis. In particular, we acknowledge the exceptional hard work of Scott Hofmann, Tim Vugteveen, Jeremy Lederhouse, Callie Sharp, AnnaMae Dziallo, Kendall Wald, Tanvi Majumdar, Mark Dreher, Clara Deck, Lillie Haddock, Anastasia Bernat, Rachel Daughtridge, Markos McAuliffe, Hannah Wilson, Nisha Albert, Audrey Kocher, Joel Reyes-Cabrera, Eve Gray, Mike Caballero, Matthew Carey, David Rowley, Austin Rueda,

Quinn Hiers, Madison Gargaro, Michael Heimbuch, Jonathan Colen, and Tina Arredondo.

CONFLICT OF INTEREST STATEMENT

The authors have no conficts of interest to report.

DATA AVAILABILITY STATEMENT

All files required for the data analyses and figure creation, including R codes and plant, soil, and climate data files, can be directly accessed via the Dryad online data repository (datadryad.org) at https://doi.org/10.5061/dryad.7sqv9s4w9.

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REFERENCES

Agrawal, A. A. (2020). A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology*, *101*(2), 1–24. https://doi.org/10.1002/ecy.2924

Allen, R. G., Smith, M., Pereira, L. S., & Perrier, A. (1994). An update for the calculation of reference evapotranspiration. *ICID Bulletin of the International Commission on Irrigation and Drainage*, *43*(2), 35–92.

Anderson, J. T., Willis, J. H., & Mitchell-Olds, T. (2011). Evolutionary genetics of plant adaptation. *Trends in Genetics*, *27*(7), 258–266. https://doi.org/10.1016/j.tig.2011.04.001

Aspinwall, M. J., Lowry, D. B., Taylor, S. H., Juenger, T. E., Hawkes, C. V., Johnson, M. V. V., Kiniry, J. R., & Fay, P. A. (2013). Genotypic variation in traits linked to climate and aboveground productivity in a widespread C4 grass: Evidence for a functional trait syndrome. *New Phytologist*, *199*(4), 966–980. https://doi.org/10.1111/nph.12341

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beguería, S., & Vicente-Serrano, S. M. (2017). *SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index* (R package version 1.7). https://cran.r-project.org/package=SPEI

Behrman, K. D., Keitt, T. H., & Kiniry, J. R. (2014). Modeling differential growth in switchgrass cultivars across the central and southern Great Plains. *Bioenergy Research*, *7*(4), 1165–1173. https://doi.org/10.1007/s12155-014-9450-8

Blanquart, F., Kaltz, O., Nuismer, S. L., & Gandon, S. (2013). A practical guide to measuring local adaptation. *Ecology Letters*, *16*(9), 1195–1205. https://doi.org/10.1111/ele.12150

Casler, M. D., Tobias, C. M., Kaeppler, S. M., Buell, C. R., Wang, Z.-Y., Cao, P., Schmutz, J., & Ronald, P. (2011). The switchgrass genome: Tools and strategies. *The Plant Genome*, *4*(3), 273–282. https://doi.org/10.3835/plantgenome2011.10.0026

Casler, M. D., Vogel, K. P., Taliaferro, C. M., Ehlke, N. J., Berdahl, J. D., Brummer, E. C., Kallenbach, R. L., West, C. P., & Mitchell, R. B. (2007). Latitudinal and longitudinal adaptation of switchgrass populations. *Crop Science*, *47*(6), 2249–2260. https://doi.org/10.2135/cropsci2006.12.0780

Casler, M. D., Vogel, K. P., Taliaferro, C. M., & Wynia, R. L. (2004). Latitudinal adaptation of switchgrass populations. *Crop Science*, *44*(1), 293–303. https://doi.org/10.2135/cropsci2004.2930

Chen, W., Wu, Y., Fritschi, F. B., & Juenger, T. E. (2021). The genetic basis of the root economics spectrum in a perennial grass. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(47), 1–10. https://doi.org/10.1073/pnas.2107541118

Creutzig, F., Ravindranath, N. H., Berndes, G., Bolwig, S., Bright, R., Cherubini, F., Chum, H., Corbera, E., Delucchi, M., Faaij, A., Fargione, J., Haberl, H., Heath, G., Lucon, O., Plevin, R., Popp, A., Robledo-Abad, C., Rose, S., Smith, P., ... Masera, O. (2015). Bioenergy and climate change mitigation: An assessment. *GCB Bioenergy*, *7*, 916–944. https://doi.org/10.1111/gcbb.12205

