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NOTE AND UNIQUE PHENOMENA

Comparative establishment and yield of bioenergy sorghum and maize following pre-emergence waterlogging

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Abstract

Biofuel feedstocks grown on marginal lands, such as those that experience ephemeral waterlogging, reduce interference with food agriculture. As early-season extreme precipitation events in the U.S. Midwest continue to increase, waterlogging tolerance may play an important role in the productivity of annual biofuel cropping systems. We assessed the establishment and yield of photoperiod-sensitive sorghum [*Sorghum bicolor* (L.) Moench] and maize (*Zea mays* L.) after extreme early-season rainfall events in central Illinois. We used paired sorghum and maize transects, spanning from low-lying poorly drained areas to higher better drained areas, to evaluate the response of both cropping systems throughout the 2020 growing season. Sorghum maintained 25% mean emergence rates in areas that experienced the most severe waterlogging, but maize failed to establish under the same conditions. Despite the low establishment, sorghum yields in the poorly drained areas were upwards of 50% of those found in the better drained, whereas maize yields were zero areas in the poorly drained locations. The yield compensation in sorghum resulted from increased tillering, higher productivity per stem, and subsequently higher productivity per plant, which illustrates the greater phenotypic plasticity of sorghum compared to maize. Land managers who are currently seeking to grow annual cellulosic feedstocks on soils that are vulnerable to transient soil waterlogging will likely have more success with photoperiod-sensitive bioenergy sorghum than maize.

1 | INTRODUCTION

The expansion of novel bioenergy feedstock production potentially competes with fertile land used for food agriculture (Tenenbaum, 2008). In the U.S. Midwest, a significant portion of land currently used for maize (*Zea mays* L.) production has low yield stability (Basso et al., 2019) and could be transferred to bioenergy with minimal loss of food production. Using land with lower yield potential, often termed marginal land (e.g., Yang et al., 2021), could alleviate this competition while meeting the second-generation cellulosic biofuel requirements mandated by the U.S. Renewable Fuel Standard (Oliver & Khanna, 2017). However, bioenergy crops grown on marginal land must overcome significant abiotic stress (Quinn et al., 2015) including ponding and soil waterlogging that is common on poorly drained, low-lying soils throughout the U.S. Midwest (Kaur et al., 2020; Paul et al., 2020).

Abbreviations: AMSL, above mean sea level; DW, dry weight; LAI, leaf area index; SPAD, Soil Plant Analysis Development.

Although perennial bioenergy feedstocks display moderate to high tolerance of ponding and soil waterlogging (Quinn et al., 2015), annual feedstocks are often more desirable because of their amenability to existing farming practices and infrastructure. In these annual cropping systems, which are typically dominated by rotations of maize and soybean [*Glycine max* (L.) Merr.], heavy rainfall and resultant waterlogged soils cause significant reductions in crop yield (Kaur et al., 2020) particularly in low-lying topographical areas (e.g., von Haden & Dornbush, 2016). It has been estimated that 2.5% of the total agricultural landscape is prone to seasonal inundation in parts of the Midwest (Paul et al., 2020), and about 15% of farmers identify portions of their land as marginal due to ponding susceptibility (Yang et al., 2021). Crop yield losses due to excess moisture are nearly as large as those caused by drought (Li et al., 2019) and may account for 10–20% of the total maize crop loss cost throughout the United States (Bailey-Serres et al., 2012). However, as an emerging annual bioenergy feedstock, sorghum [*Sorghum bicolor* (L.) Moench] displays moderate tolerance of waterlogging (Quinn et al., 2015; Tari et al., 2013) and therefore may provide better yields than maize when grown in areas susceptible to transient waterlogging.

The urgency to identify biofuel crops tolerant to soil waterlogging is compounded by the predicted increases in future precipitation in the U.S. Midwest. Over the last several decades, this region has received increasingly more total precipitation (Ford et al., 2021) and more frequent extreme springtime precipitation (Feng et al. 2016). The intensity of springtime precipitation, frequency of extreme precipitation events, and fraction of total precipitation occurring during extreme events are expected to increase in parts of the U.S. Midwest throughout the 21st century (Cook et al., 2008; Singh et al., 2013). Importantly, early-season precipitation amounts have increased in recent decades (Dai et al., 2016), which can affect both plant establishment (i.e., emergence) and early-season growth. Without adaptation, these changes in precipitation regimes are expected to cost US$3 billion per year in damage to U.S. maize crops alone (Rosenzweig et al., 2002).

