CrossMark

Inter-Annual Precipitation Variability Decreases Switchgrass Productivity from Arid to Mesic Environments

Lara G. Reichmann[1] · Harold P. Collins[2] · Virginia L. Jin[3] · Mari-Vaughn V. Johnson[4] · Jim R. Kiniry[2] · Robert B. Mitchell[5] · H. Wayne Polley[2] · Philip A. Fay[2]

Abstract

Cellulosic biofuels are an important source of renewable biomass within the alternative energy portfolio. Switchgrass (*Panicum virgatum* L.), a perennial C_4 grass native to North America, is widely studied as a biofuel feedstock for its consistently high yields and minimal input requirements. The influences of precipitation amount and temporal variability on the fertilizer response of switchgrass productivity are not fully understood. Moreover, global climate models predict changes in rainfall patterns towards lower and increasingly variable soil water availability in several productive areas worldwide, which may impact net primary production of biofuel crops. We conducted a meta-analysis of aboveground net primary production of switchgrass from 48 publications encompassing 82 different locations, 11 soil types, 52 switchgrass cultivars, fertilizer inputs between 0 to 896 kg N ha^{-1} year^{-1}, and 1 to 6 years of annual productivity measures repeated on the same stand. Productivity of the lowland ecotype doubled with N rates > 131 kg N ha^{-1} year^{-1}, but upland ecotype productivity increased only by 50%. Results showed an optimum N rate of 30 to 60 kg N ha^{-1} year^{-1} for both ecotypes, after which biomass gain per unit of N added decreased. Growing season precipitation (GSPPT) and inter-annual precipitation variability (inter-PPTvar) affected both ecotypes similarly. Long-term mean annual precipitation (MAP) differentially affected lowland and upland productivity, depending on the N level. Productivity responses to MAP and GSPPT were similar for both upland and lowland ecotypes at none or low N rates. When N increased beyond 60 kg N ha^{-1} year^{-1}, lowland cultivars had a greater growth response to MAP than uplands. Productivity increased with increasing GSPPT and MAP and had a positive linear response to MAP ranging from 600 to 1200 mm year^{-1}. One third of the variability in switchgrass production was accounted for by inter-PPTvar. After accounting for MAP, sites with higher inter-PPTvar had lower switchgrass productivity than sites with lower inter-PPTvar. Increased inter-annual variation in precipitation reduced production of both ecotypes. Predicted changes in the amount and timing of precipitation thus likely will exert greater influence on production of upland than lowland ecotypes of switchgrass.

Keywords *Panicum virgatum* L. · Primary production · Precipitation variability · Nitrogen fertilization · Resource limitation

✉ Lara G. Reichmann
lara.reichmann@berkeley.edu

[1] Plant and Microbial Biology, UC Berkeley, 111 Koshland Hall, Berkeley, CA 94720, USA

[2] USDA-ARS Grassland, Soil and Water Research Laboratory, 808 E Blackland Rd, Temple, TX 76502, USA

[3] USDA-ARS, Agroecosystem Management Research Unit, 251 Filley Hall, UNL, East Campus, Lincoln, NE 68583, USA

[4] USDA-NRCS, 808 E Blackland Rd, Temple, TX 76502, USA

[5] USDA-ARS Wheat, Sorghum, and Forage Research Unit, 251 Filley Hall, UNL, East Campus, Lincoln, NE 68583, USA

Introduction

Cellulosic biofuels are likely to be part of the future energy portfolio to meet the Congressional mandate that ~ 25% of US gasoline consumption should come from renewable sources (EISA 2007, DOE 2011). The use of perennial native grasses has the potential to mitigate global climate change, with fewer environmental impacts than intensive cropping from corn-based ethanol [1]. Switchgrass (*Panicum virgatum* L.) is a perennial, warm-season C_4 grass native to North America. Switchgrass is ideal for its consistently high yields with minimal inputs, and for its success in lands less well-suited to food or commodity production [2, 3]. Ideally, biomass sources of energy will be resilient to changes in climate. Climate change scenarios predict increased precipitation variability with more

🍒 Springer

frequent and severe droughts and extreme rain events in several highly productive regions, worldwide [4]. Switchgrass productivity increases with annual precipitation both when grown in monocultures and in mixtures [5]. Increased rainfall variability decreased productivity in arid and semiarid ecosystems, even when mean annual rainfall amounts remained constant [6, 7]. Changes in precipitation amount and variability are thus likely to impact switchgrass productivity.

Switchgrass populations show local adaptations to temperature and habitat [8, 9]. Populations of "lowland" ecotypes thrive in floodplains of the southern USA, whereas "upland" ecotypes better tolerate freezing temperatures and shorter growing seasons in drier regions of the northern US [10, 11]. In addition, lowland ecotypes are 25 to 50% more productive than upland ecotypes [5, 12, 13], in part due to their early growth initiation, thicker leaves, and higher water use efficiency [13]. As a result, ecotypes may respond differently to climate change. For example, traits that favor productivity of lowland ecotypes, such as high water use efficiency, may provide resilience to lowland ecotypes during periods of low precipitation. In contrast, upland ecotypes may be more limited by low growing season precipitation (GSPPT) than lowland ecotypes [12].

Nitrogen (N) limitation is widespread across terrestrial ecosystems [14–16]. The harvest of high-yielding crops results in high soil N withdrawals that must be replenished with fertilizer inputs for sustained high yields. Perennial plant species can reduce the negative effects of N fertilizers due to their N recycling capacity during senescence and belowground N storage compared to annual crops [17, 18]. For this reason, perennials may be preferred over annuals in cellulosic biofuel production systems. Increasing fertilizer N use has negative consequences on ecosystems by increasing carbon emissions from fertilizer production, the fossil fuels expended to apply these fertilizers, and the amount of reactive N in the global N cycle, which can later result in eutrophication and ground water pollution [19–21]. However, there is a broad range of variability among perennials in their effects on N cycling [22, 23]. Switchgrass populations that originated in warm climates in lower latitudes have a longer growing season, higher tiller mass, C/N ratios, and higher overall productivity than switchgrass from cooler, high-latitude populations [11, 13]. High-latitude switchgrass populations show traits associated with shorter growing seasons, such as high nutrient concentration, rapid tissue turnover, and overall higher rates of physiological processes. The higher yield of lowlands suggests a higher N requirement for lowlands than uplands. On the other hand, uplands higher leaf N content may result in demand for N comparable to that of larger lowlands. Thus, the effects of N fertilization on productivity of upland and lowland switchgrass remain unclear [5, 12].

