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RESEARCH ARTICLE

Long-term yields in annual and perennial bioenergy crops in the Midwestern United States

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Abstract

Many yield predictions in perennial bioenergy species have been made based on data collected during the establishment phase of growth or a limited number of long-term studies. Few studies compare multiple perennial crops with the dominant agricultural vegetation of the landscape over long time periods. Here, we present the results of 11 years of perennial crop management on fertile agricultural soils in central Illinois, compared with conventional row crop maize/soybean (*Zea mays* L., *Glycine max* L.) production. We examined the long-term productivity and drought susceptibility of *Miscanthus* x *giganteus* Greef et. Deu. ex. Hodkinson et Renvoize (miscanthus), *Panicum virgatum* L., Cave-in-Rock cultivar (switchgrass), and a native prairie mix, in contrast to annual maize/soybean agriculture. Long-term yields for miscanthus and switchgrass failed to reach initial predictions made during the establishment phase; however, in miscanthus, the 11th year of production shows little progressive yield loss with age, exceeding the modeled limit for the onset of age-related decline. Harvest timing and differences in yields from hand and machine harvests in perennial crops likely contribute to overestimates of potential yields. Application of fertilizer to mature miscanthus resulted in significant increases in yield after a severe drought, though modeled effects of management and drought in miscanthus point to a more complex mechanism for yield response.

KEYWORDS

bioenergy/biofuels, DAYCENT model, drought, miscanthus, perennial grasses, root allocation, yields

1 | INTRODUCTION

The rapid growth in renewable and alternative energy development over the last two decades has increased the public interest in bioenergy and the need for bioenergy feedstocks for the production of liquid biofuels. Bioenergy crops for carbon mitigation are part of the "bioenergy with carbon capture and storage" (BECCS) strategy (Robertson et al., 2017; Rosen, 2018), a method of energy production with a smaller carbon footprint than fossil fuel combustion. Research continues on the feasibility and sustainability of biomass production for biofuel conversion (Davis et al., 2012; de Souza et al., 2013; Gauder et al., 2011; Jain et al., 2010), and the long-term ecological effects of perennial bioenergy crops. While bioenergy feedstocks are being investigated based on their individual adaptations for different climate zones, few studies offer direct comparisons of multiple potential feedstocks in a long-term dataset (Borkowska & Molas, 2013; Iqbal et al., 2015; Robertson et al., 2017; Sanford et al., 2016). Additionally, the longevity of perennial crops leads to compounding effects of stand age and climate effects that are less well characterized.

While maize grain (*Zea mays* L., an annual crop) constitutes the dominant feedstock for bioethanol produced in the United States (IEA [International Energy Agency], 2019), and occupies 28 M ha of farmland, concern over the division of resources between food and fuel production, and the fertilizer and pest management demands of maize have increased interest in perennial feedstocks for second-generation cellulosic bioethanol (Anderson-Teixeira et al., 2013; Sanford et al., 2016; Somerville et al., 2010). Perennial crops have lower fertilizer and management demands than conventional row crops, and benefit the soil through reduced use of pesticides and decreased soil erosion through reduced tillage frequency. Perennial crops provide important ecosystem services with the potential for high yields (Arundale et al., 2014; Davis et al., 2012; Robertson et al., 2008; Smith et al., 2013), but also have a lag in establishment and full productivity that make them less enticing to farmers and land managers (Arundale, Dohleman, Heaton, et al., 2014; Miao & Khanna, 2017).

The University of Illinois Energy Farm was established in 2008 to investigate the long-term productivity and feasibility of three perennial bioenergy crop systems: miscanthus (*Miscanthus* x *giganteus* Greef et. Deu. ex. Hodkinson et Renvoize), switchgrass (*Panicum virgatum* L., Cave-in-Rock cultivar), and a 28-species prairie mixture. Research on the site has contributed to understanding nutrient dynamics, carbon sequestration, and ecosystem services of perennial monocultures and prairie mixtures (Anderson-Teixeira et al., 2013; Arundale, Dohleman, Heaton, et al., 2014; Arundale, Dohleman, Voigt, et al., 2014; Davis et al., 2012; Hudiburg et al., 2016; Kantola et al., 2017; Masters et al., 2015; Robertson et al., 2017; Smith et al., 2013). Due to the long lifespan of perennial crops and the pressure of a rapidly developing field, biofuel feedstock research has been weighted toward studies of young, establishment-phase stands (<5 years old) (Davis et al., 2012; Anderson-Teixeira et al., 2013; Smith et al., 2013; Cadoux et al., 2014; Robertson et al., 2017. For long-term studies, see Sanford et al., 2016; Wang et al., 2020). Short-term studies, which demonstrate adaptability of individual crops to a growing environment, can fail to capture maximum potential productivity if the perennial crop stands do not reach maturity in the course of the study or experience establishment challenges like frost or drought (Anderson-Teixeira et al., 2013 vs. this study). In contrast, early estimates of productivity may overestimate yields due to optimal timing, that is, over the course of a decade, a perennial crop will likely experience climate variability that may reduce cumulative yield. After 11 years, perennial crops at the Energy Farm have entered the "rotational phase" of the perennial grass life cycle, when managers begin to consider turning over and replanting the mature crop. Modeled predictions show that productivity will begin to decline as the stand approaches 15 years of age (Miao & Khanna, 2017).

Here, we present 11 years of biomass data from the Energy Farm demonstrating the responses of three perennial bioenergy crops to climate variability, fertilization, and stand age in direct comparison with annual maize and soybean (*Glycine max* L.), with the intention of improving estimates of yields in bioenergy feedstocks, an invaluable resource for growers and policy makers interested in bioenergy crops. Here, we present three hypotheses suggested by ecological theories of perennial plant growth and adaptation (Isbell et al., 2015; Knapp et al., 2001; McNaughton et al., 1983; Sarmiento, 1992; Volaire et al., 2014). We hypothesize that perennial systems will be less influenced by inter-annual climatic variability than annual crops. We hypothesize that despite repeated demonstrations of its efficient N cycling in N-rich soils, high-yielding miscanthus will eventually become N limited and respond to fertilization. Lastly, we hypothesize that by the 11th growing season, the effect of stand age will be evident in declining yields in the perennial monocultures. We compared productivity of fertilized and unfertilized miscanthus and examined the effects of fertilization on biomass allocation. We used the DAYCENT biogeochemical model to disentangle the compounding effects of stand age and drought on miscanthus productivity over time, with implications for perennial crop longevity in the face of future climate variability.

2 | MATERIALS AND METHODS

The University of Illinois Energy Farm (40°3′46″N, 88°11′46″W) is located in Urbana, IL, United States. The Energy Farm was established in 2008, on land previously used for more than 100 years of row crop agricultural production on former tallgrass prairie. Soils consist of Dana silt loam (fine-silty, mixed, superactive, mesic Oxyaquic Argiudolls); Flanagan silt loam (fine smectitic, mesic, Aquic Argiudolls); Blackberry silt loam (fine-silty, mixed superactive, mesic Oxyaquic Argiudolls); and Drummer silty clay loam (fine-silty, mixed superactive, mesic Typic Endoaquolls). Mean annual temperature is 10.9°C, and mean annual precipitation is 1051 mm (Angel, 2010; 1981–2015 average), with highest rainfall occurring in the months of May, June, and July.

The experiment consists of replicated plots of four vegetation types: a maize–maize–soybean rotation, monoculture plots of miscanthus and switchgrass, and a 28-species restored prairie (see Zeri et al., 2011 for complete species list). Plots of each vegetation type were arranged in a randomized block design, with one 3.8-ha plot (minimum size needed to incorporate an eddy covariance tower, see Moore et al., 2020, 2021), and four 0.7-ha plots.

Soybean was alternated with maize every third year (2010, 2013, 2016) to mimic conventional row crop production in this area. Nitrogen fertilizer was applied prior to maize planting as 28% urea ammonium nitrate at 168 kg N ha^{-1} (2008, 2011, 2014) and 202 kg N ha^{-1} (2009, 2012, 2015, 2017, 2018). Until 2017, maize was fertilized at a lower rate in the first year of maize rotation because calculated N needs included an N credit from the previous soybean year. From 2017 onward, maize was fertilized consistently at 202 kg N ha^{-1} to better represent local practice (Timothy Mies, personal communication). Miscanthus was propagated by rhizomes cloned from a single stock, as described in by Heaton et al. (2008), while switchgrass and prairie were broadcast seeded, and maize was planted by drill seeding. Delayed planting in 2008 and a harsh winter in 2008–2009 resulted in high mortality of juvenile miscanthus rhizomes; requiring replanting in 2009 and partial replanting in 2010 (see Smith et al., 2013). Miscanthus was unfertilized from 2008 to 2013, after which half of each miscanthus plot received 56 kg N ha^{-1} granular urea from 2014 to 2018. Switchgrass was fertilized with granular urea, at 56 kg N ha^{-1} from 2010 to 2018. Soybean and prairie were not fertilized. Row crop plots were chisel plowed each fall following maize harvest according to the regional convention, and worked with a field cultivator (Sunflower Mfg., AGCO Corp.) in spring prior to planting both maize and soybean. Perennial crops were untilled after establishment (see Table S1: Management).

