ORIGINAL ARTICLE

Biofuels

Comparative productivity of six bioenergy cropping systems on marginal lands in the Great Lakes Region, United States

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Abstract

Growing lignocellulosic crops on marginal lands is a promising solution for sustainable biofuel production. We evaluated the productivity of bioenergy cropping systems (switchgrass [Panicum virgatum L., var. Cave-In-Rock], miscanthus [Miscanthus \times giganteus, 'Illinois clone'], hybrid poplar [Populus nigra \times P. maximowiczii A. Henry 'NM6'], native grasses [five species], early successional vegetation, and restored prairie vs. historical vegetation [as reference control]) with and without nitrogen fertilization on low-fertility former cropland at five sites in the Great Lakes Region, United States. We reported biomass yields for the first 7 years after establishment. Switchgrass was most consistently productive across all sites but miscanthus was more productive at three of the five sites. When averaged across sites, years, and nitrogen (N) treatments, biomass yields followed the order miscanthus > switchgrass > hybrid poplar \approx native grasses > restored prairie > early successional vegetation \approx historical vegetation, but varied substantially by crop and site, with a significant crop by site interaction. Yields of miscanthus and switchgrass peaked after four-five growing seasons and declined thereafter, while yields of both native grasses and restored prairie increased throughout 6 years with no sign of follow-on decline, suggesting that polycultures may outperform monocultures over the long term. Yields of early successional vegetation-similar in composition to historical vegetation at each site-did not improve with time. Nitrogen fertilization increased the yields of all cropping systems at all sites. Our results demonstrate the viability of low-productivity former cropland for long-term bioenergy production and suggest there is no single crop best suited for all low fertility soils.

INTRODUCTION 1

Growing lignocellulosic crops on so-called "marginal" lands has been proposed as a promising solution to support biofuel production and to minimize its potential conflict with the production of food, feed, and fiber (Gelfand et al., 2013; Kang et al., 2013; Robertson et al., 2008; 2017). Marginal is an economic term that varies spatially and temporally based on the local economic context (Richards et al., 2014; Stoof et al., 2015). Generally, marginal lands are poorly suited for

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cultivation of field crops due to poor soil and climatic conditions (Gelfand et al., 2013; Kang et al., 2013). However, they are suitable for growing perennial grasses and short rotation trees that are better adapted to highly erodible, nutrient deficient, or droughty soils (Gelfand et al., 2013). Although some marginal lands may support economically sustainable lignocellulosic biomass production, empirical studies that evaluate the comparative productivity of candidate bioenergy feedstocks on marginal lands differing in climate and soil properties are lacking.

Not all marginal lands are desirable for bioenergy production. First, converting land to bioenergy production can create carbon debt that may take decades to centuries to recapture. Alternatively, carbon debt can be avoided or minimized by growing bioenergy crops on marginal lands with low initial carbon stocks, whether in soil or tree biomass (Fargione et al., 2008; Gelfand et al., 2011, 2013). Second, many marginal lands support habitats and species of conservation concern and are likewise undesirable for bioenergy conversion (Robertson et al., 2017). Thus, locating bioenergy crops on degraded former cropland not now forested or with low soil carbon stocks will likely avoid these concerns and may also facilitate the eventual repatriation of these lands. Also, sound management practices could enhance soil carbon sequestration, improve soil and water quality, and support other ecosystem services such as biodiversity benefits (Kang et al., 2013; Werling et al., 2014). That said, projected biomass production, the strongest predictor of energy yield per ha (Sanford et al., 2017), is likely to be highly variable on marginal lands due to their variability in soil and generally low fertility.

Perenniality is one of the most desirable traits for a bioenergy crop for many reasons such as high energy return on investment, greater soil carbon (C) and nitrogen (N) retention, and biodiversity and conservation benefits (Mosier et al., 2021; Robertson et al., 2017). Two herbaceous perennial grasses in particular have received much attention for potential to serve as bioenergy crops. Giant miscanthus (Miscanthus \times giganteus) and switchgrass (Panicum virgatum L.) have both been grown and studied extensively. In pairwise comparisons, especially on arable cropland, miscanthus yields tend to outperform switchgrass often by a factor of two or more (Heaton et al., 2004). In contrast, in North America switchgrass is a native cosmopolitan grass with associated biodiversity benefits, whereas miscanthus has considerably less biodiversity value (Williams & Feest, 2019) and is potentially invasive (Pitman et al., 2015). Both miscanthus and switchgrass can be cultivated on marginal lands without irrigation or heavy fertilization (Mehmood et al., 2017), although miscanthus establishment can be tricky due to high risk of winter kill rhizome mortality (Sanford et al., 2016). Other perennials, including fast growing trees which respond well to short-rotation coppicing, have also received considerable attention. The short rotation woody crop hybrid poplar (Pop-

- Miscanthus and switchgrass performed well on marginal lands in the upper US Midwest.
- Switchgrass performed better over a wide range of soils and climates.
- Monocultures out-yielded polycultures initially, but polycultures may outperform monocultures over the long term.
- Nitrogen fertilization increased the productivity of all cropping systems at all sites.
- No single crop appears best suited for all low fertility soils in the upper US Midwest.

ulus spp.) is suitable for cultivation in many regions of the United States, and its 5- to 6-year rotation and density provide supply chain flexibility that complements annually harvested herbaceous crops. In some cases, early successional (unmanaged) vegetation can be as productive as switchgrass (Gelfand et al., 2013). Also, native grass mixtures and restored prairie can provide sufficient biomass to be tenable biomass sources for bioenergy production (Gelfand et al., 2013; Sanford et al., 2016, 2017).

Studies of biomass production that contrast monocultures and polycultures often produce mixed results (Robertson et al., 2017 and references therein). Available limited evidence suggests the productivity difference between monocultures and polycultures may depend on stand age. For example, a 3-year study conducted on Conservation Reserve Program lands in Oklahoma found higher biomass yields with a monoculture, but the eventual yield decrease was greater for the monoculture than the polyculture over time (Venuto & Daniel, 2010). Similarly, Tilman et al. (2006) observed significantly higher biomass yields in polycultures than monocultures a decade after stand establishment. It thus seems timely to investigate the temporal variation of the productivity of monocultures and polycultures when considering long-term production potentials of biomass crops.

Complicating this comparison, switchgrass and miscanthus monocultures are often provided supplemental nitrogen while this is far less common for the polycultures discussed above. This is in part because perennial lignocellulosic crops are highly efficient in nutrient recycling (Mosier et al., 2021; Roley et al., 2021; Valentine et al., 2012; Yang & Udvardi, 2018). As a result, nutrient removal from perennial biomass is generally significantly lower than from annual crops (Masters et al., 2016). Thus, fertilizer requirements are generally lower and in some cases may be unnecessary. Miscanthus, for example, is mainly responsive to nitrogen fertilizer in infertile soils (Lewandowski et al., 2000). Switchgrass responds to N fertilizer in only about 50% of US field trials, likely



FIGURE 1 Great Lakes Bioenergy Research Center's (GLBRC's) bioenergy lands experimental sites located in Michigan and Wisconsin. Inset is a map of United States with Michigan and Wisconsin highlighted.

due to associative N fixation (Roley et al., 2019). Little is known, however, about the benefit, if any, of fertilization to polycultures systems grown on marginal lands.

Here, we compare biomass production among seven candidate bioenergy cropping systems across five marginal land sites in the upper US Midwest over a 5- to 7-year period. Sites differ in climate and soil properties, and we evaluate production with and without added N fertilizer. We hypothesize that greater biomass yields will occur with monocultures than polycultures over the short term but biomass yields of polycultures will outperform monocultures over the long term. We also hypothesize that N fertilization will increase biomass yields of all cropping systems tested at all sites.

2 | MATERIALS AND METHODS

2.1 | Study sites

This study was conducted from 2012 to 2020 at the Great Lakes Bioenergy Research Center's (GLBRC's) Bioenergy Land Experiment (formerly Marginal Land Experiment) sites in Michigan and Wisconsin (https://lter.kbs.msu.edu/ research/long-term-experiments/marginal-land-experiment/, Figure 1):

- Michigan Central–Lake City (latitude: 44.3095, longitude: -85.2031, altitude: 372 m a.s.l).
- Michigan North–Escanaba (latitude: 45.7646, longitude: -87.1838, altitude: 206 m a.s.l).

- Michigan South–Lux Arbor (latitude: 42.4763, longitude: -85.4518, altitude: 295 m a.s.l).
- Wisconsin Central–Hancock (latitude: 44.1191, longitude: -89.5332, altitude: 332 m a.s.l).
- Wisconsin North–Rhinelander (latitude: 45.6668, longitude: -89.2186, altitude: 498 m a.s.l).

These sites were selected based on a history of low productivity (Kasmerchak & Schaetzl, 2018). Prior to establishment of the experiment, the vegetation of both Michigan Central and Michigan North was unimproved pasture, and Michigan South was land abandoned from alfalfa or row crops for over 20 years. Wisconsin Central was unmanaged for several years, and Wisconsin North was in small grain crops in the unirrigated corners of a field with a center-pivot irrigation system.

Monthly total precipitation, total snowfall, and mean temperatures during the study period (2013–2020) and 30-year monthly averages (1991–2020) were obtained from the National Oceanic & Atmospheric Administration database (www.ncdc.noaa.gov/cdo-web/datatools/). The weather stations nearest to Michigan Central, Michigan South, Wisconsin Central, and Wisconsin North were respectively located ~42, 20, 0.2, and 20 km distant. For Michigan North, precipitation and monthly snowfall data were obtained from a weather station ~14 km away and temperature and 30-year snowfall data from a weather station ~125 km away (Tables S1–S15).

Soils of the sites are described in Kasmerchak and Schaetzl (2018) as follows:

- Michigan Central soils are moderately well-drained Spodosols that formed in outwash or sandy till over sandy outwash.
- Michigan North soils are well-drained and moderately welldrained Alfisols that formed in gravelly sandy loam till.
- Michigan South soils are well-drained Alfisols that formed in pitted outwash with a thin loess cap.
- Wisconsin Central soils are excessively drained Entisols that formed in sandy outwash, and
- Wisconsin North soils are well-drained Spodosols that also formed in sandy outwash.
 - In Michigan South, erosion may have occurred in the past by deep tillage and there is also evidence of bioturbation. In no other location is there clear evidence of erosion or bioturbation. There is also no evidence of a high-water table in any location, although there is evidence of water table fluctuations in Michigan Central and Michigan North (Kasmerchak & Schaetzl, 2018). Soil chemical and other characteristics appear in Table 1. Volumetric soil water content data were obtained from the GLBRC's Sustainability Data Catalog (Table S16, https:// data.sustainability.glbrc.org), based on 1-h weather observations.

2.2 | Experimental design, establishment, and management

In 2013, six bioenergy cropping systems and one historical reference system were established at each site in a randomized complete block design with four replicates, except Wisconsin Central had three replicates. Bioenergy cropping systems included:

- Miscanthus (*Miscanthus* × giganteus, 'Illinois clone'),
- switchgrass (Panicum virgatum L., var. Cave-In-Rock),
- hybrid poplar (*P. nigra* × *P. maximowiczii* A. Henry 'NM6'),
- native grasses (five-species mix),
- · early successional vegetation, and
- restored prairie (18-species mix).

Species compositions and seeding rates appear in Table 2. The reference system consisted of the historical (existing) vegetation at each site. The early successional system was populated by colonization and species that emerged from the existing seed bank after receiving the same preplant plot preparations as the planted systems. Plots in Michigan Central and Michigan North were 19.5 m \times 19.5 m; plots in Michigan South, Wisconsin Central, and Wisconsin North were 19.5 m \times 12.2 m, except for hybrid poplar systems which were 19.5 m

 \times 19.5 m at all sites. Adjacent plots were separated by 3- to 15-m wide mown alleyways.

Soils were prepared for planting in fall 2012 and summer 2013 and crops were established in summer 2013. For soil preparation, the existing vegetation was mowed and Herbicides were applied to plots planted to bioenergy crops. Herbicides were applied based on recommendations by Michigan State University and University of Wisconsin extension agronomists (Table S17). Before crop establishment, glyphosate and 2,4-D ester were applied on all systems to control existing vegetation. At two sites, conservation tillage preceded planting to remove legacy furrows (chisel plow plus secondary tillage at Michigan South and disc plow plus secondary tillage at Wisconsin North); other sites were planted without tillage (Table S18).

Miscanthus rhizomes with one to two active growing points (industry standard) were hand planted to a depth of 10-15 cm at a 76 cm \times 76 cm spacing interval within and between rows. Switchgrass, native grasses, and restored prairie species were planted using a Truax No Till Seed Drill (Truax Company Inc.). Hybrid poplar cuttings were hand planted with 2.4 m between rows and 1.5 m within rows. Early successional vegetation consisted of the preexisting seed bank plus novel recruitment (Table 2).

After initial crop establishment in 2013, poorly established plants in miscanthus and hybrid poplar stands were individually replanted in the following years. Winter kill rhizome mortality is the main reason for miscanthus replanting. Fungal disease pressure and deer browsing are the main reasons for hybrid poplar replanting. In 2014, miscanthus was individually replanted at all five sites and hybrid poplar at Michigan Central, Wisconsin Central, and Wisconsin North. In 2015, miscanthus was individually replanted at all sites, except Michigan Central, and hybrid poplar at all sites except Michigan North. In 2016, both miscanthus and hybrid poplar were individually replanted at Wisconsin Central and Wisconsin North. In 2017, miscanthus was individually replanted at Michigan Central and Wisconsin North, and hybrid poplar at Michigan South. In 2016, poplar plots were fenced to 3 m in order to discourage deer browsing at all sites. Fungal disease and deer browsing of hybrid poplar were monitored by visual observations.

After crop establishment, herbicides were applied as needed based on recommendations by Michigan State University and University of Wisconsin extension agronomists (Table \$17).

2.3 | Nitrogen fertilization

Plots were split at establishment for an N fertilizer treatment (i.e., +N and 0N). In summer 2014, only the +N split-plots of the early successional system were fertilized.

TABLE 1 Chemical characteristics, classification, and slope of soils at Bioenergy Land Experiment study sites in Michigan and Wisconsin.