Precipitation variability can impact productivity independently from the effects of long-term mean annual precipitation (MAP) [24–26]. For example, in annual crops, inter-annual variability in precipitation accounted for 30 to 60% of the variability in yield [26], while in a perennial-dominated ecosystem the inter-annual variability in precipitation explained 11 to 18% of ANPP variability [27]. In contrast, increased intra-annual PPT variability (intra-PPTvar) may have neutral to positive effects on ANPP in dry sites, but negative effects in more mesic sites [28, 29], depending on whether greater intra-PPTvar increases or decreases the soil water content. Switchgrass can grow roots to > 2-m depth, [30–32], and therefore precipitation variability, may affect switchgrass productivity less than other species with shallower rooting systems [30, 32].

Increased precipitation variability may cause drying-rewetting cycles and result in "leaky" ecosystems with higher losses of reactive N and increased N limitation than under constant soil moisture conditions [33, 34]. Small water pulses can stimulate microbial activity, but large pulses are required to stimulate vascular plant activity [35]. Thus, during longer drought periods, N mineralization may continue without plant uptake, resulting in inorganic N accumulation susceptible to loss by leaching during subsequent wet periods [36]. In agroecosystems, increased intra- or inter-annual precipitation variability will likely reduce the effectiveness of N fertilization compared to less variable precipitation.

This review evaluates published switchgrass productivity studies to determine ecotypic-specific productivity responses to interactions of intra- and inter-annual variation in precipitation with N fertilization. We predicted that (1) N fertilization increases switchgrass productivity in lowland more than upland ecotypes; (2) growing season precipitation limits upland productivity more than lowlands; (3) increasing precipitation enhances the response of switchgrass productivity to N fertilizer, with upland ecotype productivity maximizing at lower rates of N addition than lowland ecotypes. With respect to precipitation variability, we predicted that (1) increased precipitation variability decreases the productivity of both ecotypes, and (2) any decrease in switchgrass productivity with increasing precipitation variability may be partially offset by N fertilization.

Methods

Data Collection

We assembled a database of peer-reviewed studies reporting switchgrass productivity in experiments conducted under ambient precipitation in stands ≥ 2 years old growing in plots with area > 3 m^2 (Supplementary Material 1, Table S1). We included only studies in which plots were harvested once per year, either at the end of the growing season or after the first killing frost. All studies identified

switchgrass ecotype, cultivar, soil type, site location, N fertilization rate (kg ha^{-1} year^{-1}), harvest date, and dry matter yield (DM Mg ha^{-1} year^{-1}). If yearly yield data was not included in the publication, we obtained it from the authors. We excluded yield data from the establishment year because immature stands usually have significantly lower productivity than subsequent years due to weed competition [12, 37, 38].

For each location, we compiled total annual precipitation (PPT), and growing season precipitation (GSPPT) for the years that the experiments were carried out from values reported in the study or from NOAA [39] for the weather station nearest to each study site. GSPPT was calculated as the sum of monthly PPT from frost-free months, or as the PPT between the first frost-free month and harvest date, whichever occurred first.

In total, our database included 48 peer-reviewed publications (Supplementary Material 1, Table S1), half of which were used in previously published syntheses [5, 12]. These 48 publications span 82 locations, 11 soil types, 52 switchgrass cultivars (21 lowland and 31 upland), fertilizer rates ranging 0 to 896 kg N ha^{-1} year^{-1}, and 1 to 6 years of biomass measures repeated on the same stand. All 75 US sites were located east of the Rocky Mountains; 2 sites were in southern Canada, 3 in Italy, and the remaining 2 in the UK (Supplementary Material 1, Fig. S1).

To examine the relationship between switchgrass productivity, long-term mean annual precipitation (MAP) and PPT variability, we used the Climate Research Unit's (CRU TS 3.22) gridded monthly data [40]. We extracted monthly precipitation data for a 30-year period (1983–2013) for each switchgrass planting location by computing distance vectors between the experimental sites and the CRU gridded data [R version 3.2.0, "ncdf" package, 41]. We then calculated intra-PPTvar for each site by calculating the coefficient of variation (the ratio of the standard deviation to the mean, CV) of mean monthly precipitation for each year in the 30-year period ($n = 12$ values in each calculation of CV), then averaging CV values over 30 years. To calculate the inter-annual precipitation variability (inter-PPTvar), we first calculated the total annual precipitation for each year in the 30-year range, and then calculated the standard deviation and the CV of total annual precipitation for a 5-year moving average. Lastly, we averaged the 5-year CVs to obtain one 30-year mean inter-PPTvar for each location. The moving average approach in the inter-PPTvar calculation was used to account for the negative relationship between standard deviation and sample size that would result in reduced CVs when calculated over a 30-year period. The 5-year range was chosen for comparing CVs to the majority of field studies, which usually span between 4 and 8 years (see Supplementary Material 2 for more details on the rationale for the PPT-related variables).

Data Analysis

Nitrogen Level Effects

Rates of N fertilization were divided into four categories, with comparable numbers of experiments in each: (1) No N added, (2) low N ($0 < $ kg N ha^{-1} year^{-1} ≤ 60), (3) medium N ($60 < $ kg N ha^{-1} year^{-1} ≤ 130), and (4) high N ($>$ 130 kg N ha^{-1} year^{-1}). To test for differences in productivity between ecotypes and levels of N fertilization, we fit linear mixed models with ecotype, fertilizer level, and their interaction as fixed effects [42, 43]. For this analysis, we used all individual year data from 82 study sites ($n = 1203$).