Peak biomass was collected for each crop annually when leaf area index (LAI) measurements (measured weekly, not shown) reached a plateau indicating biomass was no longer increasing in the system. LAI was used instead of plant growth stage so that a common metric could be used for maize, soybean, and non-grain-producing perennials. Aboveground biomass was collected biometrically, with several randomly placed quadrats collected in each field, oven-dried, weighed, and averaged. A 0.5625-m^2 quadrat was used for miscanthus, maize, and soybean; a 0.36-m^2 quadrat was used for switchgrass and prairie. Belowground biomass was averaged from roots and rhizomes collected from three 5.08-cm diameter cores of 30-cm depth collected within the quadrat during the aboveground sampling. Cores from each location were combined and plant root material was separated from soil by elutriation.

Harvest/removal biomass and litter were collected by hand with 0.5625 m^2 (miscanthus, maize, and soybean) or 0.36 m^2 (prairie and switchgrass) quadrats within 2 days prior to mechanized harvest at a height of 10–15 cm. Perennial crops were not harvested in 2008. Harvest date for perennial crops was determined by weather—all perennial crops were allowed to dry in the field prior to harvest to maximize retranslocation of nutrients (Masters et al., 2015), and then harvested when conditions allowed. Therefore, harvest dates fell between November and April, with prairie and switchgrass normally harvested in November and December, respectively, and miscanthus harvested in February or March. Field harvest measurements for prairie ended in 2016 when management changed to incorporate biomass burning in the field for invasive species control. All biomass was oven-dried at 60 C to constant mass, and weighed to calculate yield.

2.1 | Statistics

While miscanthus establishment in the US Midwest has been estimated between 3 and 5 years (Anderson et al., 2011; Arundale, Dohleman, Heaton, et al., 2014; Clifton-Brown & Lewandowski, 2000), the drought of 2012, in the fifth year of perennial crop growth on this site, was sufficient disturbance to either reduce productivity or prevent the crop from achieving full productivity at maturity, resulting in the need to define the life stages of the perennial crops for statistical purposes as "pre-drought" (2010–2011), "drought" (2012), and "post-drought" (2013–2018). The relatively small biomass in 2008 and 2009 in miscanthus, switchgrass, and prairie is attributed to first- and second-year growth in an establishing perennial crop. Peak biomass values from 2008 and 2009 were excluded from statistical analysis of perennial crops.

Differences in biomass between crops were tested using a complete block repeated measures ANOVA with crop, year, and their interaction as fixed factors. We used complete block repeated measures ANOVA with crop as fixed factor to test differences in biomass between crops during pre-drought (2010–2011), drought (2012), and post-drought (2013–2018) years. We tested differences in biomass between fertilized and unfertilized miscanthus using a complete block repeated measures ANOVA with fertilized or unfertilized crop, year, and their interaction as fixed factors. For each perennial crop, differences in biomass between the pre-drought (i.e., 2010–2011) and drought/post-drought (2012–2018) phases were tested using a simple ANOVA with developmental stage as fixed factor. Data were transformed to ensure normality and homogeneity of variances. All statistical tests were conducted with Statgraphics Centurion XVI (Statistical Graphics Corporation).

2.2 | Model description and simulations

In 2012, the combination of abnormally low snowfall during preceding winters and the generally dry conditions associated with the La Niña weather pattern led to a severe drought that continued into 2013 and drastically reduced crop yields throughout the US Midwest (Mallya et al., 2013; Rippey, 2015). In the absence of a climate control treatment, we used the DAYCENT biogeochemical model to disentangle the impacts of drought and stand age on productivity (Del Grosso et al., 2005; Parton et al., 1998). The DAYCENT biogeochemical model simulates the effects of climate and land use on ecosystem carbon and nutrient cycling and has been extensively validated for use in grassland and crops, including high-yielding lignocellulosic bioenergy crops (Adler et al., 2007; Anderson-Teixeira et al., 2009; Blanc-Betes et al., 2021; Campbell et al., 2014; Chamberlain et al., 2011; Cheng et al., 2013, 2014; Davis et al., 2010; Del Grosso et al., 2006; Hudiburg et al., 2016; Parton et al., 2001). Model inputs included vegetation cover, daily precipitation and temperature, soil texture, and nitrogen deposition, as well as current and historical land use practices. Historical simulations were built on reconstructions of the original biome based on the Olson et al. (2001) classification followed by agricultural history and historical management practices, and by integrating site-specific climate reconstructions of historic daily weather records from CRU-NCEP (1901–1979). The NCEP reanalyzes 2.5 × 2.5 degrees 6-hour time step from 1948 and beyond that uses observed variability to estimate daily values for the period covering 1901–1947 (Viovy, 2018). Agricultural history included maize–soybean rotations, alfalfa, and wheat. Soil carbon stocks were simulated to represent the pre-agricultural native prairie levels with a subsequent decline as the land was cultivated each year for the annual crops. Following the agricultural history, the Energy Farm simulations were run from 2008 to 2019 duplicating the site management (Table S1). A baseline-fertilized miscanthus (56 kg N ha^{-1} y^{-1}) was simulated for the entire period for comparison with unfertilized miscanthus since the onset of the experiment.

2.3 | Model parameterization, calibration, and validation

For this study, DAYCENT was parameterized to reproduce the impacts of drought and post-drought on the productivity of miscanthus, integrating nutrient interactions. Crop-specific physiology, ontogeny, and interactions with the environment (e.g., physiological responses to light, water and nutrient availability, and developmental stage) were parameterized following dynamics reported in the literature (Anderson et al., 2011; Arundale, Dohleman, Heaton, et al., 2014; Arundale, Dohleman, Voigt, et al., 2014; Behnke et al., 2012; Boersma et al., 2015; Da Costa et al., 2019; Davis et al., 2010; Dohleman et al., 2012; Heaton et al., 2009; Holder et al., 2018; Hong et al., 2014; Hudiburg et al., 2015; Ings et al., 2013; Malinowska et al., 2020; Mann et al., 2013; Maughan et al., 2012; Miguez et al., 2008; Pyter et al., 2010; Scarlat et al., 2010; Van der Weijde et al., 2017). We optimized simulations of crop responses to drought based on field observations at the Energy Farm. Predicted productivity was optimized by adjusting carbon allocation with water and nutrient stress, the response of above- and belowground C-to-N ratios to precipitation, the regulation of shoot and root death under water stress, and nutrient translocation under severe drought. Crop productivity was further optimized by redefining potential plant productivity, response to nutrient availability, and emergence and senescence events as a function of stand age. Energy Farm data including above- and belowground biomass measurements, biomass C and N content, and soil nutrient measurements, along with local weather data and N deposition measured at a nearby weather station were used to calibrate the model. Following calibration, the model was evaluated against randomly selected observations excluded from model calibration, from both unfertilized plots and plots fertilized since 2014 at the Energy Farm. Simple linear regression and a student's t test were used to compare observed and predicted data.

The model was used to produce three data projections: growing miscanthus without fertilizer; the existing scenario, in which unfertilized miscanthus began to receive fertilizer after maturity; and a fertilized projection, where the miscanthus had been fertilized from the outset. From there, the model incorporated a disturbance in the form of water stress (the 2012 drought) and the response of all three projections was compared.

3 | RESULTS

3.1 | Yields

Maize harvest yields (grain only) machine harvested at the Energy Farm averaged 10.90 Mg dry matter (DM) ha^{-1} (173.4 bu ac^{-1}) between 2008 and 2018, not significantly different from the county-wide average of 183.7 bu ac^{-1} observed in Champaign County over the same time period

(Figure 1, Table S2; USDA NASS, downloaded 6/15/20). Maize was rotated with soybeans in 2010, 2013, and 2016. Maize yields at the Energy Farm and the county-wide average in the 2012 drought were lower than 2008–2011, but not significantly different from each other. The drought caused widespread crop loss through the region in 2012. Soybean harvest yields (grain only) the following year (2013) were comparable to 2011 and 2014 values for the region, showing no indication of drought effects on yields in annual crops beyond the drought period (Table S2; USDA-NASS, retrieved 12 May 2021).