	Horizon					$\mathbf{Mg^{d}}$			
Study site	(cm)	рН ^а	P ^b (ppm)	K ^c (ppm)	Ca ^d (ppm)	(ppm)	Soil series	Taxonomic class	Slope (%)
Michigan Central	0–10	6.2 ± 0.3	40 ± 19	44 ± 16	700 ± 143	96 ± 38	Croswell	Spodosol (Oxyaquic Haplorthods)	0–3
	10-25	$5.9~\pm~0.4$	32 ± 16	32 ± 14	$452~\pm~151$	72 ± 35			
	25-50	$6.2~\pm~0.4$	33 ± 13	30 ± 13	$282~\pm~111$	56 ± 32			
	50-100	$6.2~\pm~0.4$	23 ± 12	35 ± 27	$234~\pm~266$	73 ± 95			
Michigan North	0–10	7.0 ± 0.3	9 ± 4	63 ± 23	1166 ± 118	177 ± 23	Onaway	Alfisol (Inceptic Hapludalfs)	0–3
	10–25	6.8 ± 0.3	8 ± 3	27 ± 8	1064 ± 121	150 ± 24			
	25-50	$7.1~\pm~0.4$	8 ± 6	25 ± 15	$1014~\pm~500$	$121~\pm~44$			
	50-100	$7.8~\pm~0.3$	4 ± 6	36 ± 8	$2448~\pm~952$	152 ± 28			
Michigan South	0–10	5.0 ± 0.3	23 ± 10	104 ± 49	501 ± 92	84 ± 24	Kalamazoo/ Oshtemo	Alfisol (Typic Hapludalfs)	0–3
	10–25	5.0 ± 0.3	22 ± 8	66 ± 24	$580~\pm~182$	86 ± 36			
	25-50	5.0 ± 0.3	32 ± 13	75 ± 22	$823~\pm~330$	$129~\pm~64$			
	50-100	5.1 ± 0.2	26 ± 8	46 ± 22	$500~\pm~271$	90 ± 60			
Wisconsin Central	0–10	6.6 ± 0.3	95 ± 43	78 ± 35	480 ± 255	95 ± 30	Plainfield	Entisol (Typic Udipsamments)	0–3
	10–25	6.8 ± 0.4	85 ± 54	68 ± 44	$388~\pm~220$	80 ± 25			
	25-50	7.0 ± 0.4	68 ± 59	51 ± 30	$211~\pm~61$	58 ± 22			
	50-100	7.0 ± 0.3	86 ± 86	38 ± 15	122 ± 33	37 ± 11			
Wisconsin North	0–10	5.8 ± 0.5	287 ± 39	142 ± 50	515 ± 261	42 ± 12	Vilas	Spodosol (Entic Haplorthods)	0–3
	10–25	$5.6~\pm~0.4$	$256~\pm~46$	83 ± 19	414 ± 174	41 ± 21			
	25-50	5.3 ± 0.4	64 ± 33	62 ± 15	$250~\pm~113$	63 ± 45			
	50-100	5.4 ± 0.3	28 ± 9	58 ± 16	265 ± 152	71 ± 37			

Note: Soil chemical characteristics data were obtained from the Great Lakes Bioenergy Research Center's Sustainability Data Catalog (https://data.sustainability.glbrc.org). Data were generated from the deep-core samples (100 cm) collected from the -N treatment split-plots of all cropping systems in 2013. Soil classification information were obtained from Kasmerchak and Schaetzl (2018) and official soil series description available at United States Department of Agriculture-Natural Resources Conservation Service website (https://soilseries.sc.egov.usda.gov/osdname.aspx). Numbers denote mean \pm standard deviation (n = 28).

Abbreviations: Ca, calcium; Mg, magnesium; P, phosphorus; K, potassium.

^apH: 1:1 dry soil/water suspension.

^bBray–Kurtz P1 extraction.

°0.3 N NH₄F in 0.025 N HCl or 1 N NH₄OAc at pH 7.0.

^d1 N NH₄OAc, pH 7.0.

N fertilization was withheld until 2015 in all other systems to avoid providing weeds a competitive advantage. N fertilizer was then applied annually at 56 kg N ha⁻¹ to all +N splitplots in all systems except hybrid poplar. The fertilizer type and the machinery used in application differed between sites and years. For fertilization of early successional +N split-plots in 2014, urea (46–0–0) was applied at all Michigan sites with a Gandy Orbit Air applicator (Gandy Company) connected to a John Deere 5225 tractor (Deere and Company). Ammonium nitrate was applied at all Wisconsin sites using a Gandy 10' drop spreader (Gandy Company) connected to a Case IH 684 tractor (CNH Industrial America LLC). From 2015 to 2018, all +N split-plots, except hybrid poplar, were fertilized with Super-U (46–0–0) using a Gandy Orbit Air applicator at all Michigan sites and with Environmentally Smart Nitrogen (ESN, 44–0–0) using a Gandy 10' drop spreader at all Wisconsin sites. Super-U is a polymer-coated urea treated with 0.06% (w/w) *N*-(n-butyl) thiophosphoric triamide and 0.85% (w/w) dicyandiamide which give Super-U its urease and nitrification inhibition properties, respectively (Koch Agronomic Services, LLC). ESN is a slow N release polymer-coated urea with no urease or nitrification inhibition properties (Golden et al., 2011). In 2019 and 2020, all +N split-plots, except for hybrid poplar, were fertilized with ESN in both Michigan and Wisconsin sites using the Gandy Orbit Air applicator. Hybrid poplar +N split-plots were hand fertilized once in 2016 at 157 kg N ha⁻¹ with Super-U at all Michigan sites and with ESN at all Wisconsin sites.

Cropping system	Species and variety	Seed (PLS)/plant rate	N treatments
Switchgrass	Panicum virgatum var. Cave-in-Rock	7.85 kg ha^{-1}	$0 \text{ vs. } 56 \text{ kg } ha^{-1}$
Miscanthus	Miscanthus x giganteus, "Illinois clone"	17,200 rhizomes ha ⁻¹	0 vs. 56 kg ha $^{-1}$
Native grasses Canada wild rye Little bluestem Indiangrass Switchgrass Big bluestem	Elymus canadensis L. Schizacyrium scoparium (Michx.) Nash Sorghastrum nutans (L.) Nash Panicum virgatum var. Southlow Andropogon gerardii Vitman	1.12 kg ha ⁻¹ 2.24 kg ha ⁻¹ 1.68 kg ha ⁻¹ 1.12 kg ha ⁻¹ 1.68 kg ha ⁻¹	0 vs. 56 kg ha ⁻¹
Hybrid poplar	Populus nigra × P. maximowiczii, NM6	2778 cuttings ha ⁻¹	0 vs. 157 kg ha^{-1}
Early successional vegetation Grasses Black bent Big bluestem Bromegrass Couch grass Timothy grass Kentucky bluegrass Little bluestem Cat grass	Agrostis gigantea Roth Andropogon gerardii Vitman Bromus inermis Leyss. Elymus repens (L.) Gould Phleum pratense L. Poa pratensis L. Schizachyrium scoparium (Michx.) Nash Dactylis glomerata L.	N/A	0 vs. 56 kg ha ⁻¹
Forbs Yarrow Ragweed Indian hemp Milkweed Frost aster Hoary alyssum Spotted knapweed Creeping thistle Horseweed Wild carrot Annual fleabane Grass-leaved goldenrod Perforate St John's-wort Canada goldenrod	Achillea millefolium L. Ambrosia artemisiifolia L. Apocynum canabinum L. Asclepias syriaca L. Aster pilosus Willd. Berteroa incana (L.) DC Centaurea stoebe L. Cirsium arvense (L.) Scop Conyza canadensis (L.) Cronq Daucus carota L. Erigeron annus (L.) Pers Euthamia graminifolia (L.) Nutt Hypericum perforatum L. Solidago canadensis L.		
Restored prairie Grasses Switchgrass Canada wild rye Junegrass Little bluestem Indiangrass Big bluestem	Panicum virgatum var. Southlow Elymus canadensis L. Koeleria cristata (Ledeb.) Schult. Schizacyrium scoparium [Michx.] Nash Sorghastrum nutans [L.] Nash Andropogon gerardii Vitman	0.59 kg ha ⁻¹ 0.88 kg ha ⁻¹ 0.59 kg ha ⁻¹ 0.88 kg ha ⁻¹ 0.88 kg ha ⁻¹ 0.88 kg ha ⁻¹	0 vs. 56 kg ha ⁻¹
Forbs Meadow anemone Butterfly weed New England aster White wild indigo Showy tick-trefoil Roundhead bushclover Wild bergamot Pinnate prairie coneflower Black-eyed susan Cup plant Stiff goldenrod Showy goldenrod	Anemone canadensis L. Asclepias tuberosa L. Aster novae-angliae L. Baptisia lactea var. lacteal Desmodium canadense L. Lespedeza capitata Michx. Monarda fistulosa L. Ratibida pinnata (Vent.) Barnh. Rudbeckia hirta L. Silphium perfoliatum L. Solidago rigida L. Solidago speciosa L.	0.26 kg ha ⁻¹ 0.26 kg ha ⁻¹	

TABLE 2 Establishment of bioenergy cropping systems on Great Lakes Bioenergy Research Center's (GLBRC's) marginal land experimental sites including species and variety planted, seeding/planting rate, and the nitrogen (N) fertilization rate for each cropping system.

Abbreviation: PLS, pure live seed.

Soil pH, potassium (K), and phosphorus (P) were routinely monitored by annual soil sampling and analyzed on a 3-year cycle throughout the study period. Pelletized limestone, potash (0-0-62), and triple super phosphate (0-46-0)were added when recommended to increase pH (>5.5), K (>45–100 ppm), and P (>10–22 ppm), respectively. Pelletized limestone was added to the split-plots of all cropping systems at Michigan South in 2016 and 2019, of miscanthus and switchgrass at Wisconsin Central in 2019, and of hybrid poplar at Wisconsin North in 2019 to increase soil pH. In May 2020, except for all cropping systems at Wisconsin North and ON split-plots of the historical system at all sites, 34-56 kg K ha⁻¹ of potash was added to each split-plot using the Gandy Orbit Air applicator connected to a John Deere 6140R tractor (Deere and Company) (Table \$19). Based on soil monitoring results, 45 kg P ha⁻¹ of triple super phosphate was applied in May 2020 to all split-plots at Escanaba except the ON split-plots of the historical system.

2.4 | Harvesting biomass

All cropping systems, except hybrid poplar, were harvested within 2 weeks after the first killing frost in the fall to minimize nutrient removal and loss of biomass. Biomass for yield determination was harvested from a 2.3-m strip down the center of each split-plot in all cropping systems, except hybrid poplar and miscanthus (at Wisconsin sites) in 2014. A machine harvester (Maschinenfabrik KEMPER GmbH) was used with the harvest height adjusted to leave a 15-cm residual stubble. Hybrid poplar is a short-rotation crop harvested after several years of growth. Miscanthus at Wisconsin sites was not harvested in 2014 to facilitate snow retention and increase first-year winter survival. Harvested biomass was chopped, collected, and weighed in a forage weigh wagon. A subsample from each split-plot was collected, oven-dried (Grieve Corporation) at 66°C for 3–4 days until constant dry weight, then weighed (Ohaus Corporation). The historical system was not harvested. Instead, biomass was determined from hand-harvested samples by clipping the vegetation within a randomly placed 1-m² quadrat (0.5 m \times 2 m) at 15 cm above ground level (n = 3 per split-plot; 2015–2020). The clipped biomass was placed in paper bags, dried, and weighed as above. Hybrid poplar biomass was determined in 2018 by harvesting 22 trees from the center two rows of each split-plot using a chain saw (Husqvarna Group). The harvested biomass was chipped, weighed, and subsamples dried as above.

We report the yield for all systems, except hybrid poplar, as the mean yield (Mg ha⁻¹ year⁻¹) over 7 years (2014– 2020). Hybrid poplar yield is expressed as the mean yield over 5 years (2014–2018). All cropping systems were harvested annually over 7 years from 2014 to 2020, except hybrid poplar which was harvested 5 years after it was established. Because hybrid poplar was harvested 5 years after establishment, only to compare its yield with other cropping systems, the cumulative yield of all cropping systems from 2014 to 2018 was divided by five to calculate the mean yield over the same time frame.

2.5 | Stand counts and species composition

Stand counts for miscanthus, switchgrass, native grasses, and restored prairie systems were determined for each plot by counting the number of plants within a randomly placed 75 cm \times 75 cm quadrat (n = 4). Species composition was assessed by recording the first intercepted species at 1 m intervals along a transect line placed lengthwise across each plot (https://data.sustainability.glbrc.org/protocols/198).

2.6 | Data analysis

Statistical assumptions of normality, equal variance, and independence were checked with normal quantile-quantile and residual versus fitted plots. If statistical assumptions were not met, data were transformed, and log transformation proved to be sufficient to meet statistical assumptions. Data were analyzed using a mixed-effects model and the statistical software RStudio version 4.0.5 with the R package LmerTest (RCore Team, 2021). Site, cropping system, N treatment, and their two-way interactions were considered fixed effects while year, replicate/block nested within site, and crop nested within site were considered random effects. Akaike information criterion (AIC) and computation of analysis of variance (using the function: anova) for fitted models were used for model selection. The fixed effect: three-way interaction of site, cropping system, and N treatment was not included in the model as its inclusion did not improve the best selected model. Results were considered significant if p < 0.05. If results were significant, pairwise comparisons were performed using Tukey's post-hoc test after calculating estimated marginal means. Stand counts were analyzed with Poisson regression analysis using marginal land site and cropping system as fixed factors. If results were significant, pairwise comparisons were performed as above. Species composition was assessed as percent canopy cover of each species, where

Percent canopy cover = Species presence/Total points per

transect \times 100.

3 | RESULTS

3.1 | Weather and soil water content

Across all sites, the 30-year annual precipitation averaged from 752 mm (Michigan Central) to 875 mm (Michigan South). Over the study period (2013–2020), the average annual precipitation and average growing season precipitation (May to October) were both above their 30-year averages at all sites (Tables S1–S5). Over this period, Michigan Central had the lowest growing season precipitation and the lowest annual precipitation, except in 2014. Wisconsin North had the highest annual precipitation during the study period (1021 mm).

Across the sites, the average 30-year annual snowfall ranged between 1095 mm (Wisconsin Central) and 3360 mm (Michigan North). Over the study period, Wisconsin Central had the lowest snowfall for the period between the end of one growing season and the start of the next growing season (November to April) (Tables S6–S10). Wisconsin Central also had the lowest annual snowfall except in 2013, 2018, and 2019 (Tables S6–S10).