Our objectives were to evaluate the effects of early-season soil waterlogging on establishment and yield in bioenergy sorghum and maize and to assess the potential mechanisms of yield compensation after soil waterlogging. We hypothesized that sorghum yields would be less impacted by soil waterlogging than maize, due to the higher tolerance of seed germination to anoxia and greater propensity for tillering in sorghum (e.g., Alam et al., 2017; Al-Ani et al., 1985). To address our objectives, we took advantage of an atypical series of extreme precipitation events that occurred during the early 2020 growing season in central Illinois, when nearly 40% of the total growing season precipitation fell during the first 3 wk following planting.

Core Ideas

- Sorghum emergence was greater than maize in poorly drained, wet locations.
- Sorghum yields in the wet areas were greater than expected based on emergence.
- Greater tillering and leaf area explained sorghum yield compensation in wet areas.
- Sorghum may be more resilient to early-season soil waterlogging than maize.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted at the University of Illinois Energy Farm in Urbana, IL (40.0659, −88.1933) during the 2020 growing season. The climate is characterized as hot-summer humid continental, and the 30-yr mean annual temperature and precipitation are 10.9 ˚C and 1,009 mm, respectively (NOAA, 2010). Soils at the site are primarily moderately well drained Dana silt loams (fine-silty, mixed, superactive, mesic Oxyaquic Argiudoll), somewhat poorly drained Flanagan silt loams (fine, smectitic, mesic Aquic Argiudoll), and poorly drained Drummer silty clay loams (fine-silty, mixed, superactive, mesic Typic Enfoaquoll) (Soil Survey Staff, 2021). The soil types are associated with microtopographic landscape positions, with more well-drained soils in the upslope areas and more poorly drained soils in the depressional areas (Soil Survey Staff, 2021). Despite widespread tile drainage in the region, the low-lying soils often experience ponding and subsequent soil waterlogging when rainfall exceeds 30 mm over a 24-h period (Krichels et al., 2019).

The research site was historically used for long-term maize and soybean production, which is the dominant land use in the area (Smith et al., 2013). In 2008, 0.67-ha bioenergy research plots (122 by 55 m) were established in a randomized block design with four cropping systems including a maize–maize–soybean rotation (Anderson-Teixeira et al., 2013; Smith et al., 2013). In 2018, the maize–maize–soybean plots (hereafter referred to as “maize”) were split in half (122 by 27.5 m) to accommodate a new sorghum–sorghum–soybean rotation treatment (hereafter referred to as “sorghum”) while retaining the maize rotation (Moore et al., 2021). The paired plots were planted adjacent to each other such that the cropping systems were separated by only one row space (Supplemental Figure S1). In 2019, the maize and sorghum plots were in the soybean rotation phase, and thus both plot types were planted into soybean (Supplemental Table S1). In 2020, the maize plots

TABLE 1 Management practices for bioenergy sorghum and maize during the 2020 growing season at the University of Illinois Energy Farm in Urbana, IL

Management	Sorghum	Maize
Pre-plant herbicide date	11 May 2020	11 May 2020
Pre-plant herbicide type	Metolachlor/Atrazine	Resicore/Atrazine
Pre-plant N fertilizer date	11 May 2020	11 May 2020
Pre-plant N fertilizer type	32% urea-ammonium nitrate	32% urea-ammonium nitrate
Pre-plant N fertilizer rate, kg N ha^{-1}	112	202
Pre-plant tillage date	11 May 2020	11 May 2020
Pre-plant tillage type	Sunflower 6221 field cultivator	Sunflower 6221 field cultivator
Planting date	12 May 2020	12 May 2020
Plant variety	TAM17500	Dekalb DKC60-87RIB
Planting depth, cm	2.5	3.8
Row spacing, cm	76.2	76.2
Planting rate, seeds ha^{-1}	185,300	84,000
Post-plant herbicide date	N/A	12 June 2020
Post-plant herbicide type	N/A	Resicore/Liberty
Harvest date	1 Oct. 2020	1 Oct. 2020

were planted to maize and the sorghum plots were planted to sorghum.