All perennial crop end-of-season yields were hand harvested as total aboveground biomass (Figure 1). Miscanthus yields, harvested January–March of the following year, averaged 10.65 Mg DM ha^{-1} from 2010 to 2012. In the 2014 growing season, yield dropped significantly compared with the average of the previous 3 years (t test, $p = 0.02$), and from 2013 to 2018, the post-drought period, yield averaged 7.20 Mg DM ha^{-1}, a loss of 33% from the pre-drought (2010–2012) average. Switchgrass yields peaked in 2011 (15.51 Mg DM ha^{-1}) before the drought and remained between 4.15 and 11.46 Mg DM ha^{-1} from 2013 to 2018. End-of-season yield in prairie recovered to near pre-drought levels in 2013 and was not significantly different from 2010 to 2012 (6.15 Mg DM ha^{-1}) measurements following the drought (2013–2015, 5.99 Mg DM ha^{-1}).

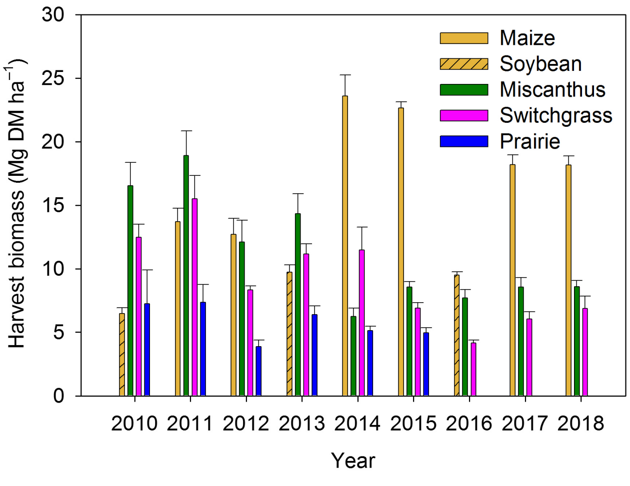

FIGURE 1 Harvest yield (hand-harvested) was grain for soybean and maize and aboveground biomass for miscanthus, switchgrass, and prairie. Bars represent average values and the error bars represent the standard error of the mean. Perennial crops were not harvested in 2008 and 2009 to encourage establishment. Yields trended upwards in 2010 and 2011 and were reduced in 2012 during the drought. Both switchgrass and prairie yields increased significantly in 2013 compared with the drought year, while miscanthus yield was not significantly different. Prairie harvest ceased in 2016, after which the prairie was managed with spring fire

Miscanthus, switchgrass, and prairie plots increased in peak biomass (hand harvested) with age from 2008 to 2010 (Figure 2) as the crops established. Peak biomasses in 2008 reflect first-year growth, and miscanthus replanting in 2009 resulted in a second year of very low biomass for miscanthus. In 2011, the year before the drought, peak biomass in perennials was not significantly different from 2010. In 2012, all crops were affected by drought conditions, with significant decreases in both peak aboveground biomass (Figure 2a) and harvested yield (Figure 1). All perennials showed an increasing trend in biomass between 2012 and 2013, though peak biomass was only significantly higher in prairie (Figure 2a). Rainfall in 2013 was within normal parameters for total precipitation by the end of the year; however, drought-like conditions persisted into March of 2013 and likely affected the early-emerging perennials and resulted in low harvest yields (Figure S1).

General linear model regression analysis of pre-drought (2010–2011) and post-drought (2013 and later) peak biomass showed a significant decrease in peak biomass following the drought for both switchgrass ($p = 0.002$) and miscanthus ($p = 0.0038$) (Figure 2a). Prairie peak biomass was reduced in the drought year (2012); however, prairie recovered more completely from the drought than the perennial monoculture crops, and pre-drought biomass was not significantly different from the average peak values between 2013 and 2016. Though drought conditions continued into early 2013 (Mallya et al., 2013), soybeans (planted May 14–15, Table S1) experienced near-normal precipitation, with no evidence of water limitation on grain yields (Figure 1).

Miscanthus was particularly affected by the drought in 2012. In the years prior to the 2012 drought, the average peak biomass for miscanthus was 22.76 Mg DM ha^{-1}, excluding the two low-yielding establishment years in 2008 and 2009. Following the drought in 2012–2013, miscanthus peak biomass never recovered to pre-drought values, averaging 12.56 Mg DM ha^{-1} between 2014 and 2016 (Figure 2a). Perennial belowground biomass was regularly 10–100× greater than belowground biomass of annual crops, both pre- and post-drought (Figure 2b). Miscanthus, which produces significant belowground biomass as rhizomes, led all species in total biomass production (Figure 2b). All perennial crops showed an increase in allocation to belowground biomass following the 2012 drought (Figure 2b).

3.2 | Miscanthus fertilization

Following the drought of 2012, perennial crops began to allocate more biomass belowground (Figure 3). In an effort

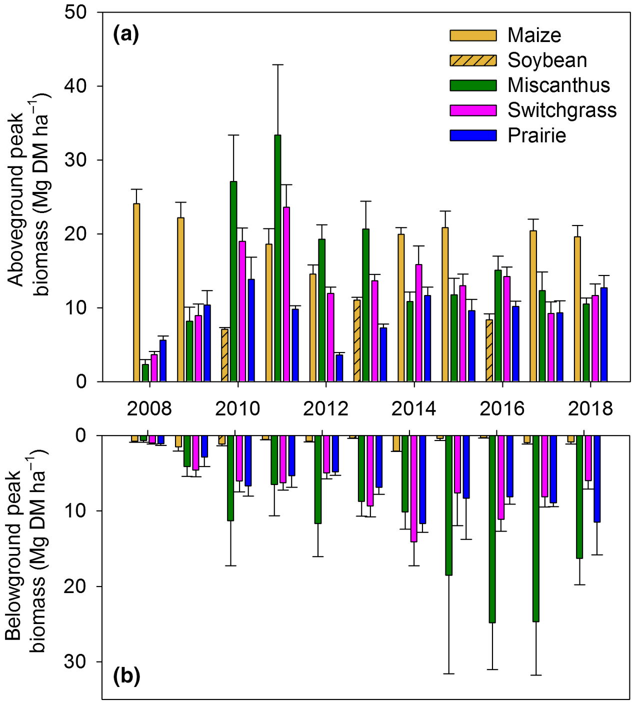

FIGURE 2 Aboveground (a) and belowground (0–30 cm), (b) biomass derived from hand harvests in four bioenergy crops from 2008 to 2018. Soybean was alternated with maize every 3 years (2010, 2013, 2016). Bars represent average values and the error bars represent the standard error of the mean

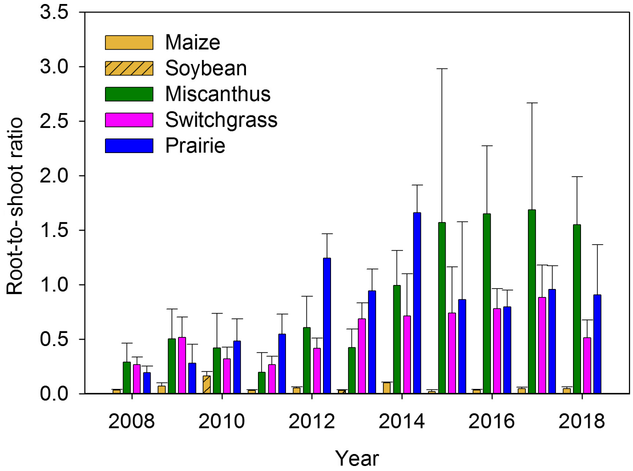

FIGURE 3 Root-to-shoot ratio derived from hand harvest biomass illustrated in Figure 2 for maize/soy (yellow), miscanthus (green), switchgrass (pink), and prairie (blue) from 2010 to 2018 shows greater biomass allocation belowground after plants reach maturity and post-drought. Bars represent average values and the error bars represent the standard error of the mean

to increase yield, half of each miscanthus plot was fertilized annually post-emergence with 56 kg ha^{-1} granular urea, beginning in the spring of 2014. With the addition of fertilizer, fertilized miscanthus harvest biomass (10.74 Mg DM ha^{-1}) increased 72% over unfertilized (6.24 Mg DM ha^{-1}) in the fall of 2014 and remained significantly higher than unfertilized through 2018. Peak aboveground biomass increased by 80% with fertilization over unfertilized in 2014 (Figure 4). From 2015 to 2018, both peak aboveground biomass (23.48 Mg DM ha^{-1}, hand harvest) and harvest yield (16.06 Mg DM ha^{-1}, hand harvest) were significantly larger ($p < 0.002$) in fertilized miscanthus plots than in unfertilized (peak = 12.42 Mg DM ha^{-1}, harvest = 8.35 Mg DM ha^{-1}).

Belowground peak biomass was not significantly different between unfertilized and fertilized plots from 2014 to 2018 (Figure 4). With fertilization, miscanthus aboveground biomass increased in proportion to belowground biomass. However, unfertilized miscanthus allocated the same amount of plant material belowground without increasing aboveground biomass, resulting in a significantly higher root-to-shoot ratio in unfertilized plots compared with fertilized (Figure 5). This difference in root-to-shoot ratio was observed from 2014 to 2018.