Nitrogen Response Efficiency and MAP Interactions

Nitrogen response efficiency (NRE) was calculated as the biomass gain per unit of N added (kg DM biomass kg^{-1} N added) [44]. We calculated the mean NRE only for those experiments that had at least 3 years of productivity data (3+ years database). We excluded experiments with only 1 year of observations due to uncertainties in the initial soil N yielding biased representations of NRE. The 3+ years database included 47 study sites, some of which may have multiple experiments conducted on different ecotypes, cultivars and N levels. The effect of site MAP on NRE was accounted for by adding MAP as a covariate in a mixed effect model with ecotype and N level as fixed effects.

Precipitation Amount and Variability

We tested GSPPT limitation on ecotype productivity with a linear model with ecotype as fixed effect, GSPPT as covariate, and yield as explanatory variable. For this analysis, we used non-fertilized experiments only.

To study the relationship between mean site switchgrass productivity, MAP and PPTvar, we first had to account for the relationship between precipitation and precipitation variability [24] that could confound the unique contribution of changes in precipitation variability to changes in productivity. We used sequential regression to control for multicollinearity and biased analyses, as a way to separate unique from shared contributions of the explanatory variables [45]. Sequential regression allowed us to study the independent effect of intra- and inter-PPTvar on switchgrass productivity after accounting for the MAP effect. The sequential regression assumes that one variable is functionally more important than the other, and thus we assigned higher priority to MAP over PPTvar (see Supplementary Material 2 for details on sequential regression).

For all the analyses, random effects terms were used to account for the variability that was not accounted for by the fixed-effects and covariates due to limited and/or unbalanced

replication. Random effects include differences in soil type or cultivars within ecotypes. Repeated measures on experimental units across years, as well as the publication record number and the study site were also included as random effects to control for the temporal, spatial, and other sources of correlation in the data.

Models were fit with the lmerTest R package [43], and non-significant terms were backward eliminated based on their p values ($\alpha = 0.05$). The analysis also calculates least squares means for the fixed factors of the model, which were used to produce the figures. When significant interactions were detected, we used the package phia [post hoc interaction analyses, 46] to evaluate multiple contrasts between factor levels with Tukey's p value adjustment for family-wise estimates, and to test the effect of the covariate (slopes) for different factor level combinations. We used the marginal and conditional R^2 to assess how the inclusion of additional predictors increased the variance explained by the models [47]. We defined outliers at each N level by ecotype combination as any individual observation outside 1.5× the interquartile range (a.k.a. box-and-whisker plot method).

Results

Lowland and upland ecotypes showed different productivity responses to N fertilizer across the 82 study sites (N level × ecotype, $p < 0.000$ l, Table 1). Averaged across all N levels, switchgrass productivity was 50% higher for lowlands than for uplands (11.45 ± 0.69 versus 7.44 ± 0.64 Mg ha^{-1} year^{-1}). Productivity in the unfertilized treatments did not differ between ecotypes (post hoc test, $p = 0.19$). In contrast to unfertilized productivity levels, lowland ecotype productivity almost doubled with high rates of N addition (7.99 ± 0.88 versus 14.69 ± 0.74 Mg ha^{-1} year^{-1}, post hoc test, $p < 0.0001$) whereas upland ecotype productivity increased by 50% (5.93 ± 0.78 versus 8.23 ± 0.77 Mg ha^{-1} year^{-1}, post hoc tests, $p = 0.01$, Fig. 1). Of the random effects, most of the variation in productivity was accounted for by the publication record number (37%), followed by experimental units (11%), soil types (5%), and cultivars within ecotypes (4%). In addition, the productivity of unfertilized lowland and upland ecotypes increased with the increasing GSPPT ($p < 0.03$). Ecotypes did not differ in their response to increasing GSPPT ($p > 0.05$, Fig. 2).

The effectiveness of N fertilizer addition, measured as the increase in biomass per kilogram of N added (nitrogen response efficiency, NRE), differed between ecotypes, N level, and across MAP (MAP × ecotype × N level, $p = 0.023$, Table 2). Overall, NRE was highest at the low rate (0–60 kg N ha^{-1} year^{-1}) of N addition, and decreased with medium (61–130 kg N ha^{-1} year^{-1}) and high N rates (> 130 kg N ha^{-1} year^{-1}) (Fig. 3). At low, medium, and high levels of N addition, the NRE for lowland ecotypes was 20, 65, and 40% higher than upland ecotypes (post

Table 1 Mixed-effects model of ecotype (lowland, upland), N level (none, low, medium, high), and their interactions on the productivity of switchgrass across 83 study sites

Effect on yield	F value	p ($> F$)
Ecotype	53.36	*< 0.0001*
N level	28.73	*< 0.0001*
Ecotype × N level	11.40	*< 0.0001*
Random effects	VC	
Exp unit ID	1.15	
Publication RN ID	3.69	
Cultivar (ecotype)	0.41	
Soil type	0.52	
Residuals	4.22	
$R^2_{(m)}$	**27%**	
$R^2_{(c)}$	**63%**	

VC variance components, $R^2_{(m)}$ marginal R^2, i.e., variance explained by fixed and covariate factors compared to a null model, $R^2_{(c)}$ conditional R^2, i.e., variance explained by the model compared to a null model

Significant p values at $\alpha = 0.05$ are shown in italics

hoc compassions $p < 0.0008$, 0.0001, and 0.07). As MAP of the sites increased, the NRE increased at low and medium N levels for lowland ecotypes, and at low N for upland ecotypes (post hoc test for MAP slopes at $p = 0.05$, Fig. 3).