On the day prior to 2020 planting, maize and sorghum plots were treated with pre-emergence herbicide, tilled using a field cultivator, and knife-fertilized with 32% urea-ammonium nitrate at 6–7 cm (Table 1). Both crops were planted on 12 May using standard 76.2 cm row spacing. In line with common agricultural practices, sorghum seeds were planted 2.5-cm deep at 185,300 seeds ha^{-1} (e.g., Schetter et al., 2021), whereas maize seeds were planted 3.8-cm deep at 84,000 seeds ha^{-1}. Sorghum plots were planted with a high biomass-yielding, photoperiod-sensitive bioenergy sorghum hybrid, TAM 17500, obtained from the Texas A&M University sorghum breeding program. Maize was treated with post-emergence herbicide 1 mo after planting, whereas sorghum was not treated likewise due to the lack of herbicide resistance in sorghum.

Five days after planting, the site experienced a 58 mm precipitation event (Figure 1) that caused short-term ponding (hours-to-days) and longer-term waterlogging (days-to-weeks) of soils in the lowland landscape positions. The soil waterlogging was exacerbated by a smaller 28-mm rain event that occurred 13 d after planting. A second extreme rainfall event of 74 mm occurred 23 d after planting, which caused additional short-term ponding and extended the long-term waterlogging in the low-lying areas. In all, 39.3% of the total growing season precipitation fell during the 1st month after planting, and thus the depressional landscape positions experienced ponding or soil waterlogging for most of the 1st month following planting.

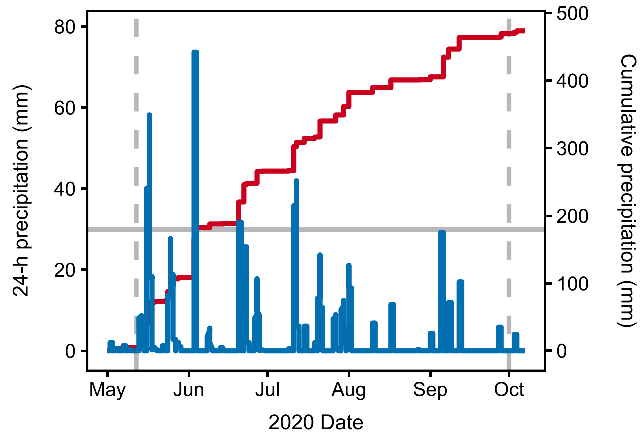

FIGURE 1 Total precipitation in 24-h windows (blue) and seasonal cumulative precipitation (red) at University of Illinois Willard Airport, located 7.4 km from the study site (MRCC, 2021). The horizontal solid line indicates the 30 mm value for 24 h precipitation that is expected to result in ponding (Krichels et al., 2019). The two vertical dashed lines show planting and harvest dates in May and October, respectively

2.2 | Transect measurements

In response to the first severe rainfall event and waterlogging, 50-m transects were established within a subarea of each of the three experimental blocks to assess the effects of waterlogging on seedling emergence and crop yields (Supplemental Figure S1). The transects were established in an East–West orientation along the primary elevational gradient (Figure 2a) such that the low end of each transect experienced