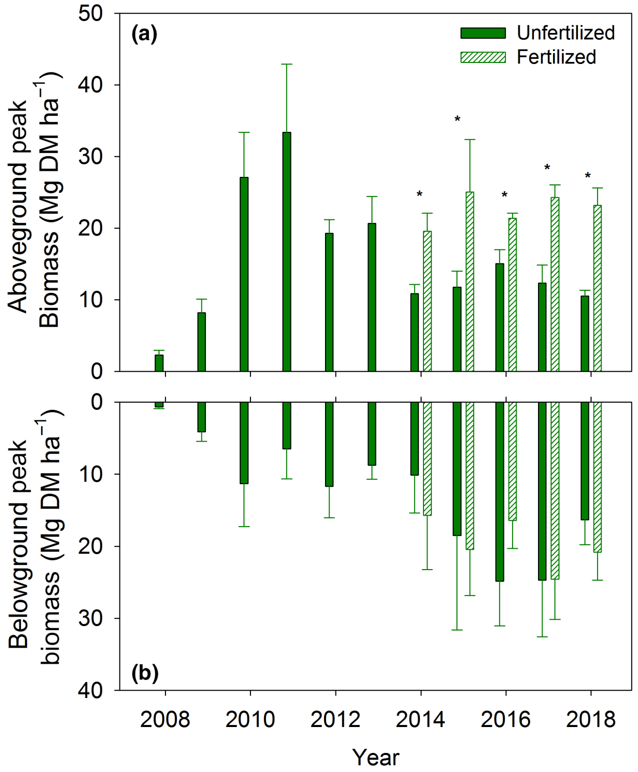

FIGURE 4 Aboveground (a) and belowground (0–30 cm), (b) biomass from hand harvests in miscanthus for unfertilized (solid) and fertilized (hatched) plots, with fertilization initiated in 50% of each plot in 2014. Asterisks indicate a significant difference between unfertilized and fertilized biomass for a given year. Bars represent average values and the error bars represent the standard error of the mean

3.3 | Model predictions

Parameterizing the DAYCENT model to meet observed productivity at the Energy Farm required both adjusting the sensitivity of crop productivity and carbon and nutrient allocation parameters to water stress and accounting for stand age. Once parameterized, the model predicted miscanthus yields with a high degree of accuracy (Figure 6a). The model predicted that fertilization during the establishment phase only marginally increased pre-drought yields at this site; however, when fertilizer application began post-drought on established miscanthus, yield improvements were indicated regardless of whether fertilizer was applied directly post-drought, or after a period of years. While all variations of the model (unfertilized, fertilized from establishment, and fertilized post-drought) were affected by the drought conditions in 2012, unfertilized miscanthus showed a continued decline with time following the drought, while miscanthus fertilized from establishment and miscanthus fertilized post-drought reached a stable level of productivity. Predicted yields for miscanthus fertilized from establishment and miscanthus fertilized post-drought were not different, indicating no benefit of early initiation of fertilization beyond the marginal increase in yield between fertilized and unfertilized miscanthus pre-drought.

4 | DISCUSSION

Initial models of potential yields from perennial crops in Illinois overestimated miscanthus yields and underestimated switchgrass yields (Davis et al., 2010; Heaton et al., 2010; Miguez et al., 2008), with maximum miscanthus yield estimated at 35.00–37.30 Mg DM ha^{-1} yr^{-1} in Champaign County, IL, where the Energy Farm is located (Khanna et al., 2008). Measurements at the Energy Farm from 2010 to 2011 in perennial crops were well below those estimates, though lower yields were attributed to an establishing crop. In 2012, the widespread drought in the Midwest resulted in reduced yields in all perennial crops, followed by continued lower-than-expected yields in the following years. As hypothesized, annual crops were strongly affected by drought conditions in 2012, but showed no legacy effects of drought. Application of fertilizer to miscanthus improved yields immediately; however, the DAYCENT model predicted that fertilizer application prior to the drought would have had little effect on yields, pointing to perpetuated drought stress as a factor in the nutrient-limited plant growth observed in miscanthus after 2013.

The DAYCENT biogeochemical model has been extensively validated for use in grassland and crops, including bioenergy feedstocks, and the model has improved with increased availability of bioenergy datasets (Adler et al., 2007; Anderson-Teixeira et al., 2009; Blanc-Betes et al., 2021; Campbell et al., 2014; Chamberlain et al., 2011; Cheng et al., 2013, 2014; Davis et al., 2010; Del Grosso et al., 2006; Hudiburg et al., 2016; Parton et al., 2001). The discrepancy between early modeled estimates for miscanthus and the realized harvest yields can be partially attributed to data collected from miscanthus yields in Europe before large-scale US trails began (Miguez et al., 2008, 2009; Somerville et al., 2010). However, a portion of the mismatch of field observations and models may be due to sampling method, that is, at peak biomass, samples are collected by hand, and despite randomization of sample site locations, human bias may contribute to some oversampling (Kozlov et al., 2014; Marvin et al., 2014; Zvereva & Kozlov, 2021). In maize, where the plant density is controlled by seed spacing at planting, hand sampling of grain can be accomplished entirely without loss from small quadrats. In perennials, hand sampling may result in more complete sampling, with less biomass discarded as litter, leading to lower-than-expected returns from machine-harvested fields. Additionally, when both machine and hand samples are collected at harvest, a harvest monitor produces a single measurement that eliminates heterogeneity within a field, while hand sampling of smaller portions of the field does the opposite. Because peak biomass samples are hand-sampled, hand-sampled harvest biomass was also presented in this paper. Additionally, the amount of time a perennial crop stands in the field before harvest contributes to biomass loss; however, comparison between the range of harvest dates at the Energy Farm and biomass lost between peak and harvest did not provide a useful trend for predicting the degree of loss over time (Figure S2).

As perennial bioenergy crop production expanded in the United States, models were verified with field measurements, including those made at the Energy Farm, and predictions were improved to more closely align with observed yields on this site (DAYCENT 4.5, Hudiburg et al., 2015). As discussed in Hudiburg et al. (2015), computer models of yield are limited by available above- and belowground data, for which long-term datasets following perennials from establishment to full maturity are uncommon. The 11-year data provided by this study serve to improve our ability to make projections into the future, as well as incorporating intra-annual variability that short-term datasets often miss and the confounding factors of stand age and nutrient availability.

Yields for maize and soybean at the Energy Farm were not significantly different from county-wide averages between 2008 and 2018 (t test, $p > 0.5$). Central Illinois counties, including Champaign County, where the Energy Farm is located, frequently rank among the most productive counties in the nation for maize and soybean (Farmweek, Mar 2, 2021). Field trials for perennial bioenergy crops in the United States were initiated in Illinois with the expectation that this productivity would contribute to optimal yields. While miscanthus has been identified as a primary bioenergy feedstock in the Midwest, young miscanthus rhizomes are susceptible to cold damage (Boersma & Heaton, 2014; Clifton-Brown & Lewandowski, 2000; Farrell et al., 2006; Jorgensen & Schwarz, 2000), creating a delay in maturation of the crop. Energy Farm miscanthus was partially replanted via rhizome propagation (Boersma & Heaton, 2014) in 2009 and 2010 following poor establishment due to extreme cold over the winter in 2008–2009. Peak biomass in 2010 approached 30.00 Mg DM ha^{-1}, not statistically different from the peak biomass in 2011, the highest peak achieved without fertilization. This peak translated to an end-of-season yield of 18.90 Mg DM ha^{-1}, still undershooting the model-predicted yields (Khanna et al., 2008). Harvest timing may also contribute to the departure from predicted yields. When crops are left standing in the field over winter to maximize retranslocation of nutrients (Masters et al., 2015), some material is lost to weather damage. Comparisons of percent aboveground biomass loss with harvest date showed that the range of Energy Farm harvest dates between 2010 and 2018 did not contribute to significant differences in yield loss in miscanthus; however, due to the goal of maximizing retranslocation,

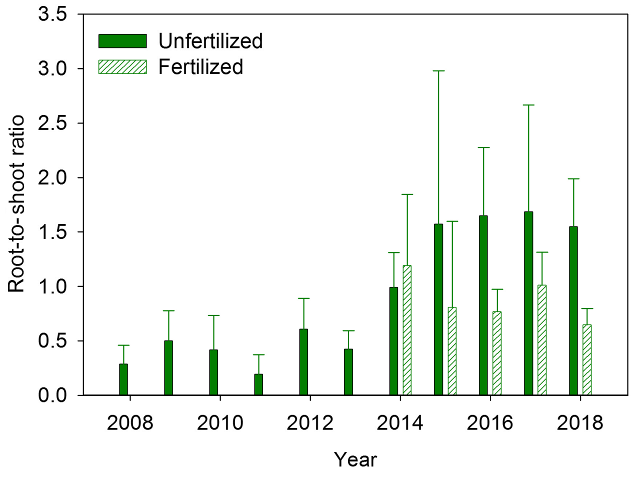

FIGURE 5 In miscanthus, both fertilized and unfertilized plots increased root-to-shoot ratio, derived from biomass data in Figure 4, after 2014. Increased aboveground biomass in fertilized miscanthus kept RS to 100–130% of pre-fertilization measurements. Root-to-shoot ratio was 40% higher in unfertilized miscanthus. Bars represent average values and the error bars represent the standard error of the mean