Fertilizer level, ecotypes, and site MAP had interactive effects on productivity (ecotype × N level × MAP, $p = 0.01$, Table 3, Fig. 4). Productivity responses to MAP were similar for both upland and lowland ecotypes at 0 and low N levels ($R^2 = 0.14$–0.33, $p = 0.005$, Fig. 4). Upland ecotype productivity increased by 1.36 Mg ha^{-1} year^{-1} for every 100 mm increase of the site MAP, compared to 0.98 Mg ha^{-1} year^{-1} for lowland ecotypes. When N increased beyond this, lowlands had a greater growth
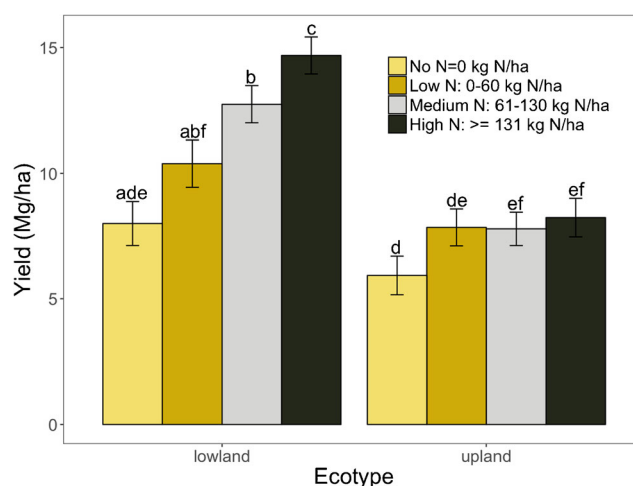

Fig. 1 Response of lowland and upland switchgrass productivity (Mg ha^{-1}) to none, low, medium, or high rates of N fertilization. Different letters denote significant differences ($p < 0.05$) between ecotype × N level combinations. See Table 1 for significance of fixed and random effects
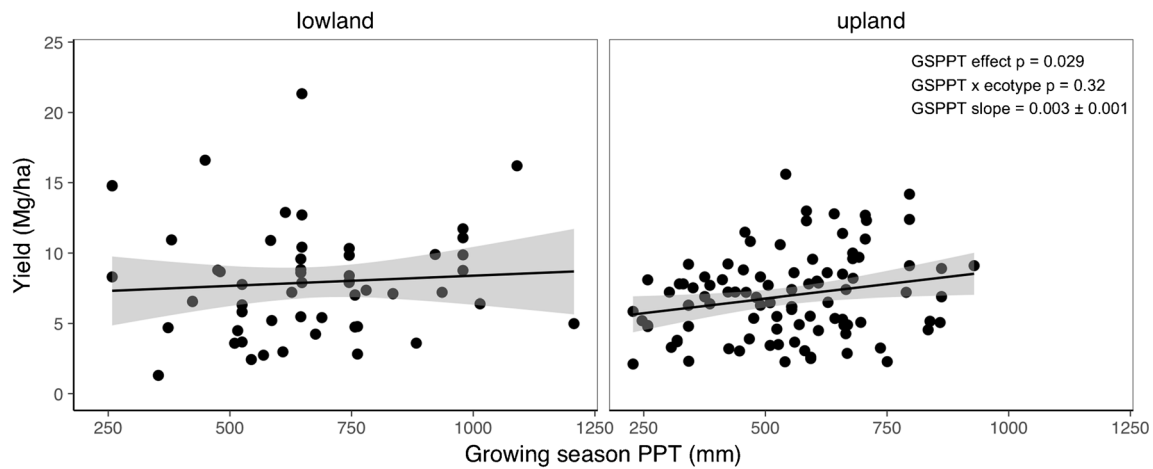
Fig. 2 Relationship between lowland and upland ecotypes productivity (Mg ha^{-1}) and growing season precipitation (GSPPT) in experiments without N fertilizer and with > 3-year duration. Solid lines show significant relationships between productivity and GSPPT at $p < 0.05$

response to MAP (higher slope) but uplands showed little to no change in productivity with MAP at medium N fertilizer level (slope ~ 0). Lowlands yield responses to MAP remained linear regardless of N level, while the very steep slope for the upland yield vs. MAP response at high N level was driven by a few data points. In both ecotypes, the yield at the lower end of MAP increased with N level with respect to the previous, lower N level, but less so for uplands.

Linear regressions showed that increased inter-PPTvar reduced switchgrass productivity across ecotypes and N levels.

Table 2 Mixed-effects models of ecotype (lowland, upland), N level (low, medium, high), mean annual precipitation (MAP), and their interactions on the mean nitrogen response efficiency (NRE) of each 189 switchgrass experiments 3+ years long across 47 sites. Ecotype and publication ID random effect terms were not significant at $\alpha = 0.1$ and removed from the final model

Effect on NRE	F value	p (>F)
Ecotype	2.46	0.12
N level	0.47	0.63
MAP	4.59	*0.03*
Ecotype × N level	3.43	*0.03*
Ecotype × MAP	0.52	0.47
MAP × N level	0.72	0.49
Ecotype × N level × MAP	3.82	*0.02*
Random effects	VC	
Site	5.7	
Soil type	0.8	
Residuals	3.5	
$R^2_{(m)}$	68%	
$R^2_{(c)}$	89%	

VC variance components, $R^2_{(m)}$ marginal R^2, i.e., variance explained by fixed and covariate factors compared to a null model, $R^2_{(c)}$ conditional R^2, i.e., variance explained by the model compared to a null model

Significant p values at $\alpha = 0.05$ are shown in italics

Switchgrass productivity decreased at a rate of 0.35 Mg ha^{-1} per percent increase in the site's inter-annual precipitation variability (%CV, $p = 0.03$, Fig. 5, Table 3). The negative effect of increasing inter-PPTvar was independent of fertilizer level and ecotype. Lastly, intra-PPTvar of the sites was not associated with changes in switchgrass yield after accounting for site MAP, regardless of whether intra-PPTvar or inter-PPTvar were prioritized ($p > 0.05$).