Across the sites, the 30-year annual temperature ranged between 4.5° C in Wisconsin North and 9.6° C in Michigan South (Tables S11–S15). For all study years, annual and growing season temperatures were highest in Michigan South. Wisconsin North had the lowest annual temperature and Michigan North had the lowest growing season temperatures (Tables S11–S15).

Volumetric soil water content data were not available for Michigan Central. Among other sites, both annual and growing season volumetric water content of both the 10 and 25 cm soil depths were higher in Michigan North and Michigan South than those in Wisconsin North and Wisconsin Central (Table S16), which was ~1.5-fold lower in Wisconsin North and approximately fivefold lower in Wisconsin Central than the Michigan locations (Table S16). Soil water content was higher at 25 cm depth than the 10-cm depth in all sites except in Wisconsin North where the opposite was observed (Table S16).

3.2 | Yields across sites and nitrogen treatment

Mean yields between 2014 and 2020 (excluding poplar) were significantly affected by the two-way interactions of crop \times site, crop \times N treatment, and site \times N treatment (Table S20). Mean yields between 2014 and 2018 (including poplar) were significantly affected by N treatment and the two-way interaction of crop \times site (Table S20).

When averaged across sites, years, and N treatments, miscanthus had the highest overall yield among cropping systems $(8.0 \pm 0.4 \text{ Mg ha}^{-1} \text{ year}^{-1}; \text{ Table 3})$, and varied by a factor of over 10 (0.8–13.6 Mg ha⁻¹ year⁻¹) across sites (Figure 2). When averaged across N treatments and years, miscanthus yields were highest in Michigan South (14.0 \pm 1.0 Mg ha⁻¹ year⁻¹, n = 52) followed by Michigan Central (10.8 \pm 0.5 Mg ha⁻¹ year⁻¹, n = 52) and Michigan North (10.6 \pm 0.8 Mg ha⁻¹ year⁻¹, n = 52). These were the highest mean yields recorded among all cropping systems. Miscanthus yields were considerably lower in Wisconsin Central (0.8 \pm 0.1 Mg ha⁻¹ year⁻¹, n = 37) and Wisconsin North (1.4 \pm 0.2 Mg ha⁻¹ year⁻¹, n = 45) and their yields were roughly 6%–7% and 10%–13% of the yields at Michigan sites, respectively. In Wisconsin North, miscanthus had the lowest mean yield among all cropping systems.

When averaged across sites, years, and N treatments, switchgrass had the second highest overall yield (6.1 \pm 0.2 Mg ha⁻¹ year⁻¹, with a range of 3.1–7.6 Mg ha⁻¹ year⁻¹), \sim 24% less than the overall average miscanthus yield for the 7year period. However, the overall average yield of switchgrass for the 7-year period was $\sim 50\%$ lower than the average miscanthus yield across Michigan sites and ~450% higher than the average miscanthus yield across Wisconsin sites for the same period (Table 3). When averaged across N treatments and years, switchgrass yields were highest in Michigan North $(7.6 \pm 0.4 \text{ Mg ha}^{-1} \text{ year}^{-1}, n = 52)$ and decreased from Michigan Central (6.9 \pm 0.3 Mg ha⁻¹ year⁻¹, n = 52), Michigan South (6.7 \pm 0.4 Mg ha⁻¹ year⁻¹, n = 52), Wisconsin North $(5.6 \pm 0.4 \text{ Mg ha}^{-1} \text{ year}^{-1}, n = 52)$, to Wisconsin Central $(3.1 \pm 0.4 \text{ Mg ha}^{-1} \text{ year}^{-1}, n = 42)$. Although switchgrass yields were lower in Wisconsin sites than in Michigan sites, switchgrass yields were the highest of all cropping systems at both Wisconsin sites (Figure 2).

When averaged across sites, years, and N treatments, hybrid poplar had the third highest overall yield among all cropping systems for the common 5-year reporting period: 3.4 ± 0.3 Mg ha⁻¹ year⁻¹, with a range of 0.9–5.0 Mg ha⁻¹ year⁻¹ (Table 3). When averaged across N treatments and years, hybrid poplar yields were greatest in Wisconsin Central $(5.0 \pm 1.2 \text{ Mg ha}^{-1}, n = 6)$ and at this site, hybrid poplar yields were the greatest among all cropping systems (Figure 2b). The second highest yields were in Michigan Central $(4.3 \pm 0.6 \text{ Mg} \text{ ha}^{-1}, n = 8)$ followed by Michigan North $(4.2 \pm 0.4 \text{ Mg ha}^{-1}, n = 8)$. The lowest yields were in Wisconsin North $(0.9 \pm 0.2 \text{ Mg ha}^{-1}, n = 8)$, which were $\sim 17\%$ –27% of the yields at other sites and were the lowest among all cropping systems in this site (Figure 2b).

When averaged across sites, years, and N treatments, native grasses had the fourth highest overall yields among all cropping systems: 4.3 ± 0.2 Mg ha⁻¹ year⁻¹, with a range of 1.4–5.4 Mg ha⁻¹ year⁻¹ (Table 3). When averaged across N treatments and years, native grass yields were highest in Michigan Central (5.4 ± 0.3 Mg ha⁻¹, n = 52) followed by Michigan South (5.4 ± 0.3 Mg ha⁻¹, n = 52), Wisconsin North

TABLE 3 Mean yields of each Great Lakes bioenergy cropping system during the study period ([2014–2020, i.e., without hybrid poplar] or [2014–2018, i.e., with hybrid poplar]) when averaged across sites, years, and nitrogen (N) treatments.

			¹ year ⁻¹)			
	2014-2018			2014-2020		
Cropping system	Mean	±SE	n	Mean	±SE	n
Switchgrass	5.68	0.36	40	6.08	0.19	250
Miscanthus-all region	6.27	0.80	40	8.02	0.44	238
Miscanthus-Michigan	10.01	0.53	24	11.66	0.45	156
Miscanthus-Wisconsin	0.65	0.13	16	1.10	0.11	82
Native grasses	3.06	0.25	40	4.34	0.17	249
Hybrid poplar	3.41	0.33	38	-	-	-
Early successional vegetation	1.44	0.12	40	1.51	0.06	269
Restored prairie	1.84	0.14	40	2.70	0.11	246
Historical vegetation	1.59	0.14	40	1.82	0.08	245

Abbreviations: n, number of replicates; SE, standard error.

(4.8 \pm 0.4 Mg ha⁻¹, n = 52), and Michigan North (4.1 \pm 0.4 Mg ha⁻¹, n = 52). Yields were lowest in Wisconsin Central and roughly 26%–35% of the yields at other sites (1.4 \pm 0.2 Mg ha⁻¹, n = 41; Figure 2a).

When averaged across sites, years, and N treatments, restored prairie yields had the fifth highest overall yields among all crops: 2.7 ± 0.1 Mg ha⁻¹ year⁻¹, with a range of 1.1–3.9 Mg ha⁻¹ year⁻¹ (Table 3). When averaged across N treatments and years, restored prairie yields were highest in Wisconsin North (3.9 ± 0.3 Mg ha⁻¹, n = 51), intermediate in Michigan sites, and lowest in Wisconsin Central (1.1 ± 0.1 Mg ha⁻¹, n = 41; Figure 2a).

When averaged across sites, years, and N treatments, historical vegetation had the second lowest overall potential yields among all cropping systems; 1.8 ± 0.1 Mg ha⁻¹ year⁻¹, with a range of which was roughly 23% of average miscanthus yield produced over 7 years (Table 3). When averaged across N treatment and years, potential yields were highest in Wisconsin North (3.1 ± 0.1 Mg ha⁻¹, n = 50) followed by Michigan South (1.9 ± 0.2 Mg ha⁻¹, n = 52), Michigan North (1.7 ± 0.1 Mg ha⁻¹, n = 50), and Wisconsin Central (1.2 ± 0.2 Mg ha⁻¹, n = 41), and lowest in Michigan Central (1.1 ± 0.1 Mg ha⁻¹, n = 52; Figure 2a) where they were the lowest among all cropping systems at the site.

When averaged across sites, years, and N treatments, early successional yields were the lowest among all cropping systems: 1.5 ± 0.1 Mg ha⁻¹ year⁻¹, with a range of 0.8–2.5 Mg ha⁻¹ year⁻¹ (Table 3). When averaged across N treatments, early successional yields were highest in Wisconsin North (2.5 ± 0.09 Mg ha⁻¹, n = 56), intermediate in Michigan North (1.5 ± 0.1 Mg ha⁻¹ year⁻¹, n = 56) and Michigan South (1.5 ± 0.1 Mg ha⁻¹ year⁻¹, n = 56), and lowest in Michigan Central (1.1 ± 0.1 Mg ha⁻¹ year⁻¹, n = 56) and Wisconsin Central (0.8 ± 0.1 Mg ha⁻¹ year⁻¹, n = 45; Figure 2a).

3.3 | Temporal yield variation

Overall miscanthus yields increased steadily from a low of $1.8 \pm 0.4 \text{ Mg ha}^{-1} \text{ year}^{-1}$ (n = 12) in 2014 to a high of $10.4 \pm 1.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$ (*n* = 37) in 2018 before gradually declining to 8.2 \pm 1.1 Mg ha⁻¹ year⁻¹ (n = 38; Figure 3a) in 2020. This trend was evident in all sites but the least productive. In Michigan South, miscanthus yields increased rapidly from 2014 (1.5 \pm 0.3 Mg ha⁻¹ year⁻¹, n = 4) to 2016 $(15.3 \pm 1.6 \text{ Mg ha}^{-1} \text{ year}^{-1}, n = 8)$ then gradually to a peak in $2018 (20.0 \pm 2.0 \text{ Mg ha}^{-1} \text{ year}^{-1}, n = 8)$ followed by a decline toward 2020 (13.5 \pm 2.3 Mg ha⁻¹ year⁻¹, n = 8; Figure 3c). In Michigan Central, miscanthus productivity rapidly and steadily increased from 2014 (3.4 \pm 0.4 Mg ha⁻¹ year⁻¹, n = 4) to a peak in 2017 (15.3 \pm 0.8 Mg ha⁻¹ year⁻¹, n = 8) and then decreased toward 2020 (9.2 \pm 0.9 Mg ha⁻¹ year⁻¹, n = 8) with a slight increase in 2019 (13.1 ± 1.3 Mg ha⁻¹ year⁻¹, n = 8; Figure 3b). In Michigan North, miscanthus yields rapidly increased from 2014 (0.6 ± 0.2 Mg $ha^{-1} year^{-1}, n = 4$) to 2017 (14.2 ± 0.9 Mg $ha^{-1} year^{-1}, n = 8$) and peaked in 2018 (14.9 \pm 1.1 Mg ha⁻¹ year⁻¹, n = 8) before it decreased toward 2020 (13.8 \pm 1.7 Mg ha⁻¹ year⁻¹, n = 8; Figure 3d). In both Wisconsin sites, miscanthus yields were so low that no temporal pattern could be identified. In Wisconsin North, miscanthus yields were highest in 2019 (1.9 \pm 0.6 Mg ha^{-1} year⁻¹, n = 7; Figure 3f) while in Wisconsin Central, it was highest in 2017 (1.4 \pm 0.3 Mg ha⁻¹ year⁻¹, n = 6; Figure 3e).

A similar pattern was evident for switchgrass: overall switchgrass yields increased steadily from 2014 to 2017 and then decreased in 2020 back to the 2014 levels (Figure 3a). Similar to the overall trend, switchgrass yields in Michigan North, Michigan Central, Michigan South, and Wisconsin Central increased from 2014 to 2017 and then decreased



FIGURE 2 Mean yields (Mg ha⁻¹ year⁻¹) of bioenergy cropping systems (switchgrass, miscanthus, native grasses, hybrid poplar, early successional vegetation, restored prairie, and historical vegetation [control]) at each study site (Michigan Central, Michigan North, Michigan South, Wisconsin Central, and Wisconsin North) between 2014 and 2020 (a, without hybrid poplar) and 2014 and 2018 (b, with poplar). Each bar represents mean \pm standard error (SE) when averaged across nitrogen (N) treatment and years. Within each study site, cropping systems not sharing the same letters are significantly different (p < 0.05, Tukey's test).

toward 2020 (Figure 3a-e). In Wisconsin North, yields of switchgrass increased from 2014 to 2016 and then decreased toward 2020 (Figure 3f).

Overall native grass yields increased gradually from 2014 to 2019 (Figure 3a). In the two northern sites and Wisconsin Central, yields increased gradually from 2014 to 2020 (Figure 3d,f). In Michigan Central, yields increased gradually

from 2014 and then fluctuated from 2018 to 2020 (Figure 3b). In Michigan South, native grass yields also increased gradually from 2014 to 2017 but remained near that level through 2020 (Figure 3c).

Overall restored prairie yields increased steadily from 2014 to 2020 (Figure 3a). Restored prairie yields in Wisconsin North, Michigan South, and Michigan North tended to



FIGURE 3 Temporal variation in mean yields (Mg ha⁻¹ year⁻¹) of bioenergy cropping systems (switchgrass, miscanthus, native grasses, early successional vegetation, restored prairie, and historical vegetation [control]) averaged across all sites (a), and at Michigan Central (b), Michigan South (c), Michigan North (d), Wisconsin Central (e), and Wisconsin North (f) between 2014 and 2020. Each data point represents mean \pm standard error when averaged across nitrogen (N) treatments.

increase from 2014 to 2020 (Figure 3c,d,f). In Michigan Central, yields increased from 2014 to 2017 and then fluctuated from 2018 to 2020 (Figure 3b). In Wisconsin Central, no temporal pattern could be identified (Figure 3e). No clear temporal pattern in yields of historical or early successional vegetations could be identified across sites (Figure 3); the highest overall potential yields of historical vegetation were in 2015.

3.4 | Yields in response to nitrogen fertilization

When averaged across all sites and years, N fertilization significantly increased the yields of all cropping systems, and miscanthus had the greatest response to N fertilization (40%) followed by switchgrass (36%), native grasses (35%), restored prairie (32%), historical vegetation (27%), and early successional vegetation (19%; Figure 4a).

When averaged across the cropping systems and years, N fertilization significantly increased yields at all marginal land sites. The magnitude of the yield increase declined from Michigan South (54%), Wisconsin North (48%), Wisconsin Central (29%), Michigan North (26%), to Michigan Central (16%) (Figure 4b).