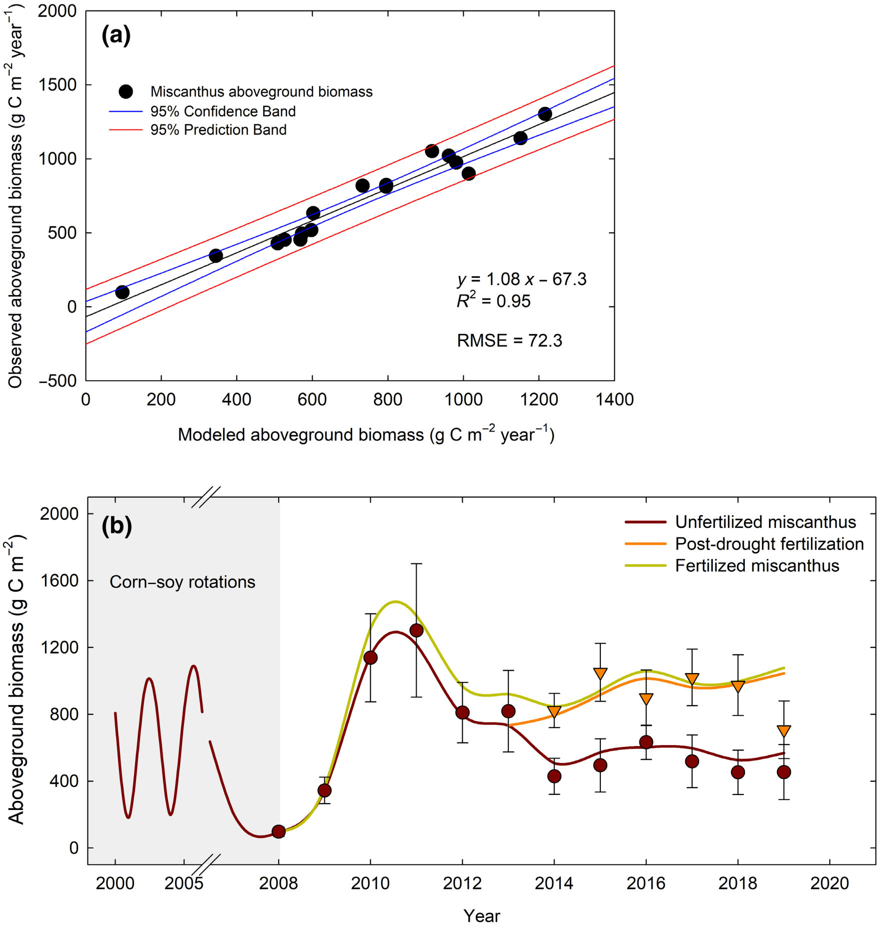

FIGURE 6 (a) DAYCENT model predictions versus measured aboveground biomass for miscanthus. (b) Model predictions for miscanthus aboveground biomass during the establishment phase and following a simulated drought in 2012. Simulations were conducted for unfertilized miscanthus (red line), miscanthus that was fertilized at the time of planting and every subsequent year (yellow line), and miscanthus that was fertilized beginning after the 2012 drought (orange line). Measured values for aboveground biomass for fertilized (post drought) and unfertilized miscanthus are shown in red circles and orange inverted triangles, respectively. Each symbol represents the average values and the error bars are plus and minus one standard deviation. Data shown were not used in calibration of the model

the perennial crops were rarely harvested early in the potential harvest window (November/December), leading to few data points in the period where peak-to-harvest loss would be minimized (Figure S2).

In the year of the Midwestern drought (2012), the month of July 2012 was the second hottest US month on record (NOAA National Centers for Environmental Information, 2021). Total average precipitation in the contiguous United States in 2012 was 67.49 cm, 9.21 cm below the 30-year climate normal (1971–2001, NOAA National Climate Data Center, 2021). Precipitation measurements in Illinois place it among the top 10 driest years on record for the state (NOAA National Centers for Environmental Information, 2021), with 61% of the continental United States in moderate-to-exceptional drought in July of 2012 (Mallya et al., 2013; NOAA National Centers for Environmental Information, 2013). Precipitation in Champaign County showed cumulative deficit for 10 of the 12 months of 2012 and rain patterns in 2013 remained disordered (Figure S1), though rainfall was adequate for annual crops to produce at normal levels. While all three perennial crop systems have demonstrated higher ecosystem water use efficiency than maize and soybean (Zeri et al., 2013), all three showed reduced yields in 2012, and while maize/soy productivity resumed pre-drought values in 2013, the perennial crops continued to produce below the 2010–2011 levels. The inability of miscanthus and switchgrass to return to pre-drought yields even with adequate moisture suggests a different limitation following the drought.

Previous studies measuring fertilized and unfertilized miscanthus in Illinois, Kentucky, Nebraska, and New Jersey found no effect of fertilization on aboveground biomass in establishing (<5 y) miscanthus (Masters et al., 2015; Maughan et al., 2012). Studies of nutrient removal in miscanthus showed limited need for N replacement due to nutrient recycling by retranslocation (Cadoux et al., 2012). It was hypothesized that the establishment of perennial crops on former agricultural lands reduced the need for nutrient additions due to legacy nitrogen in the soil. In that case, it stands to reason that Energy Farm miscanthus, planted on soil that was previously in row crop agriculture, would be sustained by legacy nitrogen during the establishment phase of growth, and evidence of N limitation would not appear until later in the life cycle, when available N was depleted, if at all. A study of fertilized and unfertilized miscanthus in Illinois from 2001 to 2006 showed no significant yield response in the first 4 years of growth (Davis et al., 2009). The strong response (~2× increase in yield following fertilization in 2014) of Energy Farm miscanthus in this study is evidence of nitrogen limitation in the seventh growing season, though nitrogen limitation may have existed in prior years when there was no comparison between fertilized and unfertilized crops. A meta-analysis of European miscanthus showed a response to N fertilizer was most common after the third year of growth (Miguez et al., 2008), while miscanthus grown in Wisconsin and Michigan from 2008 to 2016 responded to fertilization in the third and fifth growing seasons, respectively, with the fifth year increase in Michigan coinciding with the year after the drought (Wang et al., 2020). Whether nitrogen limitation was building during miscanthus establishment at the Energy Farm, was exacerbated by repeated biomass harvests, or occurred more directly as a result of the plants' efforts to recover from the drought itself cannot be determined from the experimental design of this study, though efforts to model the effect in DAYCENT point to a combination of nutrient limitation, moisture limitation, and stand age.

The DAYCENT model has been used successfully for modeling bioenergy ecosystems at this site and elsewhere in the Midwestern United State (Campbell et al., 2014; Davis et al., 2009, 2010, 2012; Del Grosso et al., 2006; Hudiburg et al., 2015). Validating and calibrating the model with local datasets produced a strong fit for our existing data, and gives us confidence in the model's ability to make predictions for this site. The projections from this model showed that changes in soil moisture alone did not produce the yield response that was observed at the Energy Farm, nor was the post-drought addition of nitrogen sufficient to recover yields to the predicted values. The lack of a single factor driving observed yields drives our hypothesis of an interaction between drought and fertilization in miscanthus. Switchgrass, which was fertilized from the outset, maintained similar peak biomass in the drought years and beyond (2012–2016), in a pattern that mimics the DAYCENT predictions for miscanthus fertilized from establishment (Figure 6).

Perennial species invest more resources than annual crops in belowground biomass (Anderson-Teixeira et al., 2009; Davis et al., 2009; Dohleman & Long, 2009; Dohleman et al., 2012; Kahle et al., 2001; Neukirchen et al., 1999), increasing soil carbon. While aboveground biomass in fertilized and unfertilized miscanthus decreased following the drought, belowground biomass increased in both fertilized and unfertilized plots, and therefore, the potential rate of carbon storage did not decrease, sustaining an important ecosystem service. Partitioning of resources to increase belowground biomass is a response to nitrogen limitation in both annual perennial plants that has been observed in herbaceous annuals, perennials, and trees (e.g Grechi et al., 2007; Hermans et al., 2006; Ingestad & Agren, 1991). However, DAYCENT modeling of the Energy Farm site predicted that nitrogen limitation alone was insufficient to cause the responses observed in the perennial crops following the drought. This suggests that routine nitrogen additions may reduce the impact of severe drought and help restore crop productivity, indicating that nutrient availability and assimilation are strong determinants of crop water use efficiency and resilience to water stress.