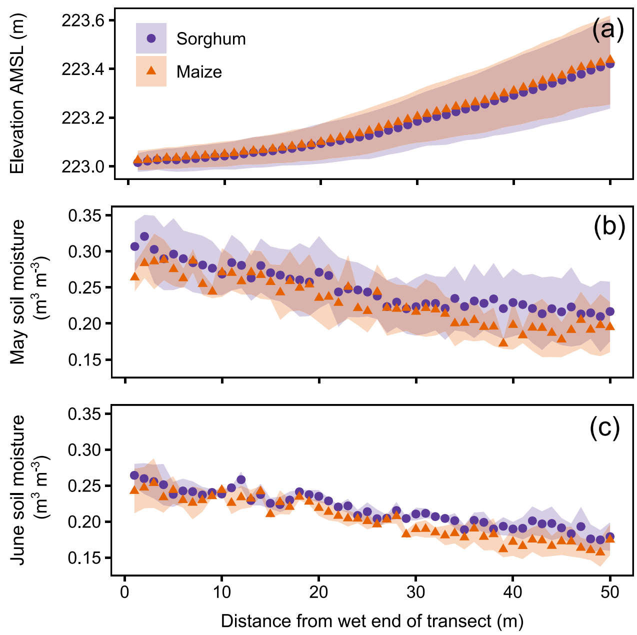

FIGURE 2 Transect patterns of (a) elevation above mean sea level (AMSL), (b) volumetric soil moisture on 27 May 2020, and (c) volumetric soil moisture on 11 June 2020. The distance from wet (m) indicates the interval along the transect with 0 m representing the area that endured the longest waterlogging and 50 m representing the area that did not experience waterlogging. The points are mean values, and the shaded areas represent ± 1 standard error ($n = 3$)

severe waterlogging while the high end remained well-drained (Figure 2b and 2c). In each block, the three rows nearest to the shared border of the two cropping systems were assigned to the transect. Thus, each pair of maize and sorghum transects was immediately adjacent, which allowed for direct comparisons of maize and sorghum at each interval along the soil moisture gradient within each transect. Throughout the study, weeds were removed manually across the transects to mitigate the effect of interspecific plant competition on the growth of maize and sorghum.

Seedling emergence was assessed on 11 June, 1 mo after planting, at 50 1-m intervals along each transect row. Care was taken to count only the main culm of each plant to correctly quantify seedling establishment (i.e., tillers were not counted). On 27 May and 11 June, soil moisture at 0-to-6-cm depth was measured at 1-m intervals using a Delta-T ML3 ThetaProbe soil moisture sensor (Delta-T Devices Ltd.). On 11 September, a late-season survey was performed to assess the total number of stems within the 50 1-m intervals. In this case, all stems were counted (including tillers) so that the total number of stems and stems plant^{-1} could be assessed.

Leaf area index (LAI) measurements were performed using a LI-COR LAI-2000 (LI-COR Biosciences) on 30 June and 1 September to estimate early- and late-season biomass, respectively. Within each of the 50 1-m intervals, four LAI subsample measurements were taken at equal distances across the two inter-row spaces to capture spatial heterogeneity. A 90° view cap was used, and the outer 68° ring was masked during post-processing to minimize the influence of vegetation from outside the 1-m interval. Skies were overcast on the two LAI measurement dates, and therefore a scattering correction was not necessary.

To assess the potential for confounding N deficiency and limitation across the transects, a Soil Plant Analysis Development (SPAD) chlorophyll content proxy was measured when maize and sorghum were near the V10 and V12 stages, respectively. The SPAD measurements were made on 7 August using a Fieldscout SPAD 502 Plus Chlorophyll Meter (Spectrum Technologies Inc.) and were taken on one plant in the middle row within each 1-m transect interval. On each plant, three measurements were taken on three locations and averaged across the youngest fully expanded leaf between the leaf margin and midrib (Ziadi et al., 2008).

Total aboveground plant yield was measured on 1 October using 76.2 by 76.2 cm quadrats spaced equidistantly at 10 locations within each transect row. All plants within each quadrat were clipped at 10 cm above the soil surface to mimic the efficiency of a forage harvester, which is typically used for whole-plant biomass harvest. Whole plants were folded and placed into fine-mesh bags, dried in ovens at 60 °C until weight was constant, and weighed for dry weight (DW). Potential ethanol yields were estimated by assuming a maize grain harvest index of 0.50 (Hütsch & Schubert, 2017) and using biomass-to-ethanol conversion factors presented in Roozeboom et al. (2019) for maize (495 L Mg grain DW^{-1} and 330 L Mg stover DW^{-1}) and sorghum (270 L Mg stover DW^{-1}). A detailed list of all measurement dates and spatial locations is given in Supplemental Table S2.