De Graaff, M. A., Jastrow, J. D., Gillette, S., Johns, A., & Wullschleger, S. D. (2014). Differential priming of soil carbon driven by soil depth and root impacts on carbon availability. *Soil Biology and Biochemistry*, *69*, 147–156. https://doi.org/10.1016/j.soilbio.2013.10.047

De Leon, N., Jannink, J. L., Edwards, J. W., & Kaeppler, S. M. (2016). Introduction to a special issue on genotype by environment interaction. *Crop Science*, *56*(5), 2081–2089. https://doi.org/10.2135/cropsci2016.07.0002in

Di Virgilio, N., Monti, A., & Venturi, G. (2007). Spatial variability of switchgrass (Panicum virgatum L.) yield as related to soil parameters in a small field. *Field Crops Research*, *101*(2), 232–239. https://doi.org/10.1016/j.fcr.2006.11.009

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. https://doi.org/10.1038/nature16489

Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P., & Guisan, A. (2013). Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. *Journal of Vegetation Science*, *24*(4), 593–606. https://doi.org/10.1111/jvs.12002

Fernando, A. L., Rettenmaier, N., Soldatos, P., & Panoutsou, C. (2018). 8 - Sustainability of perennial crops production for bioenergy and bioproducts. In E. Alexopoulou (Ed.), *Perennial grasses for bioenergy and bioproducts* (pp. 245–283). Academic Press Inc. https://doi.org/10.1016/B978-0-12-812900-5.00008-4

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., ... Zaks, D. P. M. (2011). Solutions for a cultivated planet. *Nature*, *478*(7369), 337–342. https://doi.org/10.1038/nature10452

Galliart, M., Bello, N., Knapp, M., Poland, J., St Amand, P., Baer, S., Maricle, B., Smith, A. B., & Johnson, L. (2019). Local adaptation, genetic divergence, and experimental selection in a foundation

grass across the US Great Plains' climate gradient. *Global Change Biology*, *25*(3), 850–868. https://doi.org/10.1111/gcb.14534

Galliart, M., Sabates, S., Tetreault, H., DeLaCruz, A., Bryant, J., Alsdurf, J., Knapp, M., Bello, N. M., Baer, S. G., Maricle, B. R., Gibson, D. J., Poland, J., St Amand, P., Unruh, N., Parrish, O., & Johnson, L. (2020). Adaptive genetic potential and plasticity of trait variation in the foundation prairie grass Andropogon gerardii across the US Great Plains' climate gradient: Implications for climate change and restoration. *Evolutionary Applications*, *13*(9), 2333–2356. https://doi.org/10.1111/eva.13028

Grabowski, P. P., Morris, G. P., Casler, M. D., & Borevitz, J. O. (2014). Population genomic variation reveals roles of history, adaptation and ploidy in switchgrass. *Molecular Ecology*, *23*(16), 4059–4073. https://doi.org/10.1111/mec.12845

Griffiths, M., Wang, X., Dhakal, K., Guo, H., Seethepalli, A., Kang, Y., & York, L. M. (2022). Interactions among rooting traits for deep water and nitrogen uptake in upland and lowland ecotypes of switchgrass (Panicum virgatum L.). *Journal of Experimental Botany*, *73*(3), 967–979. https://doi.org/10.1093/jxb/erab437

Heckman, R. W., Khasanova, A. R., Johnson, N. S., Weber, S., Bonnette, J. E., Aspinwall, M. J., Reichmann, L. G., Juenger, T. E., Fay, P. A., & Hawkes, C. V. (2020). Plant biomass, not plant economics traits, determines responses of soil CO2 efflux to precipitation in the C4 grass Panicum virgatum. *Journal of Ecology*, *108*(5), 2095–2106. https://doi.org/10.1111/1365-2745.13382

Joswig, J. S., Wirth, C., Schuman, M. C., Kattge, J., Reu, B., Wright, I. J., Sippel, S. D., Rüger, N., Richter, R., Schaepman, M. E., van Bodegom, P. M., Cornelissen, J. H. C., Díaz, S., Hattingh, W. N., Kramer, K., Lens, F., Niinemets, Ü., Reich, P. B., Reichstein, M., … Mahecha, M. D. (2022). Climatic and soil factors explain the two-dimensional spectrum of global plant trait variation. *Nature Ecology and Evolution*, *6*(1), 36–50. https://doi.org/10.1038/s41559-021-01616-8

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, *7*(12), 1225–1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Kiniry, J. R., Anderson, L. C., Johnson, M. V. V., Behrman, K. D., Brakie, M., Burner, D., Cordsiemon, R. L., Fay, P. A., Fritschi, F. B., Houx, J. H., Hawkes, C., Juenger, T., Kaiser, J., Keitt, T. H., Lloyd-Reilley, J., Maher, S., Raper, R., Scott, A., Shadow, A., … Zibilske, L. (2013). Perennial biomass grasses and the Mason-Dixon line: Comparative productivity across latitudes in the southern Great Plains. *Bioenergy Research*, *6*(1), 276–291. https://doi.org/10.1007/s12155-012-9254-7