The variance between early miscanthus yield predictions (Khanna et al., 2008) and the observed yields at this site are likely due to a combination of factors. Heaton et al. (2009) demonstrated that it was necessary to wait for perennial crop senescence to reduce nutrient loss with harvest, which required timing the aboveground harvest for December or later at this site and then maximizing yield by harvesting as soon as possible after senescence. Over the study period, prevailing weather patterns and farm operations at the Energy Farm have pushed miscanthus harvest later and later in the spring, often occurring in late February or early March. While this preserves soil nutrients, it results in a partial loss of aboveground material, reducing potential yields (Table S2). Exposure to the elements between December and February results in leaf loss and lodging, both of which contribute to smaller harvests.

5 | CONCLUSIONS

Long-term yields for perennial bioenergy grasses in the Midwest undershot initial predictions, and this study demonstrates that climate factors should be considered when making predictions of yields over time. Grasses allocate more biomass belowground in the mature phase than predicted by measurements and modeling conducted during the establishment phase, increasing potential for carbon allocation and storage underground. Long-term collection of data on perennial grasses shows vulnerability to extreme climate events and potential for mitigating climate effects through management strategies. Perennial grasses, while resilient in the face of extreme drought, are not immune, and effects may be long-lasting; however, empirical data and model results show that supplemental nitrogen can improve crop yields.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

All authors contributed to the experimental design. Manuscript preparation was led by Kantola with input from all co-authors. Data contributions are as follows: Kantola, Masters, and DeLucia were responsible for field measurements and analysis. Blanc-Betes and Gomez-Casanovas performed modeling and statistical analysis.

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REFERENCES

Adler, P. R., Del Grosso, S. J., & Parton, W. J. (2007). Life-cycle assessment of net greenhouse-gas flux for bioenergy cropping systems. *Ecological Applications*, *17*, 675–691. https://doi.org/10.1890/05-2018

Anderson, E., Arundale, R., Maughan, M., Oladeinde, A., Wycislo, A., & Voigt, T. (2011). Growth and agronomy of *Miscanthus* x *giganteus* for biomass production. *Biofuels*, *2*, 71–87.

Anderson-Teixeira, K. J., Davis, S. C., Masters, M. D., & DeLucia, E. H. (2009). Changes in soil organic carbon under biofuel crops. *GCB Bioenergy*, *1*, 75–96. https://doi.org/10.1111/j.1757-1707.2008.01001.x

Anderson-Teixeira, K. J., Masters, M. D., Black, C., Zeri, M., Hussain, M., Bernacchi, C., & DeLucia, E. (2013). Altered belowground carbon cycling following land-use change to perennial bioenergy crops. *Eocsystems*, *16*, 508–520. https://doi.org/10.1007/s10021-012-9628-x

Angel, J. (2010). Official 1981-2010 Climate Normals for Champaign Willard AP. Illinois State Water Survey, Prairie Research Institute, University of Illinois, IL.

Arundale, R. A., Dohleman, F. G., Heaton, E. A., McGrath, J. M., Voigt, T. B., & Long, S. P. (2014). Yields of *Miscanthus* x *giganteus* and *Panicum virgatum* decline with stand age in the Midwestern USA. *GCB Bioenergy*, *6*, 1–13.

Arundale, R. A., Dohleman, F. G., Voigt, T. B., & Long, S. P. (2014). Fertilization does significantly increase yields of stands of *Miscanthus* x *giganteus* and *Panicum virgatum* in multiyear trials in Illinois. *BioEnergy Research*, *7*, 408–416.

Behnke, G. D., David, M. B., & Voigt, T. B. (2012). Greenhouse gas emissions, nitrate leaching, and biomass yields from production of *Miscanthus* x *giganteus* in Illinois, USA. *BioEnergy Research*, *5*, 801–813.

Blanc-Betes, E., Kantola, I. B., Gomez-Casanovas, N., Hartmann, M. D., Parton, W. J., Lewis, A. L., Beerling, D. J., & DeLucia, E. H. (2021). In silico assessment of the potential of basalt amendments to reduce N_2O emissions from bioenergy crops. *GCB Bioenergy*, *13*, 224–241.

Boersma, N. N., Dohleman, F. G., Miguez, F. E., & Heaton, E. A. (2015). Autumnal leaf senescence in *Miscanthus* x *giganteus* and leaf [N] differ by stand age. *Journal of Experimental Biology*, *66*, 4395–4401. https://doi.org/10.1093/jxb/erv129

Boersma, N. N., & Heaton, E. A. (2014). Propagation method affects *Miscanthus* x *giganteus* developmental morphology. *Industrial Crops and Products*, *57*, 59–68.

Borkowska, H., & Molas, R. (2013). Yield comparison of four lignocellulosic perennial energy crop species. *Biomass and Bioenergy*, *51*, 145–153. https://doi.org/10.1016/j.biombioe.2013.01.017

Cadoux, S., Ferchaud, F., Demay, C. H., Boizard, H., Machet, J.-M., Fourdinier, E., Preudhomme, M., Chabbert, B., Gosse, G., & Mary, B. (2014). Implications of productivity and nutrient requirements on greenhouse gas balance of annual and perennial bioenergy crops. *GCB Bioenergy*, *6*, 425–438. https://doi.org/10.1111/gcbb.12065

Cadoux, S., Riche, A. B., Yates, N. E., & Machet, J.-M. (2012). Nutrient requirements of *Miscanthus* x *giganteus*: Conclusions from a review of published studies. *Biomass and Bioenergy*, *38*, 14–22. https://doi.org/10.1016/j.biombioe.2011.01.015

Campbell, E. E., Johnson, J. M. F., Jin, V. L., Lehman, R. M., Osborne, S. L., Varvel, G. E., & Paustian, K. (2014). Assessing the soil carbon, biomass production, and nitrous oxide emission impact of corn stover management for bioenergy feedstock production using DAYCENT. *BioEnergy Research*, *7*, 491–502. https://doi.org/10.1007/s12155-014-9414-z

Chamberlain, J. F., Miller, S. A., & Frederick, J. R. (2011). Using DAYCENT to quantify on-farm GHG emissions and N dynamics of land use conversion to N-managed switchgrass in the Southern U.S. *Agriculture, Ecosystems, and Environment*, *141*, 332–341. https://doi.org/10.1016/j.agee.2011.03.011

Cheng, K., Ogle, S. M., Parton, W. J., & Pan, G. (2013). Predicting methanogenesis from rice paddies using the DAYCENT ecosystem model. *Ecological Modeling*, *261–262*, 19–31. https://doi.org/10.1016/j.ecolmodel.2013.04.003

Cheng, K., Ogle, S. M., Parton, W. J., & Pan, G. (2014). Simulating greenhouse gas mitigation potentials for Chinese croplands using the DAYCENT ecosystem model. *Global Change Biology*, *20*, 948–962.

Clifton-Brown, J. C., & Lewandowski, I. (2000). Overwintering problems of newly established *Miscanthus* plantations can be overcome by identifying genotypes with improved rhizome cold tolerance. *New Phytologist*, *148*, 287–294.

Da Costa, R. M. F., Simister, R., Roberts, L. A., Timms-Taravella, E., Cambler, A. B., Corke, F. M. K., Han, J., Ward, R. J., Buckeridge, M. S., Gomez, L. D., & Bosch, M. (2019). Nutrient and drought stress: implications for phenology and biomass quality in miscanthus. *Annals of Botany*, *124*, 553–566. https://doi.org/10.1093/aob/mcy155

Davis, S. C., Anderson-Teixeira, K. J., & DeLucia, E. H. (2009). Life-cycle analysis and the ecology of biofuels. *Trends in Plant Science*, *14*, 140–146. https://doi.org/10.1016/j.tplants.2008.12.006

Davis, S. C., Parton, W. J., Del Grosso, S. J., Keough, C., Marx, E., Adler, P. R., & DeLucia, E. H. (2012). Impact of second-generation biofuel agriculture on greenhouse-gas emissions in the corn-growing regions of the US. *Frontiers in Ecology and the Environment*, *10*, 69–74. https://doi.org/10.1890/110003

Davis, S. C., Parton, W. J., Dohleman, F., Smith, C., Del Grosso, S. J., Kent, A., & DeLucia, E. H. (2010). Comparative biogeochemical cycles of bioenergy crops reveal nitrogen-fixation and low greenhouse gas emissions in a *Miscanthus* x *giganteus* agro-ecosystem. *Ecosystems*, *13*, 144–156.