2.3 | Statistical analyses

At each of the transect intervals, measurements within each plot were averaged across multiple rows where applicable. Stems per plant, late-season LAI per stem, and late-season LAI per plant, were tabulated at each transect interval using the corresponding datasets. To facilitate direct comparisons of maize and sorghum metrics across the transects, raw measurements of emergence, LAI, and yield at each transect interval were converted into relative (i.e., proportional) values by dividing each observed value by the maximum value observed in each plot such that the resulting values ranged between zero to one. Crop-level means and standard errors were calculated from the plot-level values at each transect interval. Note that for the relative values, crop-level averages equal zero or one only when the values in all three replicate plots equal zero or one, respectively.

Multiple linear regression models were used to assess whether relationships varied between cropping systems for the

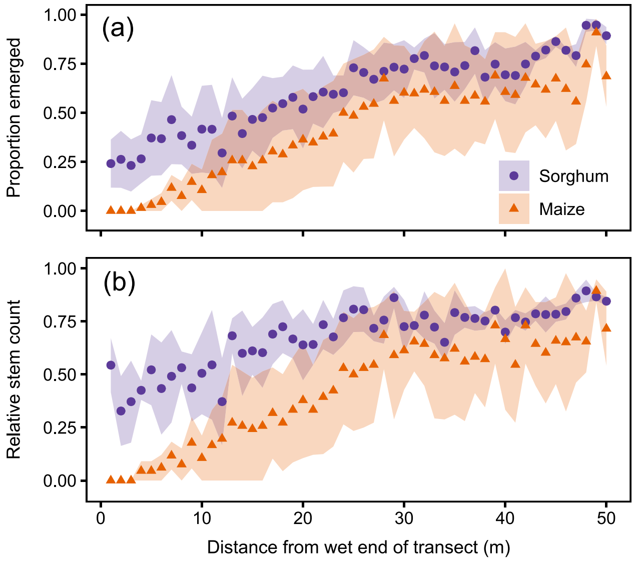

FIGURE 3 Patterns of (a) seedling emergence proportion and (b) relative stem count along the transects. Emergence and stem count were assessed on 11 June 2020 and 11 Sept. 2020, respectively. Proportion emerged and relative stem count were calculated by dividing the raw values by the maximum value observed in each plot such that the resulting values ranged between zero and one. The points are mean values, and the shaded areas represent ± 1 standard error ($n = 3$)

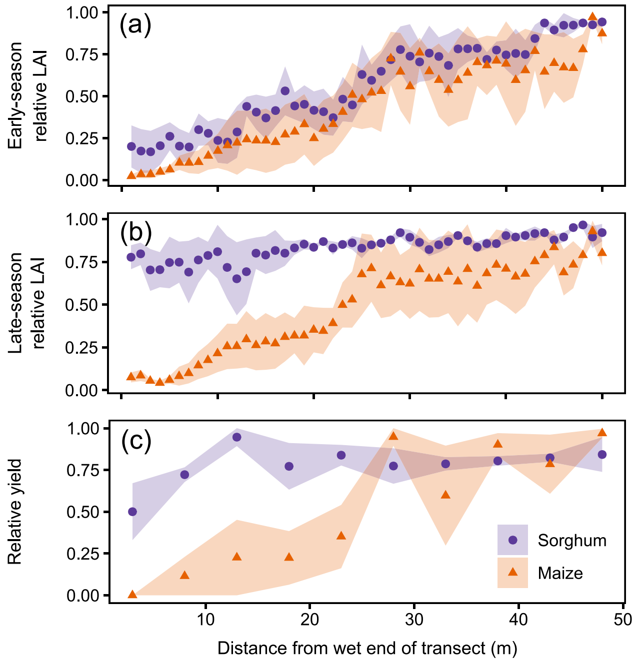

FIGURE 4 Transect patterns of (a) early-season relative leaf area index (LAI), (b) late-season relative LAI, and (c) relative biomass yield as measured on 30 June, 1 September, and 1 October, respectively. Raw measurements were converted to relative values by dividing by the maximum observed value within each plot so that the resulting values ranged between zero and one. The points are mean values, and the shaded areas represent ± 1 standard error ($n = 3$). Maximum absolute yields were 25.7 ± 4.3 Mg ha^{-1} and 13.4 ± 5.5 Mg ha^{-1} for sorghum and maize, respectively