4 | DISCUSSION

Biomass production by seven candidate bioenergy cropping systems at our five marginal land sites differed greatly by crop, site, and year. When averaged across sites, years, and N treatments, average 7-year yields ranged fivefold, from 1.5 to 8.0 Mg ha⁻¹ year⁻¹ in the order miscanthus > switchgrass > hybrid poplar \approx native grasses > restored prairie > early successional \approx historical vegetation. Although miscanthus had the highest overall yield, its yields varied by a factor of over 10 across sites and ranked highest at only three (all Michigan) of the five sites. In contrast, switchgrass yields-though 24% lower on average-were more consistent across sites and greater than miscanthus at sites with the lowest miscanthus yields. Although the overall average yield of switchgrass was ~50% lower than the average yield of miscanthus across Michigan sites, it was ~450% higher than the average yield of miscanthus across Wisconsin sites.

Overall yields of the polyculture systems (native grasses and restored prairie) were lower than yields of monoculture systems (miscanthus and switchgrass). However, polyculture yields increased gradually during the study period while monoculture yields tended to decline (by as much as 60%) three–five growing seasons after crop establishment. Hybrid poplar yields were highest at the least productive site. The early successional and historical systems had consistently low yields at all sites. N fertilization significantly increased yields of all crops (19%–40%) at all sites (16%–54%).

4.1 | Cropping system and site differences

Our results are consistent with Sanford et al. (2016), who reported higher yields for miscanthus and switchgrass relative to our other cropping systems (i.e., native grasses, early successional, and restored prairie) when grown in comparatively JAYAWARDENA ET AL.

more productive soils in southwest Michigan and southcentral Wisconsin. In the present study, miscanthus was highly productive but only in three (Michigan) of the five sites. In contrast, switchgrass yields were more consistent across sites.

Despite replanting failed plants in the initial years of stand establishment (2014–2017), site differences in miscanthus and switchgrass yields likely resulted from differences in stand uniformity, caused by various climatic and soil factors specific to each site. In the three most productive Michigan sites, miscanthus had significantly higher stand counts than in the two least productive Wisconsin sites. In contrast, switchgrass had significantly higher and consistently better stand counts across all sites (Table S21).

In the least productive site, Wisconsin Central, miscanthus had the poorest stand establishment, despite repeated replanting. Overwintering losses during the establishment period have been reported previously (Lewandowski et al., 2000). In north temperate regions such as Michigan and Wisconsin, snow serves as an insulator and its retention appears to be critical for the survival of miscanthus rhizomes during winters of stand establishment. In all study years, Wisconsin Central received the lowest snowfall, which may have contributed to its poor stand establishment and low productivity (Table S9). This was exacerbated by the sandy, excessively well-drained soils at the site. For example, volumetric water content at Wisconsin Central was roughly an order of magnitude lower than other sites (Table S16). Miscanthus productivity can decline considerably under water stress (both drought and waterlogged conditions; Pyter et al., 2007). Low water availability may also have contributed to the poor stand establishment and low productivity of this site. Similarly, volumetric water content was also low in Wisconsin North soils (especially lower in the soil profile; Table S16), despite having had the highest annual precipitation (Tables S1–S5), suggesting that high drainage may have also contributed to the low productivity here. Like Wisconsin Central, and despite the highest annual precipitation of the five sites, many farmers in the Rhinelander area rely on center-pivot irrigation to compensate for the coarse textured and excessively well drained soils.

Wisconsin North also had the coldest winters throughout the study period (Table S15) and spot replanting was required between 2014 and 2017 due to winter kill. In the following two winters (2017–2018 and 2018–2019), however, Wisconsin North also had the highest snow fall, which may have enhanced winter survival of the newly planted rhizomes (Table S10) and improved yields in 2019.

In the less productive Wisconsin sites, switchgrass was the most productive crop. This consistency can be attributed to switchgrass' low water and nutrient requirements and its ability to thrive across a wide geographical range (Mehmood et al., 2017), a versatility reflected in its genetic diversity (Lovell et al., 2021). The variety Cave-in-Rock planted



FIGURE 4 Mean yield (Mg ha⁻¹ year⁻¹) of bioenergy cropping systems (switchgrass, miscanthus, native grasses, hybrid poplar, early successional, restored prairie, and historical [control]) in response to nitrogen (N) treatments ($0N = 0 \text{ kg N ha}^{-1}$, $+N = 56 \text{ kg N ha}^{-1}$) when averaged across years and five Michigan and Wisconsin study sites (a) or when averaged across years and cropping systems (b) between 2014 and 2020. Each bar represents mean \pm standard error. Within each cropping system or marginal land site, N treatments not sharing the same letters are significantly different (p < 0.05, Tukey's test).

in this study is an upland variety and generally considered drought tolerant (Parrish & Fike, 2005; Porter Jr., 1966), which may explain why switchgrass had the highest yields of all cropping systems at the two Wisconsin sites that exhibited the lowest soil water availability among sites. Although miscanthus and switchgrass were the two most productive cropping systems in this study, additional factors remain important when selecting candidate bioenergy crops for sustainable use. These include (1) ecosystem services such as soil carbon sequestration and reduced greenhouse gas emissions (Gelfand et al., 2013), (2) pollination and other biodiversity benefits (Werling et al., 2014), and (3) soil N and microbial diversity improvement (Li et al., 2022) as well as agronomically relevant considerations such as (1) resilience to pests (Bradshaw et al., 2010; Parrish & Fike, 2005) and pathogens (Falter & Voigt, 2014; Parrish & Fike, 2005; Sykes et al., 2016), (2) cold tolerance (Lewandowski et al., 2000), and (3) crops potential to become invasive (Pittman et al., 2015; Raghu et al., 2006). Miscanthus in particular may be disadvantaged by biodiversity concerns (Pittman et al., 2015; Williams & Feest, 2019) and high establishment cost (Lewandowski et al., 2000).

Low poplar yields in Wisconsin North appeared to be caused by extensive deer browsing, which required frequent spot replanting (from 2014 to 2017). Michigan South had the lowest hybrid poplar yields across Michigan sites, apparently due to fungal disease pressure and deer browsing that resulted in poor stand establishment. As a result, spot replanting was required at this site as late as 2017. The leaf spot fungus (Marssonina spp.) is a common pathogen affecting some varieties of hybrid poplar, and warm temperatures combined with high rainfall provides favorable conditions for outbreaks (Sanford et al., 2016). The warm and moist climate of Michigan South makes these trees particularly susceptible to Marssonina spp. Selection of new hybrid poplar clones for bioenergy use should, therefore, place particular emphasis on disease and herbivore resistance in addition to biomass production potential.

In comparison to miscanthus, switchgrass, and other C_4 grasses, as a C_3 species hybrid poplar is also relatively water inefficient, and hence survives better in places where rainfall is abundant (Somerville et al., 2010). However, our sites with the lowest precipitation (i.e., Michigan Central) and volumetric water content (Wisconsin Central) had the higher hybrid poplar yields—probably because of high fungal disease pressure and deer browsing elsewhere.

The yield differences in native grasses across the sites were related to differences in stand counts, again associated with the specific soil and climatic factors at each site. The stand counts in the three most productive sites were significantly higher than the two least productive sites (Table S21). Yield was lowest in Wisconsin Central, the site with the least soil moisture availability and excessive drainage (Table S16). Similar to native grasses, restored prairie yields and stand counts were also lowest in Wisconsin Central (Tables S16 and S21). In contrast, Wisconsin North had the highest restored prairie yields and the highest annual and growing season precipitation during the study period.

Potential yields of both historical and early successional systems exhibited a clear relationship with precipitation and soil water availability. Wisconsin North had the highest yields of both historical and early successional vegetation and received the highest annual precipitation during the study period. Michigan South and Michigan North had interJAYAWARDENA ET AL.

mediate yields and received the second and third highest annual precipitation during the study period, respectively. The lowest yields were at sites with the lowest annual precipitation (Michigan Central) and with the lowest soil moisture availability (Wisconsin Central). Early successional yields were the lowest among cropping systems in three out of five sites (i.e., Michigan North, Michigan South, and Wisconsin Central). Although yields varied somewhat among sites, the overall poor performance of the early successional vegetation—somewhat lower even than the historical control—appears to make it a substandard candidate for bioenergy production on our marginal land sites.

4.2 | Temporal trends of yields

Across sites, miscanthus yields rapidly increased within the first 4-5 years after planting while switchgrass reached its maximum yields about a year earlier. This establishment trajectory is typical for miscanthus and switchgrass stands (Lewandowski et al., 2000; Stoof et al., 2015), and is a drawback of using warm season perennial grasses. Weed control during this phase is critical, but once established, maintenance is minimal (Stoof et al., 2015). After full establishment, yields of both miscanthus and switchgrass decreased toward 2020 with a higher rate of decline in switchgrass than miscanthus. By 2020, miscanthus and switchgrass yields had decreased by 22% and 60% as compared to their peak yields in 2018 and 2017, respectively. The observed yield declines in both miscanthus and switchgrass over the last few years raise questions about the long-term ability of these marginal lands to support highly productive monoculture cropping systems.

Unlike the increase, peak, and decline observed in monoculture yields, the yields of the herbaceous polyculture systems (native grasses and restored prairie) increased gradually during the study period, to the point that in 2020 native grasses outperformed switchgrass at all sites and restored prairie outperformed switchgrass at two of the five sites (Michigan South and Wisconsin North) and was similar to switchgrass at the remaining sites. If this trend were to continue (i.e., loss in monocultures/gain in polycultures), polyculture yields could prove comparably productive in the long term. However, additional data from these sites are needed to determine the persistence and long-term significance of these trends.

This pattern of polyculture dominance is consistent with that observed in small plot studies elsewhere (e.g., Tilman et al., 2006), with polyculture productivity increasing over time as more productive species begin to dominate (Griffith et al., 2011). In our study, big bluestem (*Andropogon geradii* Vitman) started to emerge as a dominant species in both native grasses and restored prairie. Big bluestem dominated the native grass system (Figure S1) at all sites except Wisconsin Central, where it accounted for only 26% of the canopy

cover as compared to 66%–80% of the cover at the other sites. In Wisconsin Central, switchgrass had a higher canopy cover than big bluestem (37% switchgrass vs. 26% bug bluestem). The other three grasses in the native grass seed mix, namely Indiangrass [*Sorghastrum nutans* (L.) Nash.], Canada wild rye (*Elymus canadensis* L.), and little bluestem [*Schizacyrium scoparium* (Michx.) Nash] poorly emerged among the tested native grasses.

Big bluestem also emerged as a dominant species in the restored prairie system at three of the five sites (Figure S1; big bluestem canopy cover: Michigan Central = 52%, Michigan South = 26%, and Wisconsin North = 41%). Grasses also dominated the remaining two sites: Kentucky bluegrass (*Poa pratensis* L.) dominated the restored prairie in Michigan North (23%), even though it was not included in the planted seed mixture and both big bluestem and switchgrass had an equal dominance (23%) in Wisconsin Central. Although big bluestem dominated the restored prairie in Michigan South, Indiangrass had a larger canopy cover (20%).

No clear temporal pattern in yields of historical or early successional vegetation could be identified across sites. The historical vegetation in Michigan South and Wisconsin North was dominated by the forb Canada goldenrod (*Solidago canadensis* L.), occupying 28% and 90% of the canopy cover, respectively, at these sites (Figure S1). Grasses dominated the remaining sites: Kentucky bluegrass in Michigan North (35%) and Wisconsin Central (30%; Figure S1) and bromegrass (*Bromus inermis* Leyss.) in Michigan Central (72%). In addition to Kentucky bluegrass, a better canopy cover of bromegrass (*Bromus inermis* Leyss.) was observed in Wisconsin Central (25%).

Grasses dominated the early successional vegetation at three sites: Kentucky bluegrass in Michigan North and Wisconsin Central, occupying 23% and 20% of the canopy cover, respectively, at these sites and Couch grass [*Elymus repens* (L.) Gould] in Michigan Central (43%; Figure S1). Forbs dominated the remaining two sites: spotted knapweed (*Centaurea stoebe* L.) in Michigan South (20%), and Canada goldenrod in Wisconsin North (85%; Figure S1).

4.3 | Yields in response to nitrogen fertilization

When averaged across sites and years, N fertilization significantly increased the yields of all cropping systems. Miscanthus and switchgrass had the highest (40% overall) and second highest yield (36% overall) increases in response to N fertilization of all cropping systems tested, respectively. A positive response of both miscanthus and switchgrass biomass yields in response to N fertilization has been noted by Heaton et al. (2004), but they report that miscanthus responds more strongly to precipitation/irrigation rather than to added N. Previously, Wang et al. (2020) investigated the yield responses of the same bioenergy cropping systems to similar N treatments (0 vs. 56 kg N ha⁻¹), but in comparatively more productive lands in southwest Michigan and southcentral Wisconsin. They found significant increases in miscanthus yields at both locations. However, they found little to no response of switchgrass biomass yield due to N fertilization. This is typical for many switchgrass N-response experiments (e.g., Fike et al., 2017; Roley et al., 2019) and even for grasslands in general (Jenkinson et al., 2004). This suggests an alternative source of N such as associative N fixation (Roley et al., 2019; Smercina et al., 2020). Our results suggest that yield responses to N fertilization may be more likely in poorer soils.

Nitrogen fertilization significantly increased the productivity of native grasses which is also consistent with Wang et al. (2020), who reported significant increase in biomass production of the same native grass mixture in response to an N application at southcentral Wisconsin. The dominance of grasses over forbs in the restored prairie helps to explain a > 30% yield increase in response to N fertilization as grasses tend to be more responsive to N fertilization than forbs (Song et al., 2011; Wang et al., 2020). Although the productivity of historical and successional vegetations increased by 27% and 19% in response to N fertilization, respectively, the magnitude of the increase was lower than in the restored prairie.

When averaged across all cropping systems and years, N fertilization significantly increased the yields at all sites. Application of N fertilizer is often a tradeoff between improving crop production and avoiding environmental contamination. Generally, these cellulosic bioenergy cropping systems tend to have the high N use efficiency and relatively low N requirements typical of perennial biomass crops in general (Mosier et al., 2021). Hence, little N fertilization may be required to improve crop production where N fixation is insufficient to meet plant N demands.