Discussion

Our results indicate that the wide range of switchgrass productivity is strongly associated with (1) the ecotype, based on plant morphology and adaptation area, (2) the long-term MAP and inter-PPTvar, and (3) ecotype-specific responses to increasing rates of N fertilizer and its interaction with the long-term MAP. We found that lowland ecotypes were 50% more productive than upland ecotypes, similar to previous multisite analyses [5, 12]. In contrast to Wang et al.'s [5] conclusions that ecotypes did not differ in their response to N addition, we found that the productivity of lowland ecotypes was twice as responsive to N additions as upland ecotypes. Greater fertilization response in lowland ecotypes may be explained by its longer growing season, and structural/physiological adaptations to warm climates that result in larger leaves, tiller mass, and overall biomass [13]. These traits may enhance water-use efficiency and stress tolerance but also result in higher tissue investment costs, such as demand for N. Upland ecotype productivity increased when fertilized at low levels (up to 60 kg N ha^{-1}), but no additional yield responses occurred for fertilizer inputs > 60 kg N ha^{-1}. We did not find support for the hypothesis that productivity would be greater in lowland than upland ecotypes compared at similar GSPPT. Due to morphological, ecophysiological, or growing season length differences, the productivity of upland ecotypes was
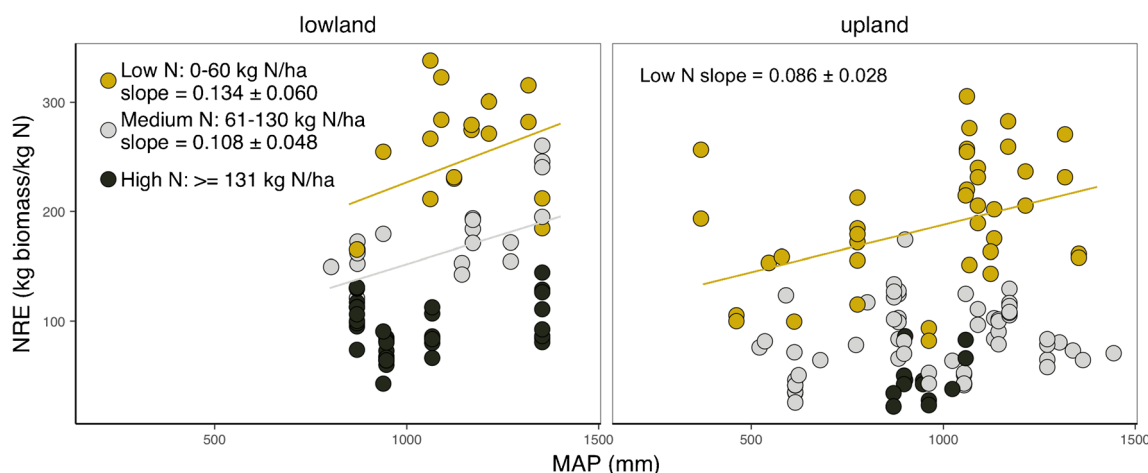
Fig. 3 Mean nitrogen response efficiency (NRE, kg biomass kg^{-1} N applied) of 3+ year long experiments in lowland and upland ecotypes as a function of 30-year mean annual precipitation (MAP, mm). Solid lines show significant relationships between NRE and MAP by N level (low, medium, high) at $p < 0.05$ (Tukey method for family-wise estimates)

more water-limited than N-limited, whereas lowland ecotype productivity was both N- and water-limited.

We found that the change in NRE as a function of MAP differed between ecotypes, indicating ecotypic constraints to productivity. Given that the growth response to fertilizer usually follows an asymptotic response curve, there should be a point at which further increases in N cause no further increase in NRE [44]. We found an optimum N rate of 30–60 kg N ha^{-1}

Table 3 Mixed-effects models of ecotype (lowland, upland), N level (none, low, medium, high), mean annual precipitation (MAP), inter-PPTvar residuals, and their interactions on the mean productivity of switchgrass from 217 switchgrass experiments 3+ years long across 54 sites. Intra-PPTvar residuals fixed effect term was not significant at $\alpha = 0.05$, and soil type, publication ID, ecotype random effect terms were not significant at $\alpha = 0.1$, and therefore were removed from the final model

Effect on yield	F value	p ($>F$)
Ecotype	2.96	0.09
N level	3.59	*0.02*
MAP	15.43	*0.0001*
Inter-PPTvar resid	4.93	*0.03*
Ecotype × N level	3.55	*0.02*
Ecotype × MAP	0.59	0.44
MAP × N level	2.38	0.07
Ecotype × N level × MAP	3.62	*0.01*
Random effects	VC	
Site	6.82	
Residuals	3.18	
$R^2_{(m)}$	56%	
$R^2_{(c)}$	86%	

VC variance components, $R^2_{(m)}$ marginal R^2, i.e., variance explained by fixed and covariate factors compared to a null model, $R^2_{(c)}$ conditional R^2, i.e., variance explained by the model compared to a null model

Significant p values at $\alpha = 0.05$ are shown in italics

for both ecotypes, after which biomass gain per unit of N added decreased. It has been shown that N uptake increases with N fertilization, with fertilizer recovery ranging from 22 to 57% [48], to 100% [37, 49] more as a result of increased N concentration in biomass than to increases in yield [50]. Because a high N concentration is not desirable in a high-quality switchgrass production system [51], reducing N inputs could be a win-win solution for both the quality and the long-term sustainability of switchgrass production for biofuels.

As predicted, MAP is a significant driver of switchgrass productivity across sites. MAP explained an extra ~30% of the variability in switchgrass productivity over that explained by Ecotype and N level (56 versus 27% variance explained). The N fertilization effect on ANPP increased significantly with MAP, with a higher magnitude of N limitation in lowlands than in uplands. N limitation of upland ecotypes may differ from our estimate, because a relatively small number of studies included uplands at the high N level. Further studies are needed to refine this estimate. We found a 2× increase in productivity across the 600 to 1200 mm year^{-1} range of MAP in these studies. Our results support the notion that the N effects on productivity are tightly related to water availability in arid-subhumid ecosystems possibly due to the direct effect of water limitation to plant growth, and its indirect effect through limitation to N mineralization when water availability decreases [15].