following pairs of relative variables: emergence/early-season LAI, emergence/late-season LAI, early-season LAI/late-season LAI, late-season LAI/yield. If the effect of crop or the interaction of crop with the dependent variable was significant, the relationships were considered to differ between cropping systems. Kendall rank correlations were used to test for monotonic trends of stems plant^{-1}, LAI stem^{-1}, LAI plant^{-1}, and chlorophyll content across the transects. Crop-level means were used for multiple regressions and Kendall rank correlations, and therefore a blocking term was not used in these models. The significance level for all tests was $\alpha = .05$, and all statistical analyses were performed in R 4.0.4 (R Core Team, 2021).

3 | RESULTS

Although the mean elevational change across the transects was only 0.4 ± 0.1 m (Figure 2a), there was a strong inverse surface soil moisture gradient for the 1st month following planting (Figure 2b and 2c). Sorghum and maize plots showed the same spatial soil moisture trends, with sorghum having marginally higher average soil moisture on both measurement dates. One month after planting, the mean proportion of seeds emerged at the wet end of the transects was 0.25 ± 0.13 for sorghum and 0.0 ± 0.0 for maize (Figure 3a). Average maximum emergence was 0.95 ± 0.03 for sorghum and 0.91 ± 0.07 for maize, and sorghum maintained higher mean emergence rates across the majority of the transects. Toward the end of the growing season, the relative stem counts at the wet end were approximately 0.41 ± 0.16 and 0.0 ± 0.0 for sorghum and maize, respectively (Figure 3b). The stem count patterns generally followed those of emergence except that sorghum relative stem count was notably higher than emergence across the wettest 25 m of the transects. Absolute emergence and stem counts are shown in Supplemental Figure S2.

Early-season relative LAI, as measured near the end of June, showed a strong gradient from low at the wet end to high at the drier end (Figure 4a). In a pattern similar to emergence, early-season relative LAI on the wetter side of the transects averaged 0.18 ± 0.13 for sorghum and 0.03 ± 0.02 for maize. For maize, the relationship between proportion emerged and early-season relative LAI was near 1:1, while in sorghum the relationship was slightly steeper (Figure 5a; $p_{slope} < .001$, $p_{crop} < .001$, $p_{crop\times slope} < .01$). However, by early September, the LAI trend in sorghum was markedly different than earlier in the growing season, with relative LAI values of 0.76 ± 0.09 at the wet end (Figures 4b and 5b; $p_{slope} < .001$, $p_{crop} < .001$, $p_{crop\times slope} < .001$). In contrast, in maize the relationship between late-season relative LAI and early-season relative LAI was near 1:1, with mean late-season relative LAI