5 | CONCLUSIONS

Our results support the hypotheses and demonstrate the viability of low productivity former cropland (so-called marginal lands) for long-term bioenergy production and suggest that there is no single crop best suited for all low fertility soils. Miscanthus yields were high but only at three (Michigan) of the five sites. Switchgrass yields were $\sim 24\%$ lower than miscanthus on average but were more consistent across all sites. Overall switchgrass yield was $\sim 50\%$ lower than the Michigan miscanthus yield but $\sim 450\%$ higher than the Wisconsin miscanthus yield. The two polyculture systems, native grass mix and restored prairie, had lower yields than other herbaceous monoculture systems. However, unlike the monocultures yields, in the polyculture systems, yields did not decline with time and yield trends suggest they may outperform the two monocultures over the long term. The yields of the early successional system were the lowest of all cropping systems and were similar to those of the historical vegetation. Yields in both systems were stable over the 7-year study period. N fertilization significantly increased yields in all cropping systems at all sites.

AUTHOR CONTRIBUTIONS

Dileepa M. Jayawardena: Formal analysis; investigation; methodology; resources; validation; visualization; writing original draft; writing—review and editing. G. Philip Robertson and Kurt D. Thelen: Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing—review and editing. Gregg R. Sanford: Conceptualization; investigation; methodology; resources; validation; visualization; writing—review and editing.

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DATA AVAILABILITY STATEMENT

Data are available at Dryad Digital Repository.

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REFERENCES

- Bradshaw, J. D., Prasifka, J. R., Steffey, K. L., & Gray, M. E. (2010). First report of field populations of two potential aphid pests of the bioenergy crop *Miscanthus* × giganteus. The Florida Entomologist, 93, 135–137. https://doi.org/10.1653/024.093.0123
- Falter, C., & Voigt, C. A. (2014). Comparative cellular analysis of pathogenic fungi with a disease incidence in *Brachypodium distachyon* and *Miscanthus* × *giganteus*. *BioEnergy Research*, 7, 958–973. https://doi.org/10.1007/s12155-014-9439-3
- Fargione, J., Hill, J., Tilman, D., Polasky, S., & Hawthorne, P. (2008). Land clearing and the biofuel carbon debt. *Science*, *319*, 1235–1238. https://doi.org/10.1126/science.1152747
- Fike, J. H., Pease, J. W., Owens, V. N., Farris, R. L., Hansen, J. L., Heaton, E. A., Hong, C. O., Mayton, H. S., Mitchell, R. B., & Viands, D. R. (2017). Switchgrass nitrogen response and estimated production

costs on diverse sites. GCB Bioenergy, 9, 1526–1542. https://doi.org/ 10.1111/gcbb.12444

- Gelfand, I., Sahajpal, R., Zhang, X., Izaurralde, R. C., Gross, K. L., & Robertson, G. P. (2013). Sustainable bioenergy production from marginal lands in the US Midwest. *Nature*, 493, 514–517. https://doi. org/10.1038/nature11811
- Gelfand, I., Zenone, T., Jasrotia, P., Chen, J., Hamilton, S. K., & Robertson, G. P. (2011). Carbon debt of Conservation Reserve Program (CRP) grasslands converted to bioenergy production. *Proceedings of the National Academy of Sciences*, *108*, 13864–13869. https://doi.org/10.1073/pnas.1017277108
- Golden, B., Slaton, N., Norman, R., Gbur, E., & Wilson, C. (2011). Nitrogen release from environmentally smart nitrogen fertilizer as influenced by soil series, temperature, moisture, and incubation method. *Communications in Soil Science and Plant Analysis*, 42, 1809–1824. https://doi.org/10.1080/00103624.2011.587568
- Griffith, A. P., Epplin, F. M., Fuhlendorf, S. D., & Gillen, R. (2011). A comparison of perennial polycultures and monocultures for producing biomass for biorefinery feedstock. *Agronomy Journal*, 103, 617–627. https://doi.org/10.2134/agronj2010.0336
- Heaton, E., Voigt, T., & Long, S. P. (2004). A quantitative review comparing the yields of two candidate C₄ perennial biomass crops in relation to nitrogen, temperature and water. *Biomass and Bioenergy*, 27, 21–30. https://doi.org/10.1016/j.biombioe.2003.10.005
- Jenkinson, D. S., Poulton, P. R., Johnston, A. E., & Powlson, D. S. (2004). Turnover of nitrogen-15-labeled fertilizer in old grassland. *Soil Science Society of America Journal*, 68, 865–875. https://doi.org/ 10.2136/sssaj2004.8650
- Kang, S., Post, W. M., Nichols, J. A., Wang, D., West, T. O., Bandaru, V., & Izaurralde, R. C. (2013). Marginal lands: Concept, assessment and management. *Journal of Agricultural Science*, 5, 129–139. https://doi. org/10.5539/jas.v5n5p129
- Kasmerchak, C. S., & Schaetzl, R. (2018). Soils of the GLBRC marginal land experiment (MLE) sites. Kellogg Biological Station Long-Term Ecological Research Special Publication. https://doi.org/10. 5281/zenodo.2578238
- Lewandowski, I., Clifton-Brown, J. C., Scurlock, J. M. O., & Huisman, W. (2000). Miscanthus: European experience with a novel energy crop. *Biomass and Bioenergy*, 19, 209–227. https://doi.org/10.1016/ S0961-9534(00)00032-5
- Li, X., Petipas, R. H., Antoch, A. A., Liu, Y., Stel, H. V., Bell-Dereske, L., Smercina, D. N., Bekkering, C., Evans, S. E., Tiemann, L. K., & Friesen, M. L. (2022). Switchgrass cropping systems affect soil carbon and nitrogen and microbial diversity and activity on marginal lands. *GCB Bioenergy*, 14(8), 918–940. https://doi.org/10.1111/gcbb. 12949
- 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., 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, 438–444. https://doi.org/10.1038/s41586-020-03127-1
- Masters, M. D., Black, C. K., Kantola, I. B., Woli, K. P., Voigt, T., David, M. B., & DeLucia, E. H. (2016). Soil nutrient removal by four potential bioenergy crops: *Zea mays, Panicum virgatum, Miscanthus×* giganteus, and prairie. Agriculture, Ecosystems & Environment, 216, 51–60. https://doi.org/10.1016/j.agee.2015.09.016

- Mehmood, M. A., Ibrahim, M., Rashid, U., Nawaz, M., Ali, S., Hussain, A., & Gull, M. (2017). Biomass production for bioenergy using marginal lands. *Sustainable Production and Consumption*, 9, 3–21. https://doi.org/10.1016/j.spc.2016.08.003
- Mosier, S., Córdova, S. C., & Robertson, G. P. (2021). Restoring soil fertility on degraded lands to meet food, fuel, and climate security needs via perennialization. *Frontiers in Sustainable Food Systems*, 5, 706142. https://doi.org/10.3389/fsufs.2021.706142
- Parrish, D. J., & Fike, J. H. (2005). The biology and agronomy of switchgrass for biofuels. *Critical Reviews in Plant Sciences*, 24, 423–459. https://doi.org/10.1080/07352680500316433
- Pittman, S. E., Muthukrishnan, R., West, N. M., Davis, A. S., Jordan, N. R., & Forester, J. D. (2015). Mitigating the potential for invasive spread of the exotic biofuel crop, *Miscanthus× giganteus*. *Biological Invasions*, 17, 3247–3261. https://doi.org/10.1007/s10530-015-0950-z
- Porter, Jr, C. L. (1966). An analysis of variation between upland and lowland switchgrass, *Panicum virgatum* L., in Central Oklahoma. *Ecology*, 47, 980–992. https://doi.org/10.2307/1935646
- Pyter, R., Voigt, T., Heaton, E., Dohleman, F., & Long, S. (2007). Growing giant miscanthus in Illinois. University of Illinois Extension.
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/
- Raghu, S., Anderson, R. C., Daehler, C. C., Davis, A. S., Wiedenmann, R. N., Simberloff, D., & Mack, R. N. (2006). Adding biofuels to the invasive species fire? *Science*, 313, 1742. https://doi.org/10.1126/ science.1129313
- Richards, B. K., Stoof, C. R., Cary, I. J., & Woodbury, P. B. (2014). Reporting on marginal lands for bioenergy feedstock production: A modest proposal. *BioEnergy Research*, 7, 1060–1062. https://doi.org/ 10.1007/s12155-014-9408-x
- 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, eaal2324. https:// doi.org/10.1126/science.aal2324
- Roley, S. S., Ulbrich, T. C., & Robertson, G. P. (2021). Nitrogen fixation and resorption efficiency differences among twelve upland and lowland switchgrass cultivars. *Phytobiomes Journal*, 5, 97–107. https:// doi.org/10.1094/PBIOMES-11-19-0064-FI
- Roley, S. S., Xue, C., Hamilton, S. K., Tiedje, J. M., & Robertson, G. P. (2019). Isotopic evidence for episodic nitrogen fixation in switchgrass (*Panicum virgatum* L.). Soil Biology and Biochemistry, 129, 90–98. https://doi.org/10.1016/j.soilbio.2018.11.006
- 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 & Environment, 216*, 344–355. https://doi. org/10.1016/j.agee.2015.10.018

- Sanford, G. R., Oates, L. G., Roley, S. S., Duncan, D. S., Jackson, R. D., Robertson, G. P., & Thelen, K. D. (2017). Biomass production a stronger driver of cellulosic ethanol yield than biomass quality. *Agronomy Journal*, 109, 1911–1922. https://doi.org/10.2134/agronj2016.08.0454
- Smercina, D. N., Evans, S. E., Friesen, M. L., & Tiemann, L. K. (2020). Impacts of nitrogen addition on switchgrass root-associated diazotrophic community structure and function. *FEMS Microbiology Ecology*, 96, fiaa208. https://doi.org/10.1093/femsec/fiaa208
- Somerville, C., Youngs, H., Taylor, C., Davis, S. C., & Long, S. P. (2010). Feedstocks for lignocellulosic biofuels. *Science*, 329, 790–792. https://doi.org/10.1126/science.1189268
- Song, L., Bao, X., Liu, X., Zhang, Y., Christie, P., Fangmeier, A., & Zhang, F. (2011). Nitrogen enrichment enhances the dominance of grasses over forbs in a temperate steppe ecosystem. *Biogeosciences*, 8, 2341–2350. https://doi.org/10.5194/bg-8-2341-2011
- Stoof, C. R., Richards, B. K., Woodbury, P. B., Fabio, E. S., Brumbach, A. R., Cherney, J., Das, S., Geohring, L., Hansen, J., Hornesky, J., Mayton, H., Mason, C., Ruestow, G., Smart, L. B., Volk, T. A., & Steenhuis, T. S. (2015). Untapped potential: Opportunities and challenges for sustainable bioenergy production from marginal lands in the Northeast USA. *BioEnergy Research*, *8*, 482–501. https://doi.org/ 10.1007/s12155-014-9515-8
- Sykes, V. R., Allen, F. L., Mielenz, J. R., Stewart, C. N., Windham, M. T., Hamilton, C. Y., Rodriguez, Jr., M., & Yee, K. L. (2016). Reduction of ethanol yield from switchgrass infected with rust caused by *Puccinia emaculata*. *BioEnergy Research*, *9*, 239–247. https://doi.org/10.1007/ s12155-015-9680-4
- Tilman, D., Hill, J., & Lehman, C. (2006). Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science*, 314, 1598–1600. https://doi.org/10.1126/science.1133306
- Valentine, J., Clifton-Brown, J., Hastings, A., Robson, P., Allison, G., & Smith, P. (2012). Food vs. fuel: The use of land for lignocellulosic 'next generation' energy crops that minimize competition with primary food production. *GCB Bioenergy*, 4, 1–19. https://doi.org/10. 1111/j.1757-1707.2011.01111.x
- Venuto, B. C., & Daniel, J. A. (2010). Biomass feedstock harvest from Conservation Reserve Program land in northwestern Oklahoma. *Crop Science*, 50, 737–743. https://doi.org/10.2135/cropsci2008.11. 0641
- 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
- Werling, B. P., Dickson, T. L., Isaacs, R., Gaines, H., Gratton, C., Gross, K. L., Liere, H., Malmstrom, C. M., Meehan, T. D., Ruan, L., Robertson, B. A., Robertson, G. P., Schmidt, T. M., Schrotenboer, A. C., Teal, T. K., Wilson, J. K., & Landis, D. A. (2014). Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proceedings of the National Academy* of Sciences, 111, 1652–1657. https://doi.org/10.1073/pnas.130949 2111
- Williams, M. A., & Feest, A. (2019). The effect of Miscanthus cultivation on the biodiversity of ground beetles (Coleoptera:Carabidae), spiders and harvestmen (Arachnida:Araneae and Opiliones). Agricultural Sciences, 10, 903–917. https://doi.org/10.4236/as.2019.107069

Yang, J., & Udvardi, M. (2018). Senescence and nitrogen use efficiency in perennial grasses for forage and biofuel production. *Journal* of Experimental Botany, 69, 855–865. https://doi.org/10.1093/jxb/ erx241

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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	Monthly total precipitation (mm)*									
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average	
Jan	90	41	30	45	75	45	44	48	43	
Feb	43	30	16	35	64	61	61	22	36	
Mar	32	29	12	120	68	20	46	60	45	
Apr	147	144	57	54	133	89	81	87	79	
May [‡]	92	73	103	104	65	99	116	123	80	
Jun ⁺	33	66	80	70	123	30	100	76	82	
Jul [‡]	29	68	37	77	55	70	83	41	70	
Aug ⁺	44	54	83	95	69	53	52	63	73	
Sep [‡]	46	82	92	74	19	56	123	42	66	
Oct [‡]	87	81	51	74	172	155	126	74	78	
Nov	80	77	62	41	63	42	52	46	56	
Dec	56	36	91	57	38	55	83	51	45	
\mathbf{GS}^{\dagger}	331	425	447	495	502	463	601	419	448	
Total	781	783	716	846	943	776	968	734	751	

Table S1. Monthly total precipitation during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Michigan Central.

*Precipitation data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Houghton Lake Roscommon County Airport, Michigan (USW00094814) located ~42 km away from the study site.

[†]Growing season

	Monthly total precipitation (mm)*									
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average	
Jan	51	48	20	37	44	47	68	60	45	
Feb	70	38	19	29	39	46	111	20	37	
Mar	50	64	32	64	54	20	40	99	45	
Apr	83	88	58	69	111	40	93	65	65	
May [‡]	44	74	133	88	104	77	-	45	80	
Jun [‡]	88	109	97	94	221	98	64	107	87	
Jul [‡]	136	58	53	112	100	98	43	163	89	
Aug [‡]	65	143	77	90	142	115	95	105	82	
Sep ⁺	49	118	92	125	73	91	202	98	93	
Oct [‡]	74	118	61	95	90	167	158	94	89	
Nov	119	94	95	60	57	76	56	82	72	
Dec	53	62	133	66	65	42	131	25	60	
\mathbf{GS}^{*}	456	620	514	604	731	647	-	612	520	
Total	883	1014	872	930	1100	919	-	964	843	

Table S2. Monthly total precipitation during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Michigan North.