After accounting for the MAP effect, sites with higher long-term inter-PPTvar had lower switchgrass productivity than sites with lower inter-PPTvar, similar to trends found in non-managed grassland systems [7]. This negative effect of inter-PPTvar on ANPP can be the result of a shift of the soil water profile towards deeper soil layers, which in turn increased water limitation for species with more shallow roots [7, 52]. Moreover, inter-PPTvar can also affect plant growth indirectly by interacting with the N cycle. Reichmann et al. [36] found that inorganic soil N increased by 2–4 times during
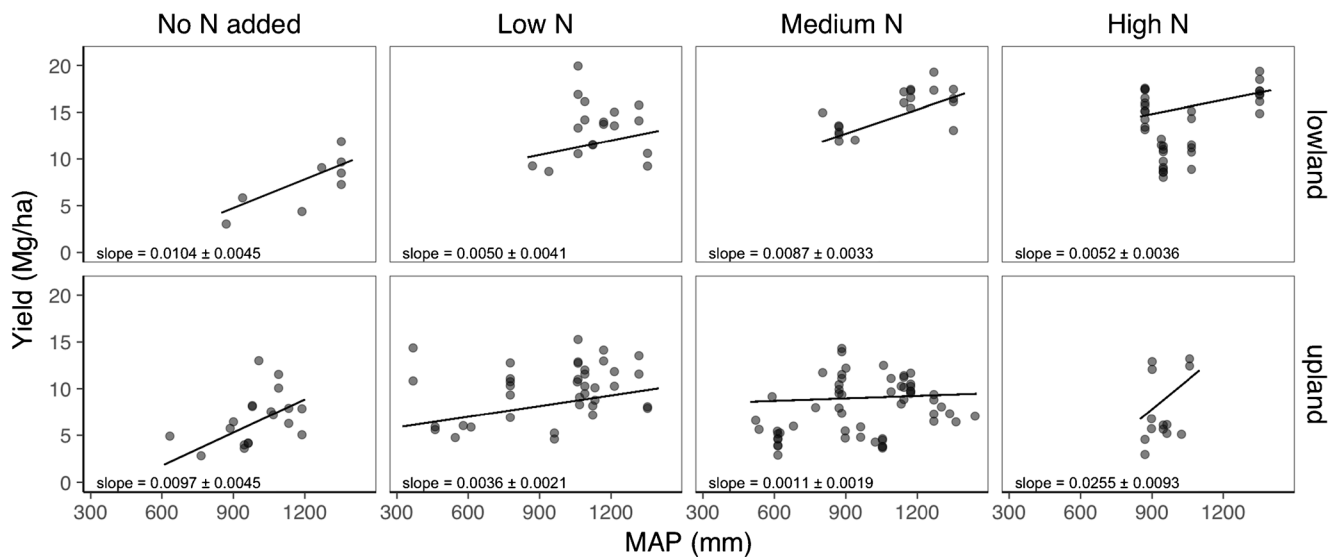
Fig. 4 Changes in lowland and upland mean productivity (Mg ha^{-1}, 3+-year-long experiment means) to none, low, medium, or high rates of N fertilization with changes in site 30-year mean annual precipitation (MAP, mm). Solid lines show mixed model covariate slope fit, which took into account the unbalanced number of experiments at each site

extreme dry years because drought prevented plant uptake but did not affect N mineralization, suggesting that increased inter-PPTvar results in an open N cycle with increased loss of reactive N, and thus possibly N limitation [also see 33]. In the present analysis, N addition did not change the relationship between inter-PPTvar and productivity. Therefore, increased inter-PPTvar affected productivity through changes in the distribution of water in the soil profile. However, not statistically significant, N addition reduced the inter-PPTvar effect in lowlands. Manipulative experiments may be able to better show the interaction between precipitation variability and N limitation.

The response of unfertilized switchgrass to increasing MAP (0.98–1.36 g m^{-2} mm^{-1}) was higher than that of native

grasslands [0.6–0.69 g m^{-2} mm^{-2}, 25], and the N fertilization effect in lowlands was also much higher (110%) than the N fertilization effect reported for various grasslands ranging from arid to temperate [18–51%; 14–16]. Our analysis implies that switchgrass alone can maintain or even increase production compared to diverse systems composed of herbaceous vegetation. Noteworthy is that these comparisons do not account for carbon costs associated with land-use change and fertilizer use in switchgrass [19, 53]. Our study included a larger number of individual studies than previously published syntheses [5, 12] and is unique in accounting for the variation in switchgrass yields that result from differences in ecotype, N fertilizer, long-term PPT, and, more importantly, inter- and intra-PPTvar across a wide range of sites with different soils,
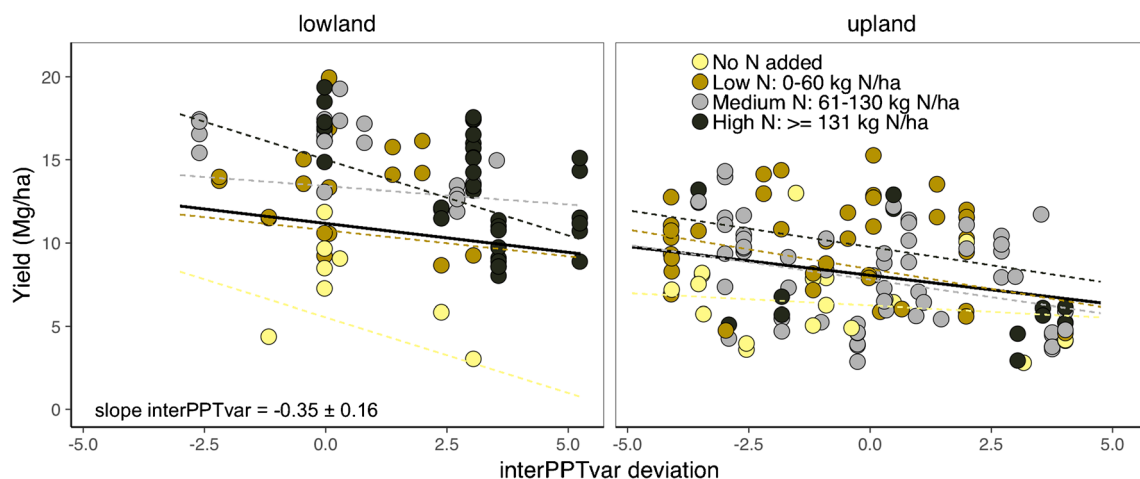

Fig. 5 Response of lowland and upland mean productivity (t ha^{-1}, 3+-year-long experiment means) to changes in site inter-annual precipitation variability after accounting for site MAP (inter-PPTvar deviations), to none, low, medium, or high rates of N fertilization. Solid lines show mixed model covariate slope estimates for ecotypes, dashed lines show N level × ecotype covariate estimates. See Table 3 for significance of fixed effects and covariate

nutrient availability, and climates. As precipitation variability is predicted to increase globally [54], results from the present analysis will aid in the design of strategies to stabilize production for biofuels and alleviate negative feedbacks such as N losses.