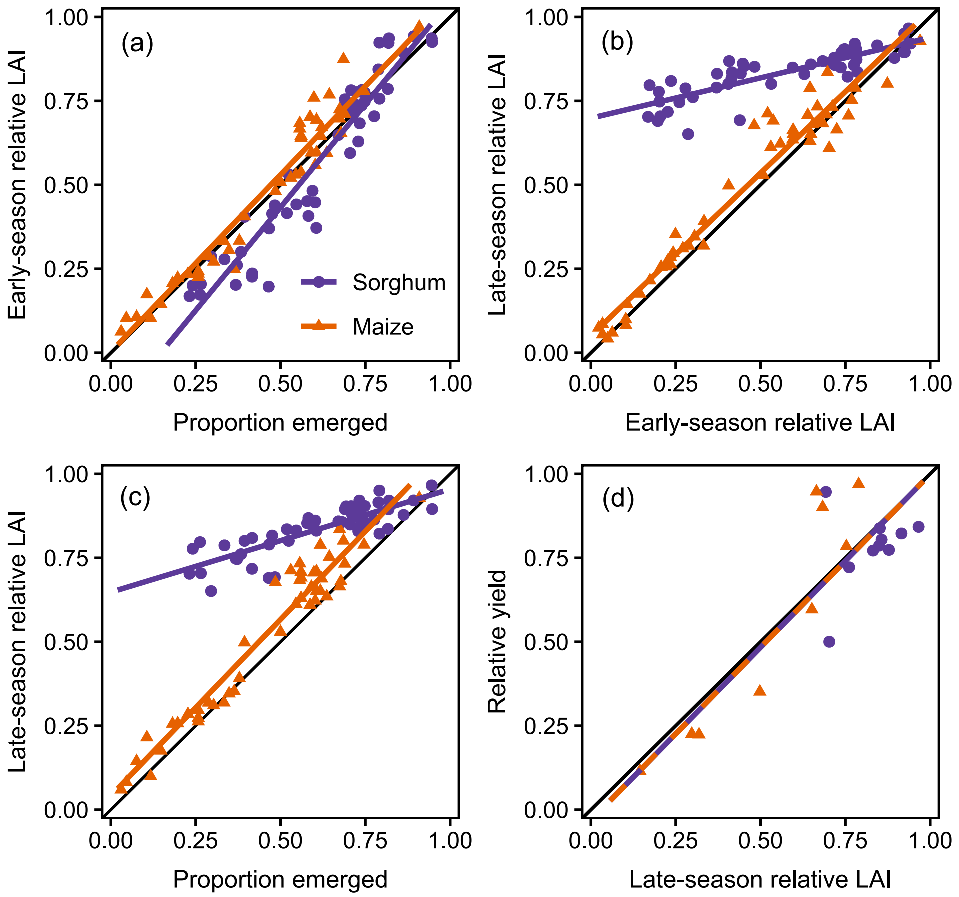

FIGURE 5 Relationships between (a) seedling proportion emerged and early-season relative leaf area index (LAI), (b) early-season relative LAI and late-season relative LAI, (c) seedling proportion emerged and late-season LAI, and (d) late-season relative LAI and relative yield. Emergence, early-season LAI, late-season LAI, and yield were measured on 11 June, 30 June, 1 September, and 1 October, respectively. Points show means for each 1-m transect interval and the lines show linear regression models. For panels (a), (b), and (c), the regression intercepts and slopes were different for sorghum and maize, while for panel (d) the slope and intercept were not statistically different between cropping systems. The 1:1 lines are shown in black

values of 0.07 ± 0.02 at the wetter end and values exceeding 0.75 only in the driest 10 m of the transect. While the relationship between maize seedling emergence and late-season relative LAI was also near 1:1, in sorghum emergence greatly underpredicted late-season relative LAI in the wet areas that experienced low seedling emergence (Figure 5c; $p_{slope} < .001$, $p_{crop} < .001$, $p_{crop×slope} < .001$). Relative yields showed similar patterns as late-season relative LAI across the transects for both cropping systems, except that sorghum had slightly lower yields compared to LAI at the wet end whereas maize had marginally higher yields compared to LAI at the drier end (Figure 4c). Nonetheless, the relationship between late-season relative LAI and relative yields ($p_{slope} < .001$) was not different between crops ($p_{crop} = .08$, $p_{crop×slope} = .06$), and the relationship fell near 1:1, indicating that late LAI was a reasonable proxy for yield (Figure 5d). When averaged across the transects, absolute biomass yields were 20.6 ± 0.9 Mg DW ha^{-1} and 8.1 ± 3.9 Mg DW ha^{-1} for sorghum and maize, respectively (Supplemental Figure S3). The mean potential ethanol yields across the transects were 5.6 ± 0.3 m^3 ha^{-1} for sorghum and 3.4 ± 1.6 m^3 ha^{-1} for maize (Supplemental Figure S3).

At the drier end of the transects, both sorghum and maize averaged approximately one stem plant^{-1}, indicating that there was minimal tillering under drier conditions (Figure 6a). Sorghum showed a clear trend toward greater tillering from drier to wetter locations ($p < .001$), but there was no significant tillering response across the transects in maize ($p = .46$). Late-season LAI stem^{-1} showed opposite spatial trends for sorghum and maize (Figure 6b), with sorghum having greater LAI stem^{-1} on the wetter end ($p < .001$) and maize having greater LAI stem^{-1} on the drier end ($p < .02$). Late-season LAI plant^{-1}, which integrates the LAI stem^{-1} and stems plant^{-1} indices, showed a clear spatial pattern in sorghum ($p < .001$), ranging from low values on the drier end to high values on the wetter end (Figure 6c). In contrast, there was no pattern of LAI plant^{-1} across the transects for maize ($p = .19$).