Komatsu, K. J., Avolio, M. L., Lemoine, N. P., Isbell, F., Grman, E., Houseman, G. R., Koerner, S. E., Johnson, D. S., Wilcox, K. R., Alatalo, J. M., Anderson, J. P., Aerts, R., Baer, S. G., Baldwin, A. H., Bates, J., Beierkuhnlein, C., Belote, R. T., Blair, J., Bloor, J. M. G., … Zhang, Y. (2019). Global change effects on plant communities are magnified by time and the number of global change factors imposed. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(36), 17867–17873. https://doi.org/10.1073/pnas.1819027116

Krishnamoorthy, K., & Lee, M. (2014). Improved tests for the equality of normal coefficients of variation. *Computational Statistics*, *29*(1–2), 215–232. https://doi.org/10.1007/s00180-013-0445-2

Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, *102*(1), 186–193. https://doi.org/10.1111/1365-2745.12187

Lovell, J. T., MacQueen, A. H., Mamidi, S., Bonnette, J., Jenkins, J., Napier, J. D., Sreedasyam, A., Healey, A., Session, A., Shu, S., Barry, K., Bonos, S., Boston, L. B., Daum, C., Deshpande, S., Ewing, A., Grabowski, P. P., Haque, T., Harrison, M., … Schmutz, J. (2021). Genomic mechanisms of climate adaptation in polyploid bioenergy switchgrass. *Nature*, *590*(7846), 438–444. https://doi.org/10.1038/s41586-020-03127-1

Lowry, D. B., Behrman, K. D., Grabowski, P., Morris, G. P., Kiniry, J. R., & Juenger, T. E. (2014). Adaptations between ecotypes and along environmental gradients in Panicum virgatum. *American Naturalist*, *183*(5), 682–692. https://doi.org/10.1086/675760

Macel, M., Lawson, C. S., Mortimer, S. R., Šmilauerova, M., Bischoff, A., Crémieux, L., Doleźal, J., Edwards, A. R., Lanta, V., Bezemer, T. M., Van Der Putten, W. H., Igual, J. M., Rodriguez-Barrueco, C., Müller-Schärer, H., & Steinger, T. (2007). Climate vs. soil factors in local adaptation of two common plant species. *Ecology*, *88*(2), 424–433. https://doi.org/10.1890/0012-9658(2007)88[424:CVSFIL]2.0.CO;2

Marwick, B., & Krishnamoorthy, K. (2019). *cvequality: Tests for the Equality of Coefficients of Variation from Multiple Groups*. (0.2.0). R software package. https://github.com/benmarwick/cvequality

Mu, Q., Guo, T., Li, X., & Yu, J. (2022). Phenotypic plasticity in plant height shaped by interaction between genetic loci and diurnal temperature range. *New Phytologist*, *233*(4), 1768–1779. https://doi.org/10.1111/nph.17904

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Napier, J. D., Grabowski, P. P., Lovell, J. T., Bonnette, J., Mamidi, S., Gomez-hughes, M. J., Vanwallendael, A., Weng, X., Handley, L. H., Kim, M. K., Boe, A. R., Fay, P. A., Fritschi, F. B., Jastrow, J. D., Lloyd-Reilley, J., Lowry, D. B., Matamala, R., Mitchell, R. B., Rouquette, F. M., Juenger, T. E. (2022). A generalist – Specialist trade-off between switchgrass cytotypes impacts climate adaptation and geographic range. *PNAS*, *119*(15), 1–10. https://doi.org/10.1073/pnas.2118879119/-/DCSupplemental.Published

Napier, J. D., Heckman, R. W., & Juenger, T. E. (2023). Gene-by-environment interactions in plants: Molecular mechanisms, environmental drivers, and adaptive plasticity. *The Plant Cell*, *35*(1), 109–124. https://doi.org/10.1093/plcell/koac322

Onogi, A., Sekine, D., Kaga, A., Nakano, S., Yamada, T., Yu, J., & Ninomiya, S. (2021). A method for identifying environmental stimuli and genes responsible for genotype-by-environment interactions from a large-scale multi-environment data set. *Frontiers in Genetics*, *12*(December), 1–15. https://doi.org/10.3389/fgene.2021.803636