References

1. Howarth RW, Bringezu S, Martinelli LA, Santoro R, Messem D, Sala OE (2009) Introduction: biofuels and the environment in the 21st century. In: Howarth RW, Bringezu S (eds) Biofuels: environmental consequences and interactions with changing land use. Proceedings of the Scientific Committee on Problems of the Environment (SCOPE) International Biofuels Project Rapid Assessment, Gummersbach Germany. Cornell University, Ithaca, pp 15–36

2. Knoll JE, Anderson WF, Strickland TC, Hubbard RK, Malik R (2012) Low-input production of biomass from perennial grasses in the Coastal Plain of Georgia, USA. BioEnergy Res 5(1):206–214. https://doi.org/10.1007/s12155-011-9122-x

3. Kiniry JR, Anderson LC, Johnson MVV, Behrman KD, Brakie M, Burner D, Cordsiemon RL, Fay PA, Fritschi FB, Houx JH III, Hawkes C, Juenger T, Kaiser J, Keitt TH, Lloyd-Reilley J, Maher S, Raper R, Scott A, Shadow A, West C, Wu Y, Zibilske L (2013) Perennial biomass grasses and the Mason-Dixon line: comparative productivity across latitudes in the southern Great Plains. BioEnergy Res 6(1):276–291. https://doi.org/10.1007/s12155-012-9254-7

4. IPCC (2007) Climate Change 2007: the physical science basis. In: Solomon S, Qin D, Manning M et al (eds) Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge 996 pages

5. Wang DAN, Lebauer DS, Dietze MC (2010) A quantitative review comparing the yield of switchgrass in monocultures and mixtures in relation to climate and management factors. GCB Bioenergy 2(1):16–25. https://doi.org/10.1111/j.1757-1707.2010.01035.x

6. Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL (2003) Productivity responses to altered rainfall patterns in a C 4-dominated grassland. Oecologia 137(2):245–251

7. Gherardi LA, Sala OE (2015) Enhanced precipitation variability decreases grass- and increases shrub-productivity. Proc Natl Acad Sci 112(41):12735–12740. https://doi.org/10.1073/pnas.1506433112

8. McLaughlin SB, Kszos LA (2005) Development of switchgrass (Panicum virgatum) as a bioenergy feedstock in the United States. Biomass Bioenergy 28(6):515–535

9. Wright L, Turhollow A (2010) Switchgrass selection as a "model" bioenergy crop: a history of the process. Biomass Bioenergy 34(6):851–868

10. Casler MD, Vogel KP, Taliaferro CM, Wynia RL (2004) Latitudinal adaptation of switchgrass populations. Crop Sci 44(1):293–303

11. Porter CL (1966) An analysis of variation between upland and lowland switchgrass, Panicum virgatum L., in Central Oklahoma. Ecology 47(6):980–992. https://doi.org/10.2307/1935646

12. Wullschleger SD, Davis EB, Borsuk ME, Gunderson CA, Lynd LR (2010) Biomass production in switchgrass across the United States: database description and determinants of yield. Agron J 102(4):1158–1168

13. Aspinwall MJ, Lowry DB, Taylor SH, Juenger TE, Hawkes CV, Johnson MV, Kiniry JR, Fay PA (2013) Genotypic variation in traits linked to climate and aboveground productivity in a widespread C(4) grass: evidence for a functional trait syndrome. New Phytol 199(4):966–980. https://doi.org/10.1111/nph.12341

14. LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89(2):371–379

15. Yahdjian L, Gherardi L, Sala OE (2011) Nitrogen limitation in arid-subhumid ecosystems: a meta-analysis of fertilization studies. J Arid Environ 75(8):675–680. https://doi.org/10.1016/j.jaridenv.2011.03.003

16. Fay PA, Prober SM, Harpole WS, Knops JMH, Bakker JD, Borer ET, Lind EM, MacDougall AS, Seabloom EW, Wragg PD, Adler PB, Blumenthal DM, Buckley YM, Chu C, Cleland EE, Collins SL, Davies KF, Du G, Feng X, Firn J, Gruner DS, Hagenah N, Hautier Y, Heckman RW, Jin VL, Kirkman KP, Klein J, Ladwig LM, Li Q, McCulley RL, Melbourne BA, Mitchell CE, Moore JL, Morgan JW, Risch AC, Schütz M, Stevens CJ, Wedin DA, Yang LH (2015) Grassland productivity limited by multiple nutrients. Nat Plants 1(7):15080. https://doi.org/10.1038/nplants.2015.80

17. Lambers H, Chapin FS, Pons TL (2008) Plant physiological ecology, 2nd edn. Springer, New York 604 pages

18. Yang J, Worley E, Wang M, Lahner B, Salt DE, Saha M, Udvardi M (2009) Natural variation for nutrient use and remobilization efficiencies in switchgrass. BioEnergy Res 2(4):257–266. https://doi.org/10.1007/s12155-009-9055-9

19. Robertson GP, Hamilton SK, Del Grosso SJ, Parton WJ (2011) The biogeochemistry of bioenergy landscapes: carbon, nitrogen, and water considerations. Ecol Appl 21(4):1055–1067. https://doi.org/10.1890/09-0456.1

20. Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai Z, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320(5878):889–892