De Souza, A. P., Arundale, R. A., Dohleman, F. G., Long, S. P., & Buckeridge, M. S. (2013). Will the exceptional productivity of *Miscanthus* x *giganteus* increase further under rising atmospheric CO_2? *Agricultural and Forest Meteorology*, *171–172*, 82–92. https://doi.org/10.1016/j.agrformet.2012.11.006

Del Grosso, S. J., Mosier, A. R., Parton, W. J., & Ojima, D. S. (2005). DAYCENT model analysis of past and contemporary soil N_2O and net greenhouse gas flux for major crops in the USA. *Soil and Tillage Research*, *83*, 9–24.

Del Grosso, S. J., Parton, W. J., Mosier, A. R., Walsh, M. K., Ojima, D. S., & Thornton, P. E. (2006). DAYCENT national-scale simulations of nitrous oxide emissions from cropped soils in the United States. *Journal of Environmental Quality*, *35*, 1451–1460. https://doi.org/10.2134/jeq2005.0160

Dohleman, F. G., Heaton, E. A., Arundale, R. A., & Long, S. P. (2012). Seasonal dynamics of above- and belowground biomass and nitrogen partitioning in *Miscanthus* x *giganteus* and *Panicum virgatum* across three growing season. *Global Change Biology Bioenergy*, *4*, 534–544.

Dohleman, F. G., & Long, S. P. (2009). More productive than maize in the Midwest: How does *Miscanthus* do it? *Plant Physiology*, *150*, 2104–2115. https://doi.org/10.1104/pp.109.139162

Farrell, A. J., Clifton-Brown, J., Lewandowski, I., & Jones, M. B. (2006). Genotypic variation in cold tolerance influences the yield of *Miscanthus*. *Annals of Applied Biology*, *149*, 337–345. https://doi.org/10.1111/j.1744-7348.2006.00099.x

Gauder, M., Graeff-Honninger, S., Lewandowski, I., & Claupein, W. (2011). Long-term yield and performance of 15 different *Miscanthus* genotypes in southwest Germany. *Annals of Applied Biology*, *166*, 126–136. https://doi.org/10.1111/j.1744-7348.2011.00526.x

Grechi, I., Vivin, P., Hilbert, G., Milin, S., Robert, T., & Gaudillere, J.-P. (2007). Effect of light and nitrogen supply on internal C:N balance and control of root-to-shoot biomass allocation in grapevine. *Environmental and Experimental Botany*, *59*, 139–149. https://doi.org/10.1016/j.envexpbot.2005.11.002

Heaton, E. A., Dohelman, F. G., & Long, S. P. (2009). Seasonal nitrogen dynamics of *Miscanthus* x *giganteus* and *Panicum virgatum*. *Global Change Biology-Bioenergy*, *1*, 297–307.

Heaton, E. A., Dohleman, F. G., & Long, S. P. (2008). Meeting US biofuel goals with less land: The potential of *Miscanthus*. *Global Change Biology*, *14*, 2000–2014. https://doi.org/10.1111/j.1365-2486.2008.01662.x

Heaton, E. A., Dohleman, F. G., Miguez, A. F., Juvik, J. A., Lozovaya, V., Widholm, J., Zabotina, O. A., McIsaac, G. F., David, M. B., Voigt, T. B., Boersma, N. N., & Long, S. P. (2010). Chapter 3 - miscanthus: A promising Biomass Crop. *Advances in Botanical Research*, *56*, 75-137.

Hermans, C., Hammond, J. P., White, P. J., & Verbruggen, N. (2006). How do plants respond to nutrient shortage by biomass allocation? *Trends in Plant Science*, *11*, 610–617. https://doi.org/10.1016/j.tplants.2006.10.007

Holder, A. J., McCalmont, J. P., McNamara, N. P., Rowe, R., & Donnison, I. S. (2018). Evapotransporation model comparison and an estimate of field scale Miscanthus canopy precipitation interception. *GCB Bioenergy*, *10*, 353–366. https://doi.org/10.1111/gcbb.12503

Hong, C. O., Owens, V. N., Bransby, D., Farris, R., Fike, J., Heaton, E., Kim, S., Mayton, H., Mitchell, R., & Viands, D. (2014). Switchgrass response to nitrogen fertilizer across diverse environments in the USA: A regional feedstock partnership report. *BioEnergy Research*, *7*, 777–788. https://doi.org/10.1007/s12155-014-9484-y

Hudiburg, T. W., Davis, S. C., Parton, W., & DeLucia, E. H. (2015). Bioenergy crop greenhouse gas mitigation under a range of management practices. *GCB Bioenergy*, *7*, 366–374.

Hudiburg, T. W., Wang, W., Khanna, M., Long, S. P., Dwivedi, P., Parton, W. J., Hartman, M., & DeLucia, E. H. (2016). Impacts of a 32-billion-gallon bioenergy landscape on land and fossil fuel use in the United States. *Nature Energy*, *1*, 1–7.

IEA (International Energy Agency). (2019). *Renewables 2019 – Analysis and forecast to 2024*. http://www.iea.org/

Ingestad, T., & Agren, G. I. (1991). The influence of plant nutrition on biomass allocation. *Ecological Applications*, *1*, 168–174. https://doi.org/10.2307/1941809

Ings, J., Mur, L. A. J., Robson, P. R. H., & Bosch, M. (2013). Physiological and growth responses to water deficit in the bioenergy crop *Miscanthus x giganteus*. *Frontiers in Plant Science*, *4*, https://doi.org/10.3389/fpls.2013.00468

Iqbal, Y., Gauder, M., Claupein, W., Graeff-Hönninger, S., & Lewandowski, I. (2015). Yield and quality development comparison between miscanthus and switchgrass over a period of 10 years. *Energy*, *89*, 268–276. https://doi.org/10.1016/j.energy.2015.05.134

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., … Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, *526*(7574), 574–577. https://doi.org/10.1038/nature15374

Jain, A. K., Khanna, M., Erickson, M., & Huang, H. (2010). An integrated biogeochemical and economic analysis of bioenergy crops in the Midwestern United States. *Global Change Biology-Bioenergy*, *2*, 217–234. https://doi.org/10.1111/j.1757-1707.2010.01041.x

Jorgensen, U., & Schwarz, K.-U. (2000). Why do basic research? A lesson from commercial exploitation of miscanthus. *New Phytologist*, *148*, 190–193.

Kahle, P., Beuch, S., Boelcke, B., Leinweber, P., & Schulten, H.-R. (2001). Cropping of *Miscanthus* in Central Europe: Biomass production and influence on nutrients and soil organic matter. *European Journal of Agronomy*, *15*, 171–184. https://doi.org/10.1016/S1161-0301(01)00102-2

Kantola, I. B., Masters, M. D., & DeLucia, E. H. (2017). Soil particulate matter increases under perennial bioenergy agriculture. *Soil Biology and Biochemistry*, *113*, 184–191.

Khanna, M., Dhungana, B., & Clifton-Brown, J. (2008). Costs of producing miscanthus and switchgrass for bioenergy in Illinois. *Biomass and Bioenergy*, *32*, 482–493. https://doi.org/10.1016/j.biombioe.2007.11.003

Knapp, A. K., Briggs, J. M., & Koelliker, J. K. (2001). Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems*, *4*, 19–28. https://doi.org/10.1007/s100210000057

Kozlov, M. V., Zverev, V., & Zvereva, E. L. (2014). Confirmation bias leads to overestimation of losses of woody plant foliage to insect herbivores in tropical regions. *PeerJ*, *2*, https://doi.org/10.7717/peerj.709

Malinowska, M., Donnison, I., & Robson, P. (2020). Morphological and physiological traits that explain yield response to drought stress in miscanthus. *Agronomy*, *10*(8), 1194. https://doi.org/10.3390/agronomy10081194

Mallya, G., Zhao, L., Song, X. C., Niyogi, D., & Govindaraju, R. S. (2013). 2012 Midwest drought in the United States. *Journal of Hydrologic Engineering*, *18*, 737–745. https://doi.org/10.1061/(ASCE)HE.1943-5584.0000786

Mann, J. J., Barney, J. N., Kyser, G. B., & Di Tomaso, J. M. (2013). *Miscanthus × giganteus* and *Arundo donax* shoot and rhizome tolerance of extreme moisture stress. *GCB Bioenergy*, *5*(6), 693–700. https://doi.org/10.1111/gcbb.12039

Marvin, D. C., Asner, G. P., Knapp, D. E., & Tupayachi, R. (2014). Amazonian landscapes and the bias in field studies of forest structure and biomass. *Proceedings of the National Academy of Sciences*, *111*, E5224–E5232. https://doi.org/10.1073/pnas.1412999111

Masters, M. D., Black, C. K., Kantola, I. B., Woli, K. P., Voigt, T., David, M. B., & DeLucia, E. H. (2015). Soil nutrient removal by four potential bioenergy crops: *Zea mays*, *Panicum virgatum*, *Miscanthus* x *giganteus*, and prairie. *Agriculture, Ecosystems and Environment*, *216*, 51–60.