*Precipitation data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Gladstone, Michigan (USC00203270) located ~14 km away from the study site. [†]Growing season

	Monthly total precipitation (mm)*									
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average	
Jan	59	37	49	39	95	47	57	107	53	
Feb	37	51	43	43	39	143	69	46	40	
Mar	2	43	16	113	134	50	73	79	48	
Apr	-	33	50	69	106	72	108	83	82	
May [‡]	42	94	167	107	86	159	123	173	100	
Jun [‡]	106	138	270	18	67	66	212	74	93	
Jul [‡]	131	110	134	94	75	21	60	32	86	
Aug ⁺	147	58	77	180	51	126	44	81	89	
Sep [‡]	27	70	64	94	11	50	129	103	78	
Oct [‡]	116	131	60	77	275	111	154	85	93	
Nov	60	86	59	47	112	71	45	55	65	
Dec	41	29	84	66	33	55	82	69	47	
\mathbf{GS}^{*}	570	601	772	572	565	534	722	548	540	
Total	-	882	1074	949	1083	972	1156	988	875	

Table S3. Monthly total precipitation during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Michigan South.

*Precipitation data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Battle Creek, Michigan (USC00200552) located ~20 km away from the study site. [†]Growing season

	Monthly total precipitation (mm)*									
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average	
Jan	31	18	8	24	47	24	48	22	29	
Feb	29	21	6	17	27	30	55	20	25	
Mar	43	25	10	150	64	23	47	91	47	
Apr	99	141	93	38	121	87	101	55	91	
May ⁺	126	54	142	64	98	161	134	98	106	
Jun [‡]	135	81	108	92	203	139	127	159	126	
Jul [‡]	48	44	46	99	104	101	182	64	105	
Aug ⁺	49	165	80	140	108	181	73	71	102	
Sep ⁺	52	67	122	299	63	146	132	50	84	
Oct [‡]	60	74	81	55	111	110	111	64	69	
Nov	78	40	66	52	16	56	56	50	50	
Dec	26	25	125	54	17	38	73	9	36	
\mathbf{GS}^{*}	470	484	579	750	686	837	759	506	592	
Total	777	754	888	1085	979	1096	1139	754	870	

Table S4. Monthly total precipitation during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Wisconsin Central.

*Precipitation data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather stations at Hancock Experimental Farm, Wisconsin (USC00473405) located ~0.2 km away from the study site.

[†]Growing season

	Monthly total precipitation (mm)*										
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average		
Jan	31	35	18	18	47	30	22	43	31		
Feb	39	34	8	18	30	30	113	9	29		
Mar	49	22	17	88	35	49	25	79	46		
Apr	113	109	82	80	157	59	90	73	75		
May [‡]	114	76	106	78	149	45	136	41	96		
Jun [‡]	140	203	87	178	188	201	109	131	115		
Jul [‡]	73	122	106	100	59	95	126	223	111		
Aug ⁺	138	171	91	207	120	54	86	56	89		
Sep [‡]	69	184	89	150	54	135	147	131	105		
Oct [‡]	114	108	94	132	124	163	80	70	86		
Nov	53	89	68	54	28	51	40	58	49		
Dec	43	45	119	49	41	37	75	15	40		
\mathbf{GS}^{\dagger}	647	865	570	845	694	693.0	686	651	601		
Total	975	1200	882	1153	1033	949.4	1051	928	873		

Table S5. Monthly total precipitation during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Wisconsin North.

*Precipitation data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Rhinelander, Wisconsin (USC00477113) located ~20 km away from the study site. ⁺Growing season

	Monthly total snowfall (mm)*									
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average	
Jan	320	392	301	384	515	147	580	366	417	
Feb	464	305	278	267	101	231	650	297	345	
Mar	148	155	40	333	246	172	174	56	211	
Apr	77	89	25	302	0	359	251	25	112	
May [‡]	23	0	0	0	0	0	0	46	2	
Jun [‡]	0	0	0	0	0	0	0	0	0	
Jul [‡]	0	0	0	0	0	0	0	0	0	
Aug ⁺	0	0	0	0	0	0	0	0	0	
Sep [‡]	0	0	0	0	0	0	0	0	0	
Oct [‡]	0	0	0	51	0	0	112	0	13	
Nov	96	328	56	229	138	103	198	106	190	
Dec	535	153	144	795	372	192	297	498	383	
NGS [¥]	-	1572	1125	1486	1937	1419	1950	1397	-	
Total	1663	1422	844	2361	1372	1204	2262	1394	1674	

Table S6. Monthly total snowfall during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Michigan Central.

*Snowfall data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Houghton Lake Roscommon County Airport, Michigan (USW00094814) located ~42 km away from the study site.

[†]Growing season

	Monthly total snowfall (mm)*										
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average		
Jan	440	606	191	266	268	568	513	608	818		
Feb	504	393	233	330	282	302	1016	216	729		
Mar	368	599	152	138	151	120	134	122	295		
Apr	221	186	48	371	0	513	97	155	325		
May ⁺	0	0	0	0	0	0	0	0	28		
Jun [‡]	0	0	0	0	0	0	0	0	0		
Jul [‡]	0	0	0	0	0	0	0	0	0		
Aug ⁺	0	0	0	0	0	0	0	0	0		
Sep [‡]	0	0	0	0	0	0	0	0	0		
Oct [‡]	0	0	0	0	0	0	25	0	33		
Nov	0	0	5	0	0	181	170	48	460		
Dec	480	317	163	536	261	217	844	213	673		
NGS [¥]	-	2264	941	1273	1237	1764	2158	2140	-		
Total	2013	2101	792	1641	962	1901	2799	1362	3360		

Table S7. Monthly total snowfall during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Michigan North.

*Snowfall data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather stations at Gladstone (USC00203270) and Big Bay (USC00200770), Michigan located ~14 km and ~125 km away from the study site, respectively.

[†]Growing season

	Monthly total snowfall (mm)*									
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average	
Jan	345	988	506	396	371	410	632	276	460	
Feb	847	710	659	507	48	600	521	629	396	
Mar	98	335	74	315	105	123	97	64	152	
Apr	-	28	3	181	84	127	55	91	53	
May [‡]	0	0	0	0	0	0	0	0	0	
Jun [‡]	0	0	0	0	0	0	0	0	0	
Jul [‡]	0	0	0	0	0	0	0	0	0	
Aug ⁺	0	0	0	0	0	0	0	0	0	
Sep [‡]	0	0	0	0	0	0	0	0	0	
Oct [‡]	13	0	0	0	0	0	13	0	13	
Nov	36	533	254	13	0	613	153	27	150	
Dec	601	29	95	892	899	67	258	113	417	
NGS [¥]	-	2711	1804	1748	1513	2159	1985	1484	-	
Total	-	2623	1591	2304	1507	1940	1729	1200	1641	

Table S8. Monthly total snowfall during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Michigan South.

*Snowfall data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Battle Creek, Michigan (USC00200552) located ~20 km away from the study site. [†]Growing season

	Monthly total snowfall (mm)*									
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average	
Jan	399	-	180	129	199	164	404	200	325	
Feb	426	181	152	269	122	145	749	247	208	
Mar	298	-	54	240	107	104	211	97	211	
Apr	75	76	0	74	0	587	79	38	69	
May [‡]	0	0	0	0	0	0	0	0	0	
Jun [‡]	0	0	0	0	0	0	0	0	0	
Jul [‡]	0	0	0	0	0	0	0	0	0	
Aug ⁺	0	0	0	0	0	0	0	0	0	
Sep [‡]	0	0	0	0	0	0	0	0	0	
Oct [‡]	0	0	0	0	0	41	0	23	8	
Nov	13	153	0	3	25	33	125	49	84	
Dec	524	25	107	526	208	153	207	131	190	
NGS [¥]	-	794	564	819	957	1233	1670	914	-	
Total	1735	435	493	1241	661	1227	1775	785	1095	

Table S9. Monthly total snowfall during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Wisconsin Central.

*Snowfall data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather stations at Hancock Experimental Farm, Wisconsin (USC00473405) located ~0.2 km away from the study site.

[†]Growing season

	Monthly total snowfall (mm)*										
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average		
Jan	275	533	211	156	383	290	242	510	305		
Feb	494	376	121	208	177	326	1321	114	312		
Mar	300	316	132	198	86	384	127	72	190		
Apr	211	576	269	241	228	751	203	257	188		
May [‡]	0	0	0	0	0	0	3	0	2		
Jun [‡]	0	0	0	0	0	0	0	0	0		
Jul [‡]	0	0	0	0	0	0	0	0	0		
Aug ⁺	0	0	0	0	0	0	0	0	0		
Sep [‡]	0	0	0	0	0	0	0	0	0		
Oct [‡]	13	28	0	0	8	26	28	163	28		
Nov	109	675	51	161	247	294	349	41	178		
Dec	520	452	210	416	280	227	556	199	376		
NGS [¥]	-	2443	1860	1064	1451	2286	2440	1886	-		
Total	1922	2956	994	1380	1409	2298	2829	1356	1580		

Table S10. Monthly total snowfall during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Wisconsin North.

*Snowfall data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Rhinelander, Wisconsin (USC00477113) located ~20 km away from the study site. [†]Growing season

	Mean monthly temperature (°C)*										
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average		
Jan	-5.2	-10.9	-9.3	-5.5	-4.3	-6.7	-9.9	-3.0	-7.2		
Feb	-6.7	-11.8	-14.5	-4.6	-2.1	-4.8	-7.4	-5.7	-6.5		
Mar	-2.5	-6.9	-2.6	1.6	-1.4	-1.8	-3.8	0.9	-1.3		
Apr	4.1	5.0	5.5	4.2	8.6	1.2	5.7	4.3	5.7		
May [‡]	14.2	12.7	13.9	13.2	11.9	15.9	10.9	11.6	12.6		
Jun [‡]	17.7	18.2	16.4	17.1	18.5	18.2	16.5	18.5	17.7		
Jul [‡]	20.0	17.2	19.4	20.7	19.8	21.1	20.9	22.2	19.9		
Aug ⁺	18.3	18.3	19.2	21.1	17.6	21.0	17.8	19.7	18.8		
Sep ⁺	14.0	13.8	17.2	16.8	16.3	16.3	15.8	13.8	14.6		
Oct [‡]	8.7	8.1	8.5	10.1	10.9	7.6	7.3	5.9	8.2		
Nov	0.7	-0.9	4.8	5.2	1.0	-1.2	-1.4	4.9	1.9		
Dec	-7.5	-2.7	1.9	-4.0	-6.8	-2.4	-2.2	-2.3	-3.6		
\mathbf{GS}^{*}	15.5	14.7	15.8	16.5	15.8	16.7	14.9	15.3	15.3		
Total	6.3	5.0	6.7	8.0	7.5	7.0	5.8	7.6	6.7		

Table S11. Mean monthly temperature during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Michigan Central.

*Temperature data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Houghton Lake Roscommon County Airport, Michigan (USW00094814) located ~42 km away from the study site.

[†]Growing season

	Mean monthly temperature (°C)*										
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average		
Jan	-6.8	-13.2	-9.7	-6.6	-5.5	-7.6	-9.8	-5.0	-8.2		
Feb	-7.7	-12.2	-13.9	-5.0	-3.8	-8.7	-10.2	-5.9	-7.2		
Mar	-4.1	-8.2	-3.2	-0.8	-3.1	-4.2	-4.1	-1.5	-2.9		
Apr	1.0	1.3	3.8	1.8	4.4	-0.7	2.7	1.2	3.0		
May [‡]	7.7	9.8	11.8	10.1	8.0	12.5	7.3	9.5	9.9		
Jun [‡]	14.0	14.6	13.6	15.3	15.8	14.8	13.7	17.0	15.4		
Jul [‡]	18.0	18.0	19.1	19.3	17.6	19.6	20.1	20.9	18.7		
Aug ⁺	19.2	16.2	-	19.5	16.0	18.3	17.1	18.6	18.4		
Sep ⁺	14.2	14.1	17.8	15.9	15.9	14.9	15.2	13.3	14.4		
Oct [‡]	8.2	6.9	7.8	9.4	10.2	4.9	7.4	4.5	7.6		
Nov	0.0	-2.6	4.1	5.7	-0.6	-2.5	-2.0	3.5	1.0		
Dec	-9.1	-4.2	-0.2	-5.1	-7.6	-2.9	-4.6	-3.4	-4.8		
\mathbf{GS}^{*}	13.6	13.3	-	14.9	13.9	14.2	13.5	14.0	14.1		
Total	4.6	3.4	-	6.6	5.6	4.9	4.4	6.0	5.4		

Table S12. Mean monthly temperature during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Michigan North.

*Temperature data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Big Bay, Michigan (USC00200770) located 125 km away from the study site. [†]Growing season

	Mean monthly temperature (°C)*										
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average		
Jan	-3.1	-9.3	-5.7	-3.2	-1.9	-4.0	-5.2	-0.6	-4.0		
Feb	-4.1	-7.9	-10.0	-1.5	2.2	-1.6	-2.2	-2.2	-2.8		
Mar	-0.2	-2.1	1.1	6.2	2.5	1.1	1.4	4.4	2.6		
Apr	-	8.9	9.9	8.8	11.6	4.4	9.6	8.1	9.1		
May [‡]	18.1	15.2	17.2	15.2	13.9	18.7	14.5	14.0	15.4		
Jun [‡]	19.8	20.2	19.4	20.2	20.1	20.6	19.1	20.9	20.2		
Jul [‡]	22.2	18.6	19.9	22.7	21.6	21.9	23.7	23.5	21.9		
Aug ⁺	19.2	20.0	19.9	22.6	19.1	21.8	21.2	21.6	21.1		
Sep ⁺	17.3	15.8	18.1	19.0	18.5	-	19.1	15.7	17.2		
Oct [‡]	11.2	10.6	11.3	13.6	13.1	-	10.5	10.6	10.9		
Nov	2.9	1.2	7.3	7.6	3.4	1.3	1.4	8.0	4.4		
Dec	-3.2	0.3	4.5	-2.6	-4.1	0.1	1.1	0.0	-1.3		
\mathbf{GS}^{*}	18.0	16.7	17.6	18.9	17.7	-	18.0	17.7	17.8		
Total	-	7.6	9.4	10.7	10.0	-	9.5	10.3	9.6		

Table S13. Mean monthly temperature during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Michigan South.