21. Schmer MR, Liebig MA, Hendrickson JR, Tanaka DL, Phillips RL (2012) Growing season greenhouse gas flux from switchgrass in the northern great plains. Biomass Bioenergy 45:315–319. https://doi.org/10.1016/j.biombioe.2012.05.026

22. Wedin DA, Tilman D (1990) Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84(4):433–441. https://doi.org/10.1007/bf00328157

23. Butler T, Muir J, Huo C, Guretzky J (2013) Switchgrass biomass and nitrogen yield with over-seeded cool-season forages in the southern Great Plains. BioEnergy Res 6(1):44–52. https://doi.org/10.1007/s12155-012-9225-z

24. Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. Science 291(5503):481–484

25. Sala OE, Gherardi LA, Reichmann LG, Jobbagy EG, Peters DP (2012) Legacies of precipitation fluctuations on primary production: theory and data synthesis. Proc R Soc Lond Ser B Biol Sci 367:3135–3144

26. Ray DK, Gerber JS, MacDonald GK, West PC (2015) Climate variation explains a third of global crop yield variability. Nat Commun 6:5989. https://doi.org/10.1038/ncomms6989

27. Knapp AK, Briggs JM, Koelliker JK (2001) Frequency and extent of water limitation to primary production in a mesic temperate grassland. Ecosystems 4(1):19–28

28. Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK (2002) Rainfall

variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298(5601):2202–2205

29. Heisler-White JL, Blair JM, Kelly EF, Harmoney K, Knapp AK (2009) Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Glob Chang Biol 15(12):2894–2904. https://doi.org/10.1111/j.1365-2486.2009.01961.x

30. Tufekcioglu A, Raich JW, Isenhart TM, Schultz RC (1998) Fine root dynamics, coarse root biomass, root distribution, and soil respiration in a multispecies riparian buffer in Central Iowa, USA. Agrofor Syst 44(2–3):163–174

31. Kiniry JR, Tischler CR, Van Esbroeck GA (1999) Radiation use efficiency and leaf CO2 exchange for diverse C4 grasses. Biomass Bioenergy 17(2):95–112. https://doi.org/10.1016/S0961-9534(99)00036-7

32. Mann JJ, Barney JN, Kyser GB, DiTomaso JM (2012) Root system dynamics of Miscanthus × giganteus and Panicum virgatum in response to rainfed and irrigated conditions in California. BioEnergy Res 6(2):678–687. https://doi.org/10.1007/s12155-012-9287-y

33. Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141(2):221–235. https://doi.org/10.1007/S00442-004-1519-1

34. Jin V, Haney R, Fay P, Polley W (2013) Soil type and moisture regime control microbial C and N mineralization in grassland soils more than atmospheric CO2-induced changes in litter quality. Soil Biol Biochem 58:172–180

35. Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220

36. Reichmann LG, Sala OE, Peters DPC (2013) Water controls on nitrogen transformations and stocks in an arid ecosystem. Ecosphere 4(1):art11. https://doi.org/10.1890/es12-00263.1

37. Parrish DJ, Fike JH (2005) The biology and agronomy of switchgrass for biofuels. Crit Rev Plant Sci 24(5–6):423–459

38. Miesel JR, Renz MJ, Doll JE, Jackson RD (2012) Effectiveness of weed management methods in establishment of switchgrass and a native species mixture for biofuels in Wisconsin. Biomass Bioenergy 36(Journal Article):121–131. https://doi.org/10.1016/j.biombioe.2011.10.018

39. NOAA Climate Data Online Global historical weather and climate data archive. http://www.ncdc.noaa.gov/cdo-web/-t=secondTabLink

40. Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 dataset. Int J Climatol 34(3):623–642. https://doi.org/10.1002/joc.3711

41. R Core Team (2015) R: A language and environment for statistical computing. Version:Retrieved from http://www.R-project.org/

42. Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B (2014) 'lme4' version 1.1–7. Version: retrieved from https://github.com/lme4/lme4/ http://lme4.r-forge.r-project.org/

43. Kuznetsova A, Brockhoff PB, Christensen RHB (2016) 'lmerTest' Version 2.0–30. Version:

44. Pastor J, Bridgham SD (1999) Nutrient efficiency along nutrient availability gradients. Oecologia 118(1):50–58

45. Graham MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology 84(11):2809–2815

46. De Rosario-Martinez H, John Fox, R Core Team (2015) phia: post-hoc interaction analysis. R package. Version:0.2–0. Retrieved from https://github.com/heliosdrm/phia

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

48. Stout WL, Jung GA (1995) Biomass and nitrogen accumulation in switchgrass: effects of soil and environment. Agron J 87(4):663–669

49. Lemus R, Parrish DJ, Wolf DD (2009) Nutrient uptake by 'Alamo' switchgrass used as an energy crop. Bioenergy Res 2(1–2):37–50

50. Jach-Smith LC, Jackson RD (2015) Nitrogen conservation decreases with fertilizer addition in two perennial grass cropping systems for bioenergy. Agric Ecosyst Environ 204:62–71. https://doi.org/10.1016/j.agee.2015.02.006

51. Agblevor FA, Rejaj B, Evans RJ, Johnson KD (1992) Pyrolytic analysis and catalytic upgrading of lignocellulosic materials by molecular beam mass spectrometry. In: Klass DL (ed) Energy from biomass wastes XVI. Elsevier Applied Science, Chicago, pp 767–795

52. Sala OE, Gherardi LA, Peters DPC (2015) Enhanced precipitation variability effects on water losses and ecosystem functioning: differential response of arid and mesic regions. Clim Chang 131(2):213–227. https://doi.org/10.1007/s10584-015-1389-z

53. Searchinger T, Heimlich R, Houghton RA, Dong F, Elobeid A, Fabiosa J, Tokgoz S, Hayes D, Yu T-H (2008) Use of US croplands for biofuels increases greenhouse gases through emissions from land-use change. Science 319(5867):1238–1240

54. IPCC (2012) Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. In: Field CB, Barros V, Stocker TF et al (eds) A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge 582 pages