Maughan, M., Bollero, G., Lee, D. K., Darmody, R., Bonos, S., Cortese, L., Murphy, J., Gaussoin, R., Sousek, M., Williams, D., Williams, L., Miguez, F., & Voigt, T. (2012). *Miscanthus* x *giganteus* productivity: The effects of management in different environments. *GCB Bioenergy*, *4*, 253–265.

McNaughton, S. J., Wallace, L. L., & Coughenour, M. B. (1983). Plant adaptation in an ecosystem context: Effects of defoliation, nitrogen, and water on growth of an African C4 sedge. *Ecology*, *64*, 307–308. https://doi.org/10.2307/1937078

Miao, R., & Khanna, M. (2017). Costs of meeting a cellulosic biofuel mandate with perennial energy crops: Implications for policy. *Energy Economics*, *64*, 321–334. https://doi.org/10.1016/j.eneco.2017.03.018

Miguez, F. E., Villamil, M. B., Long, S. P., & Bollero, G. A. (2008). Meta-analysis of the effects of management factors on *Miscanthus* x *giganteus* growth and biomass production. *Agricultural and Forest Meteorology*, *148*, 1280–1292.

Miguez, F. E., Zhu, X., Humphries, S., Bollero, G. A., & Long, S. P. (2009). A semimechanistic model predicting the growth and production of the bioenergy crop *Miscanthus* x *giganteus*: Description, parameterization and validation. *GCB-Bioenergy*, *1*, 282–296.

Moore, C. E., Berardi, D. M., Blanc-Betes, E., Dracup, E. C., Egenreither, S., Gomez-Casanovas, N., Hartman, M. D., Hudiburg, T., Kantola, I. B., Masters, M. D., Parton, W. J., Van Allen, R., von Haden, A. C., Yang, W. H., DeLucia, E. H., & Bernacchi, C. J. (2020). The carbon and nitrogen cycle impacts of reverting perennial bioenergy switchgrass to an annual maize crop rotation. *GCB Bioenergy*, *12*, 941–954. https://doi.org/10.1111/gcbb.12743

Moore, C. E., von Haden, A. C., Burnham, M. B., Kantola, I. B., Gibson, C. D., Blakely, B. J., Dracup, E. C., Masters, M. D., Yang, W. H., DeLucia, E. H., & Bernacchi, C. J. (2021). Ecosystem-scale biogeochemical fluxes from three bioenergy crop candidates: How energy sorghum compares to maize and miscanthus. *GCB Bioenergy*, *13*, 445–458. https://doi.org/10.1111/gcbb.12788

Neukirchen, D., Hiken, M., Lammel, J., Czpionka-Krause, U., & Olfs, H.-W. (1999). Spatial and temporal distribution of the root system and root nutrient content of an established *Miscanthus* crop. *European Journal of Agronomy*, *11*, 301–309. https://doi.org/10.1016/S1161-0301(99)00031-3

NOAA National Centers for Environmental Information. (2013). State of the climate: National climate report for annual 2012. Retrieved from https://www.ncdc.noaa.gov/sotc/national/201213

NOAA National Centers for Environmental Information. (2021). State of the climate: Global Climate report for annual 2020. Retrieved from https://www.ncdc.noaa.gov/sotc/global/202013

NOAA National Climate Data Center. (2021). US climate normals. Retrieved October 25, 2021 from https://www.ncei.noaa.gov/products/land-based-station/us-climate-normals

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, *51*, 933–938. https://doi.org/10.1641/0006-3568(2001)051

Parton, W. J., Hartman, M., Ojima, D., & Schimel, D. (1998). DAYCENT and its land surface submodel: Description and testing. *Global and Planetary Change*, *19*, 35–48.

Parton, W. J., Holland, E. A., Del Grosso, S. J., Hartman, M. D., Martin, R. E., Mosier, A. R., Ojima, D. S., & Schimel, D. S. (2001). Generalized model for NO_x and N_2O emissions from soils. *Journal of Geophysical Research: Atmospheres*, *106*, 17403–17419.

Pyter, R. J., Dohleman, F. G., & Voigt, T. B. (2010). Effects of rhizome size, depth of planting and cold storage on *Miscanthus* x *giganteus* establishment in the Midwestern United States. *Biomass and Bioenergy*, *34*, 1466–1470.

Rippey, B. R. (2015). The U.S. drought of 2012. *Weather and Climate Extremes*, *10*, 57–64. https://doi.org/10.1016/j.wace.2015.10.004

Robertson, G. P., Dale, V. H., Doering, O. C., Hamburg, S. P., Melillo, J. M., Wander, M. M., Parton, W. J., Adler, P. R., Barney, J. N., Cruse, R. M., Duke, C. S., Fearnside, P. M., Follett, R. F., Gibbs, H. K., Goldemberg, J., Mladenoff, D. J., Ojima, D., Palmer, M. W., Sharpley, A., … Wilhelm, W. W. (2008). Sustainable biofuels redux. *Science*, *322*, 49–50. https://doi.org/10.1126/science.1161525

Robertson, G. P., Hamilton, S. K., Barham, B. L., Dale, B. E., Izaurralde, R. C., Jackson, R. D., Landis, D. A., Swinton, S. M., Thelen, K. D., & Tiedje, J. M. (2017). Cellulosic biofuel contributions to a sustainable energy future: Choices and outcomes. *Science*, *356*(1349), 1–11.

Rosen, J. (2018). The carbon harvest. *Science*, *359*, 733–737. https://doi.org/10.1126/science.359.6377.733

Sanford, G. R., Oates, L. G., Jasrotia, P., Thelen, K. D., Robertson, G. P., & Jackson, R. D. (2016). Comparative productivity of alternative cellulosic bioenergy cropping systems in the North Central USA. *Agriculture, Ecosystems and Environment*, *216*, 344–355. https://doi.org/10.1016/j.agee.2015.10.018

Sarmiento, G. (1992). Adaptive strategies of perennial grasses in South American savannas. *Journal of Vegetation Science*, *3*, 325–336. https://doi.org/10.2307/3235757

Scarlat, N., Martinov, M., & Dallemand, J.-F. (2010). Assessment of the availability of agricultural crop residues in the European Union: Potential and limitations for bioenergy use. *Waste Management*, *30*, 1889–1897. https://doi.org/10.1016/j.wasman.2010.04.016

Smith, C. M., David, M. B., Mitchell, C. A., Masters, M. D., Anderson-Teixeira, K. J., Bernacchi, C. J., & DeLucia, E. H. (2013). Reduced nitrogen losses after conversion of row crop agriculture to perennial biofuel crops. *Journal of Environmental Quality*, *42*, 219–228. https://doi.org/10.2134/jeq2012.0210

Somerville, C., Youngs, H., Taylor, C., Davis, S. C., & Long, S. P. (2010). Feedstocks for lingnocellulosic biofuels. *Science*, *329*, 790–792.

Van der Weijde, T., Huxley, L. M., Hawkins, S., Sembiring, E. H., Farrar, K., Dolstra, O., Visser, R. G. F., & Trindade, L. M. (2017). Impact of drought stress on growth and quality of miscanthus for biofuel production. *GCB Bioenergy*, *9*, 770–782. https://doi.org/10.1111/gcbb.12382

Viovy, N. (2018). *CRUNCEP Version 7—Atmospheric Forcing Data for the Community Land Model*. Research Data Archive at the National Center for Atmospheric Research, Computational and Information Systems Laboratory. Retrieved from http://rda.ucar.edu/datasets/ds314.3/

Volaire, F., Barkaoui, K., & Norton, M. (2014). Designing resilient and sustainable grasslands for a drier future: Adaptive strategies, functional traits and biotic interactions. *European Journal of Agronomy*, *52*, 81–89. https://doi.org/10.1016/j.eja.2013.10.002

Wang, S., Sanford, G. R., Robertson, G. P., Jackson, R. D., & Thelen, K. D. (2020). Perennial bioenergy crop yield and quality response to nitrogen fertilization. *BioEnergy Research*, *13*, 157–166. https://doi.org/10.1007/s12155-019-10072-z

Zeri, M., Anderson-Teixeira, K., Hickman, G., Masters, M., DeLucia, E., & Bernacchi, C. J. (2011). Carbon exchange by establishing biofuel crops in central Illinois. *Agriculture, Ecosystems and Environment*, *144*, 319–329. https://doi.org/10.1016/j.agee.2011.09.006

Zeri, M., Hussain, M. Z., Anderson-Teixeira, K. J., DeLucia, E., & Bernacchi, C. J. (2013). Water use efficiency of perennial and annual bioenergy crops in central Illinois. *Journal of Geophysical Research: Biogeosciences*, *118*, 581–589. https://doi.org/10.1002/jgrg.20052

Zvereva, E. L., & Kozlov, M. V. (2021). Biases in ecological research: Attitudes of scientists and ways of control. *Scientific Reports*, *11*, 226. https://doi.org/10.1038/s41598-020-80677-4

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