*Temperature data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Battle Creek, Michigan (USC00200552) located ~20 km away from the study site. [†]Growing season

	Mean monthly temperature (°C)*										
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average		
Jan	-7.4	-13.1	-8.0	-9.0	-6.6	-8.3	-9.9	-5.3	-8.9		
Feb	-8.3	-	-12.8	-5.2	-2.3	-7.7	-9.1	-7.3	-6.9		
Mar	-4.7	-	0.4	3.1	-0.9	-0.4	-2.7	1.6	-0.4		
Apr	3.4	5.3	7.9	6.5	8.6	1.2	6.4	5.1	6.7		
May [‡]	14.2	13.3	15.1	13.5	12.3	17.5	11.4	12.6	13.7		
Jun [‡]	18.0	20.5	18.2	18.7	19.2	19.7	18.2	19.5	19.1		
Jul [‡]	21.4	18.8	20.6	21.5	20.8	21.8	22.1	22.8	21.2		
Aug ⁺	20.3	20.3	19.9	21.4	18.6	21.0	18.9	21.0	20.2		
Sep [‡]	16.8	15.5	18.8	17.5	17.4	16.9	16.7	14.9	15.8		
Oct ⁺	8.3	7.9	9.7	10.9	9.6	7.1	7.7	6.0	8.8		
Nov	0.0	-3.5	4.8	5.6	0.4	-2.1	-1.8	4.4	1.2		
Dec	-9.9	-3.9	0.6	-6.4	-7.2	-3.4	-4.0	-3.7	-5.7		
\mathbf{GS}^{*}	16.5	16.0	17.0	17.2	16.3	17.3	15.8	16.1	16.5		
Total	6.0	-	7.9	8.2	7.5	6.9	6.2	7.6	7.1		

Table S14. Mean monthly temperature during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Wisconsin Central.

*Temperature data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather stations at Hancock Experimental Farm, Wisconsin (USC00473405) located ~0.2 km away from the study site.

[†]Growing season

	Mean monthly temperature (°C)*										
Month	2013	2014	2015	2016	2017	2018	2019	2020	30-year average		
Jan	-11.1	-16.7	-12.2	-10.5	-8.9	-11.7	-12.8	-7.9	-11.8		
Feb	-11.4	-15.6	-16.6	-7.7	-5.4	-11.6	-13.4	-9.8	-10.1		
Mar	-7.2	-9.2	-3.1	0.4	-4.1	-4.3	-6.3	-1.3	-3.7		
Apr	0.6	1.2	4.7	4.0	5.7	-1.9	3.2	2.1	3.7		
May [‡]	11.5	11.3	12.2	11.9	9.8	15.8	9.1	10.9	11.4		
Jun [‡]	15.6	17.6	15.6	17.4	17.1	17.6	16.3	17.3	16.7		
Jul [‡]	19.1	16.9	18.8	19.7	18.9	19.5	20.3	20.5	19.1		
Aug ⁺	17.4	17.2	17.1	19.6	16.2	18.9	16.9	18.3	17.9		
Sep ⁺	13.6	12.6	16.6	15.2	15.0	14.8	14.6	12.1	13.5		
Oct [‡]	6.3	6.2	7.1	8.4	8.3	4.1	5.7	2.9	6.3		
Nov	-2.5	-5.9	2.3	3.6	-2.2	-4.7	-3.9	1.9	-1.4		
Dec	-13.6	-7.1	-1.9	-8.2	-10.7	-5.4	-6.9	-6.2	-8.2		
\mathbf{GS}^{*}	13.9	13.6	14.6	15.4	14.2	15.1	13.8	13.7	14.2		
Total	3.2	2.4	5.0	6.2	5.0	4.3	3.6	5.1	4.5		

Table S15. Mean monthly temperature during the study period (2013-2020) and 30-year monthly averages (1991-2020) at Wisconsin North.

*Temperature data were obtained from the National Oceanic & Atmospheric Administration (NOAA) weather station at Rhinelander, Wisconsin (USC00477113) located ~20 km away from the study site. [†]Growing season

	Mean monthly volumetric water content (cm ⁻³ /cm ⁻³)*											
	Michig	an North	Michig	an South	Wise Ce	consin ntral	Wise	consin orth				
Month	10 cm depth	25 cm depth	10 cm depth	25 cm depth	10 cm depth	25 cm depth	10 cm depth	25 cm depth				
Jan	0.21	0.28	0.30	0.34	0.02	0.03	0.16	0.17				
Feb	0.17	0.26	0.30	0.34	0.02	0.03	0.16	0.15				
Mar	0.23	0.30	0.30	0.35	0.04	0.05	0.15	0.15				
Apr	0.32	0.35	0.31	0.35	0.04	0.05	0.22	0.21				
May [‡]	0.30	0.33	0.29	0.35	0.05	0.06	0.24	0.23				
Jun [‡]	0.28	0.30	0.23	0.31	0.05	0.07	0.21	0.21				
Jul [‡]	0.23	0.24	0.16	0.25	0.04	0.05	0.14	0.13				
Aug [‡]	0.20	0.20	0.18	0.24	0.05	0.06	0.14	0.13				
Sep ⁺	0.26	0.27	0.22	0.29	0.06	0.07	0.18	0.18				
Oct [‡]	0.29	0.30	0.29	0.33	0.07	0.08	0.23	0.23				
Nov	0.30	0.31	0.31	0.35	0.06	0.08	0.22	0.23				
Dec	0.25	0.30	0.32	0.34	0.03	0.05	0.19	0.20				
\mathbf{GS}^{*}	0.26	0.27	0.23	0.29	0.05	0.06	0.19	0.18				
Total	0.25	0.29	0.27	0.32	0.04	0.06	0.19	0.18				

Table S16. Mean monthly volumetric water content at each marginal land site (Michigan North, Michigan South, Wisconsin Central, and Wisconsin North).

*Volumetric water content data were obtained from the Great Lakes Bioenergy Research Center's Sustainability Data Catalog (<u>https://data.sustainability.glbrc.org</u>).

[†]Growing season

Note: Volumetric water content data were not available from Michigan Central. Monthly mean values were averaged across study years and the data availability differed among sites [Michigan North (Jan-Jun, n=4; Jul-Dec, n=5), Michigan South (Jan-Nov, n=5; Dec, n=6), Wisconsin Central (Jan-Nov, n=3; Dec, n=4), and Wisconsin North (Jan-Jun, n=4; Jul-Dec, n=5)].

Site	Cropping system	2012	2013	2014	2015	2016	2017	2018	2019
	Switchgrass	4.68 L ha ⁻¹ Glyphosate, 1.17 L ha ⁻¹ 2,4-D ester	n/a	2.80 kg ha ⁻¹ Glyphosate, 0.56 kg ha ⁻¹ Quinclorac 75 DF, 0.56 kg ha ⁻¹ 2,4-D ester	2.24 kg ha ⁻¹ Glyphosate	n/a	n/a	n/a	n/a
Michigan Central	Miscanthus	4.68 L ha ⁻¹ Glyphosate, 1.17 L ha ⁻¹ 2,4-D ester	2.34 L ha ⁻¹ Glyphosate, 0.56 kg ha ⁻¹ Quinclorac, 1.17 L ha ⁻¹ 2,4-D ester	2.80 kg ha ⁻¹ Glyphosate, 0.56 kg ha ⁻¹ Quinclorac 75 DF, 0.56 kg ha ⁻¹ 2,4-D ester	2.24 kg ha ⁻¹ Glyphosate, 0.56 kg ha ⁻¹ Quinclorac 75 DF, 1.12 kg ha ⁻¹ 2,4-D ester	n/a	n/a	n/a	n/a
	Native grasses	4.68 L ha ⁻¹ Glyphosate, 1.17 L ha ⁻¹ 2,4-D ester	4.68 L ha ⁻¹ Glyphosate	2.80 kg ha ⁻¹ Glyphosate, 0.56 kg ha ⁻¹ Quinclorac 75 DF, 0.56 kg ha ⁻¹ 2,4-D ester	n/a	n/a	1.5% (v/v) Glyphosate	n/a	n/a

Table S17: Pesticides applied before and after the establishment of crops in the six bioenergy cropping systems at each marginal land site during the study period. Blue (lighter) font denote pesticides that were applied before crop establishment; none were applied in 2020.

	Hybrid poplar	4.68 L ha ⁻¹ Glyphosate, 1.17 L ha ⁻¹ 2,4-D ester	2.34 L ha ⁻¹ Glyphosate, 0.56 kg ha ⁻¹ Quinclorac, 1.17 L ha ⁻¹ 2,4-D ester	0.39 kg ha ⁻¹ Scepter® 70 DF, 0.84 kg ha ⁻¹ Assure® II	2.24 kg ha ⁻¹ Glyphosate, 0.39 kg ha ⁻¹ Scepter® 70 DF, 7.01 L ha ⁻¹ Prowl® H2O, 0.84 kg ha ⁻¹ Assure® II	n/a	1.5% (v/v) Glyphosate, 0.4% (v/v) Assure® II	n/a	2.24 kg ha ⁻¹ Glyphosate, 0.39 kg ha ⁻¹ Scepter®, 7.01 L ha ⁻¹ Prowl® H2O
	Early successional vegetation	4.68 L ha ⁻¹ Glyphosate, 1.17 L ha ⁻¹ 2,4-D ester	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	Restored prairie	4.68 L ha ⁻¹ Glyphosate, 1.17 L ha ⁻¹ 2,4-D ester	4.68 L ha ⁻¹ Glyphosate	n/a	n/a	n/a	n/a	n/a	n/a
n South	Switchgrass	4.68 L ha ⁻¹ Glyphosat,2. 34 L ha ⁻¹ 2,4-D ester	2.34 L ha ⁻¹ Glyphosate, 0.56 kg ha ⁻¹ Quinclorac 75 DF, 0.58 L ha ⁻¹ 2,4-D ester	0.56 kg ha ⁻¹ Quinclorac 75 DF, 0.56 kg ha ⁻¹ 2,4-D ester	n/a	n/a	n/a	n/a	n/a
Michiga	Miscanthus	4.68 L ha ⁻¹ Glyphosat,2. 34 L ha ⁻¹ 2,4-D ester	Glyphosate (unknown), 4.09 L ha-1 2,4-D ester, 1.02 kg ha ⁻¹ Quinclorac 75 DF,	2.80 kg ha ⁻¹ Glyphosate, 0.56 kg ha ⁻¹ Quinclorac 75 DF, 0.56 kg ha ⁻¹ 2,4-D ester	0.56 kg ha ⁻¹ Quinclorac 75 DF, 1.12 kg ha ⁻¹ 2,4-D ester	n/a	n/a	n/a	n/a

		4.68 L ha ⁻¹ Atrazine®						
Native grasses	4.68 L ha ⁻¹ Glyphosat,2. 34 L ha ⁻¹ 2,4-D ester	2.34 L ha ⁻¹ Glyphosate, 0.56 kg ha ⁻¹ Quinclorac 75 DF, 0.58 L ha ⁻¹ 2,4-D ester	n/a	n/a	n/a	2.24 kg ha ⁻¹ 2,4-D ester	n/a	n/a
Hybrid poplar	4.68 L ha ⁻¹ Glyphosat,2. 34 L ha ⁻¹ 2,4-D ester	Glyphosate (unknown), 0.39 kg ha ⁻¹ Scepter® 70 DF, 7.01 L ha ⁻¹ Prowl® H2O	Glyphosate (unknown), 0.39 kg ha ⁻¹ Scepter® 70 DF, 0.84 kg ha ⁻¹ Assure® II	n/a	n/a	n/a	n/a	3.36 kg ha ⁻¹ Glyphosate (generic), 0.39 kg ha ⁻¹ Scepter®, 7.01 L ha ⁻¹ Prowl® H2O
Early successional vegetation	4.68 L ha ⁻¹ Glyphosat,2. 34 L ha ⁻¹ 2,4-D ester	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Restored prairie	4.68 L ha ⁻¹ Glyphosat,2. 34 L ha ⁻¹ 2,4-D ester	2.34 L ha ⁻¹ Glyphosate	n/a	n/a	n/a	n/a	n/a	n/a

	Switchgrass	4.68 L ha ⁻¹ Glyphosate, 2.34 L ha ⁻¹ 2,4-D ester	4.68 L ha ⁻¹ Glyphosate	4.68 L ha ⁻¹ Glyphosate, 2.34 L ha ⁻¹ 2,4-D ester	n/a	n/a	n/a	n/a	n/a
	Miscanthus	4.68 L ha ⁻¹ Glyphosate, 2.34 L ha ⁻¹ 2,4-D ester	4.68 L ha ⁻¹ Glyphosate, 0.46 kg ha ⁻¹ Quinclorac 75 DF, 2.80 kg ha ⁻¹ Atrazine	4.68 L ha ⁻¹ Glyphosate, 2.34 L ha ⁻¹ 2,4-D ester	1.12 kg ha ⁻¹ Quinclorac 75 DF, 2.34 L ha ⁻¹ 2,4-D ester	n/a	2.24 kg ha ⁻¹ Glyphosate	n/a	n/a
	Native grasses	4.68 L ha ⁻¹ Glyphosate, 2.34 L ha ⁻¹ 2,4-D ester	4.68 L ha ⁻¹ Glyphosate	n/a	n/a	n/a	n/a	n/a	n/a
	Hybrid poplar	4.68 L ha ⁻¹ Glyphosate, 2.34 L ha ⁻¹ 2,4-D ester	4.68 L ha ⁻¹ Glyphosate, 0.39 kg ha ⁻¹ Scepter® 70 DF, 7.01 L ha ⁻¹ Pendulum® aquacap	0.27 kg ha ⁻¹ Scepter® 70 DF, 4.68 L ha ⁻¹ Pendulum® aquacap	n/a	n/a	n/a	n/a	2.24 kg ha ⁻¹ Glyphosate, 0.39 kg ha ⁻¹ Scepter®, 7.01 L ha ⁻¹ Prowl® H2O
Michigan North	Early successional vegetation	4.68 L ha ⁻¹ Glyphosate, 2.34 L ha ⁻¹ 2,4-D ester	4.68 L ha ⁻¹ Glyphosate	n/a	n/a	n/a	n/a	n/a	n/a