Provin, T. (2014). Chapter 5.2 - Total carbon and nitrogen and organic carbon via thermal combustion analyses. In F. J. Sikora & K. P. Moore (Eds.), *Soil test methods from the Southeastern United States* (Issue 419, pp. 149–154). Southern Cooperative Series. https://aesl.ces.uga.edu/sera6/PUB/MethodsManualFinalSERA6.pdf

R Core Team. (2021). *R: A language and environment for statistical computing (4.1.0)*. R Foundation for Statistical Computing https://www.r-project.org/

Rawls, W. J., Pachepsky, Y. A., Ritchie, J. C., Sobecki, T. M., & Bloodworth, H. (2003). Effect of soil organic carbon on soil water retention. *Geoderma*, *116*(1–2), 61–76. https://doi.org/10.1016/S0016-7061(03)00094-6

Reich, P. B. (2014). The world-wide "fast-slow" plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211

Reichmann, L. G., Collins, H. P., Jin, V. L., Johnson, M. V. V., Kiniry, J. R., Mitchell, R. B., Polley, H. W., & Fay, P. A. (2018). Interannual precipitation variability decreases switchgrass productivity from arid to Mesic environments. *Bioenergy Research*, *11*(3), 614–622. https://doi.org/10.1007/s12155-018-9922-3

Reichstein, M., Bahn, M., Mahecha, M. D., Kattge, J., & Baldocchi, D. D. (2014). Linking plant and ecosystem functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(38), 13697–13702. https://doi.org/10.1073/pnas.1216065111

Saltz, J. B., Bell, A. M., Flint, J., Gomulkiewicz, R., Hughes, K. A., & Keagy, J. (2018). Why does the magnitude of genotype-by-environment interaction vary? *Ecology and Evolution*, *8*(12), 6342–6353. https://doi.org/10.1002/ece3.4128

Samson, F. B., & Knopf, F. L. (1996). *Prairie conservation: Preserving North America's Most endangered ecosystem*. Island Press.

Sanderson, M. A., Reed, R. L., Ocumpaugh, W. R., Hussey, M. A., Van Esbroeck, G., Read, J. C., Tischler, C. R., Hons, F. M., & Hons, P. M. (1999). Switchgrass cultivars and germplasm for biomass feedstock production in Texas. *Bioresource Technology*, *67*(3), 209–219. https://doi.org/10.1016/S0960-8524(98)00132-1

Sengupta, M., Xie, Y., Lopez, A., Habte, A., Maclaurin, G., & Shelby, J. (2018). The National Solar Radiation Data Base (NSRDB). *Renewable and Sustainable Energy Reviews*, *89*, 51–60. https://doi.org/10.1016/j.rser.2018.03.003

Van Kleunen, M., & Fischer, M. (2005). Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist*, *166*(1), 49–60. https://doi.org/10.1111/j.1469-8137.2004.01296.x

Walter, I. A., Allen, R. G., Elliott, R. L., Howell, T. A., Itenfisu, D., Jensen, M. E., & Snyder, R. L. (2005). The ASCE sandardized reference evapotranspiration equation. In *Final Report*. Environmental and Water Resources Institute of the American Society of Civil Engineers. https://doi.org/10.1061/9780784408056

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827. www.nature.com/nature

Wullschleger, S. D., Davis, E. B., Borsuk, M. E., Gunderson, C. A., & Lynd, L. R. (2010). Biomass production in switchgrass across the United States: Database description and determinants of yield. *Agronomy Journal*, *102*(4), 1158–1168. https://doi.org/10.2134/agronj2010.0087

Zandalinas, S. I., & Mittler, R. (2022). Plant responses to multifactorial stress combination. *New Phytologist*, *234*(4), 1161–1167. https://doi.org/10.1111/nph.18087

Zhang, L., Juenger, T. E., Lowry, D. B., & Behrman, K. D. (2019). Climatic impact, future biomass production, and local adaptation of four switchgrass cultivars. *GCB Bioenergy*, *11*(8), 956–970. https://doi.org/10.1111/gcbb.12609

Zhang, L., MacQueen, A., Bonnette, J., Fritschi, F. B., Lowry, D. B., & Juenger, T. E. (2021). QTL × environment interactions underlie ionome divergence in switchgrass. *G3: Genes, Genomes, Genetics*, *11*(7), jkab144. https://doi.org/10.1093/g3journal/jkab144

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How to cite this article: Ricketts, M. P., Heckman, R. W., Fay, P. A., Matamala, R., Jastrow, J. D., Fritschi, F. B., Bonnette, J., & Juenger, T. E. (2023). Local adaptation of switchgrass drives trait relations to yield and differential responses to climate and soil environments. *GCB Bioenergy*, *15*, 680–696. https://doi.org/10.1111/gcbb.13046