	Restored prairie	4.68 L ha ⁻¹ Glyphosate, 2.34 L ha ⁻¹ 2,4-D ester	4.68 L ha ⁻¹ Glyphosate	n/a	n/a	n/a	n/a	n/a	n/a
entral	Switchgrass		3.36 kg ha ⁻¹ Roundup® Power Max, 0.56 kg ha ⁻¹ Quinclorac SPC 75 DF, 1.17 L ha ⁻¹ 2,4-D LV4 ester	2.24 kg ha ⁻¹ Roundup® Power Max	n/a	1.54 kg ha ⁻¹ Roundup® Power Max, 2.45 kg ha ⁻¹ Prowl® H2O, 1.12 kg ha ⁻¹ Quinclorac SPC 75 DF, 2.34 L ha ⁻¹ 2,4-D LV4 ester	1.54 kg ha ⁻¹ Roundup® Weather Max, 3.36 kg ha ⁻¹ Prowl® H2O, 3.51 L ha ⁻¹ 2,4-D LV4 ester	n/a	n/a
Wisconsin C	Miscanthus	2.34 L ha ⁻¹ Roundup® Power Max, 2.34 L ha ⁻¹ 2,4-D LV4 ester	1.54 kg ha ⁻¹ Roundup® Power Max, 0.56 kg ha ⁻¹ Quinclorac SPC 75 DF, 1.17 L ha ⁻¹ 2,4-D LV4 ester, 0.035 kg ha ⁻¹ Clarity®, 3.51 L ha ⁻¹ Prowl® H2O	1.54 kg ha ⁻¹ Roundup® Power Max, 0.84 kg ha ⁻¹ Quinclorac SPC 75 DF, 3.51 L ha ⁻¹ 2,4-D LV4 ester	2.34 L ha ⁻¹ Roundup® Power Max, 3.51 L ha ⁻¹ 2,4-D LV4 ester	1.49 kg ha ⁻¹ Quinclorac SPC 75 DF, 0.56 kg ha ⁻¹ 2,4-D LV4 ester, 2.34 L ha ⁻¹ 2,4-D LV4 ester	 1.54 kg ha⁻¹ Roundup® Weather Max, 2.24 kg ha⁻¹ 2,4-D LV4 ester, 3.51 L ha⁻¹ 2,4-D LV4 ester 	n/a	n/a

Native grasses	2.34 L ha ⁻¹ Roundup® Power Max, 2.34 L ha ⁻¹ 2,4-D LV4 ester	3.36 kg ha ⁻¹ Roundup® Power Max	3.51 L ha ⁻¹ 2,4-D LV4 ester	3.51 L ha ⁻¹ 2,4-D LV4 ester	2.24 kg ha ⁻¹ 2,4-D LV4 ester, 2.34 L ha ⁻¹ pints 2,4-D LV4 ester	1.54 kg ha ⁻¹ Roundup® Weather Max, 3.36 kg ha ⁻¹ Prowl® H2O, 2.24 kg ha ⁻¹ 2,4-D LV4 ester, 3.51 L ha ⁻¹ 2,4-D LV4 ester	n/a	n/a
Hybrid poplar	2.34 L ha ⁻¹ Roundup® Power Max, 2.34 L ha ⁻¹ 2,4-D LV4 ester	1.54 kg ha ⁻¹ Roundup® Power Max, 0.39 kg ha ⁻¹ Scepter®, 7.01 L ha ⁻¹ Pendulum® Aqua Cap	1.54 kg ha ⁻¹ Roundup® Power Max, 0.39 kg ha ⁻¹ Scepter®, 7.01 L ha ⁻¹ Pendulum® Aqua Cap	7.01 L ha ⁻¹ Pendulum® Aqua Cap	0.84 kg ha ⁻¹ Fusilade II	 1.54 kg ha⁻¹ Roundup® Weather Max, 2.24 kg ha⁻¹ 2,4-D LV4 ester, 3.51 L ha⁻¹ Fusilade II 	n/a	2.24 kg ha ⁻¹ Glyphosate, 0.39 kg ha ⁻¹ Scepter®, 7.01 L ha ⁻¹ Prowl® H2O
Early successional vegetation	2.34 L ha ⁻¹ Roundup® Power Max, 2.34 L ha ⁻¹ 2,4-D LV4 ester	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Restored prairie	2.34 L ha ⁻¹ Roundup® Power Max, 2.34 L ha ⁻¹ 2,4-D LV4 ester	3.36 kg ha ⁻¹ Roundup® Power Max	n/a	n/a	n/a	n/a	n/a	n/a

	Switchgrass	n/a	2.24 kg ha ⁻¹ Roundup® Power Max, 0.84 kg ha ⁻¹ 2,4-D LV4 ester, 0.56 kg ha ⁻¹ Quinclorac SPC 75 DF, 1.17 L ha ⁻¹ 2,4-D LV4 ester	2.34 L ha ⁻¹ 2,4-D LV4 ester	n/a	1.54 kg ha ⁻¹ Roundup® Power Max, 2.45 kg ha ⁻¹ Prowl® H2O	n/a	n/a	n/a
Wisconsin North	Miscanthus	n/a	1.54 kg ha ⁻¹ Roundup® Power Max, 0.56 kg ha ⁻¹ Quinclorac SPC 75 DF, 1.17 L ha ⁻¹ 2,4-D LV4 ester, 0.035 kg ha ⁻¹ Clarity®, 3.51 L ha ⁻¹ Prowl® H2O	0.84 kg ha ⁻¹ Quinclorac SPC 75 DF, 2.34 L ha ⁻¹ 2,4-D LV4 ester	2.34 L ha ⁻¹ Roundup® Power Max, 3.51 L ha ⁻¹ 2,4-D LV4 ester	1.54 kg ha ⁻¹ Roundup® Power Max, 0.56 kg ha ⁻¹ Quinclorac SPC 75 DF, 1.12 kg ha ⁻¹ 2,4-D LV4 ester, 2.45 kg ha ⁻¹ Prowl® H2O	1.54 kg ha ⁻¹ Roundup® Weather Max, 1.12 kg ha ⁻¹ Quinclorac SPC 75 DF, 3.36 kg ha ⁻¹ Prowl® H2O	n/a	n/a
	Native grasses	n/a	2.24 kg ha ⁻¹ Roundup® Power Max, 0.84 kg ha ⁻¹ 2,4-D LV4 ester, 0.56 kg ha ⁻¹ Quinclorac SPC 75 DF,	n/a	3.51 L ha ⁻¹ 2,4-D LV4 ester	0.56 kg ha ⁻¹ Quinclorac SPC 75 DF, 1.12 kg ha ⁻¹ 2,4-D LV4 ester	n/a	n/a	n/a

		1.17 L ha ⁻¹ 2,4-D LV4 ester						
Hybrid poplar	n/a	1.54 kg ha ⁻¹ Roundup® Power Max, 0.39 kg ha ⁻¹ Scepter®, 7.01 L ha ⁻¹ Pendulum® Aqua Cap	1.75 L ha ⁻¹ Intensity One	2.34 L ha ⁻¹ Roundup® Power Max, 7.01 L ha ⁻¹ Pendulum® Aqua Cap, 0.15 kg ha ⁻¹ Oust, 0.39 kg ha ⁻¹ Scepter®	n/a	1.54 kg ha ⁻¹ Roundup® Weather Max, 3.36 kg ha ⁻¹ Prowl® H2O	n/a	3.36 kg ha ⁻¹ Glyphosate (generic)
Early successional vegetation	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Restored prairie	n/a	2.24 kg ha ⁻¹ Roundup® Power Max, 0.84 kg ha ⁻¹ 2,4-D LV4 ester	n/a	n/a	n/a	n/a	n/a	n/a

Note: n/a=not applied.

Site	Cropping system	Soil preparation agronomic practice	Equipment details
Michigan	Switchgrass	No till	-
Central	Miscanthus	No till	-
	Native grasses	No till	-
	Hybrid poplar	No till	-
	Early successional vegetation	No till	-
	Restored prairie	No till	-
Michigan	Switchgrass	No till	-
North	Miscanthus	No till	-
	Native grasses	No till	-
	Hybrid poplar	No till	-
	Early successional vegetation	No till	-
	Restored prairie	No till	-
Michigan	Switchgrass	Chisel plowed to a depth of 20-25 cm	John Deere chisel plow
South	C	Field cultivated twice to a depth of 10-15 cm	John Deere 960 10' field cultivator
		Culti-mulched	John Deere 970 12 ft Culti-mulcher
	Miscanthus	Chisel plowed to a depth of 20-25 cm	John Deere chisel plow
		Field cultivated twice to a depth of 10-15 cm	John Deere 960 10' field cultivator
	Native grasses	Chisel plowed to a depth of 20-25 cm	John Deere chisel plow
		Field cultivated twice to a depth of 10-15 cm	John Deere 960 10' field cultivator
		Culti-mulched	John Deere 970 12 ft Culti-mulcher
	Hybrid poplar	Chisel plowed to a depth of 20-25 cm	John Deere chisel plow
		Field cultivated twice to a depth of 10-15 cm	John Deere 960 10' field cultivator
	Early successional vegetation	Chisel plowed to a depth of $20-25$ cm	John Deere chisel plow
		Field cultivated twice to a depth of 10-15 cm	John Deere 960 10' field cultivator
	Restored prairie	Chisel plowed to a depth of 20-25 cm	John Deere chisel plow
		Field cultivated twice to a depth of 10-15 cm	John Deere 960 10' field cultivator
		Culti-mulched	John Deere 970 12 ft Culti-mulcher
Wisconsin	Switchgrass	No till	-
Central	Miscanthus	No till	-
	Native grasses	No till	-
	Hybrid poplar	No till	-

Table S18. Details of agronomic practices and equipment used during soil preparation for the establishment of six bioenergy cropping systems (miscanthus, switchgrass, native grasses, hybrid poplar, early successional, and restored prairie) at Michigan and Wisconsin marginal lands.

	Early successional vegetation Restored prairie	No till No till	-	
Wisconsin	Switchgrass	Disc plowed	NA	
North	Miscanthus	Disc plowed	NA	
	Native grasses	Disc plowed	NA	
	Hybrid poplar	Disc plowed	NA	
	Early successional vegetation	Disc plowed	NA	
	Restored prairie	Disc plowed	NA	

Note: NA = Equipment details not available

Site	Cropping system	K fertilization rate (kg ha ⁻¹) in each split-plot		
		+N	0N	
Michigan Central	Switchgrass	45	45	
C	Miscanthus	45	45	
	Native grasses	45	45	
	Hybrid poplar	45	45	
	Early successional vegetation	45	45	
	Restored prairie	45	45	
	Historical vegetation	45	0	
Michigan North	Switchgrass	56	56	
C	Miscanthus	56	56	
	Native grasses	56	56	
	Hybrid poplar	56	56	
	Early successional vegetation	56	56	
	Restored prairie	56	56	
	Historical vegetation	56	0	
Michigan South	Switchgrass	34	34	
C	Miscanthus	34	34	
	Native grasses	34	34	
	Hybrid poplar	34	34	
	Early successional vegetation	34	34	
	Restored prairie	34	34	
	Historical vegetation	34	0	
Wisconsin Central	Switchgrass	56	56	
	Miscanthus	56	56	
	Native grasses	56	56	
	Hybrid poplar	56	56	
	Early successional vegetation	56	56	
	Restored prairie	56	56	
	Historical vegetation	56	0	

Table S19. Details of potassium (K) fertilizer application in bioenergy cropping systems at each marginal land site in 2020.

Table S20. p values	from	mixed	effects	model
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Response variable	Crop	Site	N treatment	p value Crop × Site	Crop × N treatment	Site × N treatment
Mean biomass production excluding poplar, i.e., 2014-2020 (Mg ha ⁻¹ yr ⁻¹)	<0.001	<0.001	<0.001	<0.001	0.007	0.001
Mean biomass production including poplar, i.e., 2014-2018 (Mg ha ⁻¹ yr ⁻¹)	<0.001	<0.001	0.007	<0.001	0.175	0.112

Cropping system	Site	Mean stand count ± SD	Multiple comparison letters from poisson
·		(m ⁻²)	regression analysis
	Michigan Central	33.8 ± 3.9	а
	Michigan North	33.0 ± 3.4	a
Switchgrass	Michigan South	34.0 ± 7.4	а
	Wisconsin Central	34.9 ± 4.2	а
	Wisconsin North	38.7 ± 0.9	а
	Michigan Central	26.9 ± 3.9	а
	Michigan North	19.8 ± 3.8	b
Miscanthus	Michigan South	22.5 ± 2.9	ab
	Wisconsin Central	5.0 ± 2.5	с
	Wisconsin North	1.9 ± 2.6	d
	Michigan Central	24.8 ± 4.6	а
Nution	Michigan North	6.0 ± 7.5	b
Native	Michigan South	21.8 ± 7.4	а
grasses	Wisconsin Central	8.9 ± 6.0	b
	Wisconsin North	20.0 ± 3.7	a
	Michigan Central	20.7 ± 7.2	а
D (1	Michigan North	14.5 ± 7.0	bc
Kestored	Michigan South	14.6 ± 6.7	bc
prairie	Wisconsin Central	11.1 ± 2.7	с
	Wisconsin North	19.2 ± 5.2	ab

Table S21: Stand counts of miscanthus, switchgrass, native grass, and restored prairie systems across study sites in 2017 and 2019

Note: Stand counts were not applicable for early successional and historical vegetation. Multiple comparison letters are given for each crop across sites. SD = standard deviation



Figure S1: Percent canopy cover of each species at each mixed-species cropping system (1. Michigan North: Restored prairie, 2. Michigan North: Historical vegetation, 3. Michigan North: Native grasses, 4. Michigan North: Early successional vegetation, 5. Wisconsin Central: Restored prairie, 6. Wisconsin Central: Historical vegetation, 7. Wisconsin Central: Native grasses, 8. Wisconsin Central: Early successional vegetation, 9. Michigan Central: Restored prairie, 10. Michigan Central: Historical vegetation, 11. Michigan Central: Native grasses, 12. Michigan Central: Early successional vegetation, 13. Michigan South: Restored prairie, 14. Michigan South: Historical vegetation, 15. Michigan South: Native grasses, 16. Michigan South: Early successional vegetation, 17. Wisconsin North: Restored prairie, 18. Wisconsin North: Historical vegetation, 19. Wisconsin North: Native grasses, 20. Wisconsin North: Early successional vegetation) divided into ten percent canopy cover classes (0-10, 10-20, 20-30, 30-40, 40-50, 50-60, 60-70, 70-80, 80-90, and 90-100).