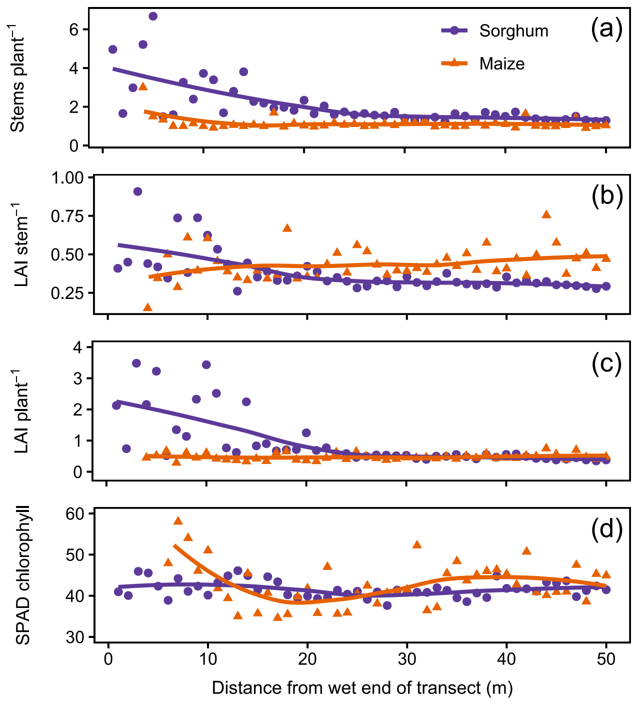

FIGURE 6 Transect patterns of (a) stems per plant, (b) late-season leaf area index (LAI) per stem, (c) late-season LAI per plant, and (d) Soil and Plant Analysis Development (SPAD) chlorophyll. Plant counts, stems, late-season LAI, and SPAD chlorophyll were measured on 11 June, 11 September, 1 September, and 7 August, respectively. Each point shows mean value among the three replicates, and the solid lines show locally estimated scatterplot smoothing curves for trend visualization

Chlorophyll content values overlapped between cropping systems (Figure 6d), and there was no evidence for monotonic trends across the transects for sorghum (p = .58) or maize (p = .51).

4 | DISCUSSION

During a growing season when intense post-planting precipitation events caused long-term soil waterlogging in low-lying areas, bioenergy sorghum demonstrated greater resilience to adverse early season growing conditions than maize. Specifically, when compared to maize, sorghum seedling establishment and biomass yields were less impaired by the stresses imposed by the water-saturated soils. Moreover, bioenergy sorghum yields in soils that were waterlogged during the early part of the growing season were much greater than expected based on seedling emergence rates, suggesting that sorghum has wider phenotypic plasticity that helped compensate for poor establishment and excess water stress. Considering that bioenergy cropping systems benefits are greatest when targeted toward marginally productive landscapes (Robertson et al., 2017), our results indicate that bioenergy sorghum may be a desirable annual feedstock where portions of the landscape are known to experience ephemeral ponding and soil waterlogging.

4.1 | Plant establishment

Both sorghum and maize suffered from lower relative seedling establishment in wetter locations compared to drier locations, but sorghum was able to maintain establishment in the wettest locations where maize establishment failed. Considering that the low-lying areas became ponded and waterlogged within 5 d of planting, it is likely that the poor seedling establishment resulted from a combination of low seed germination rates and high pre-emergence seedling mortality. Both the degree and duration of oxygen deficiency have been shown to strongly negatively affect both sorghum and maize seed germination efficacy (Al-Ani et al., 1985; Khosravi & Anderson, 1990). In line with our findings, Al-Ani et al. (1985) reported that sorghum seed germination was slightly more tolerant of low oxygen conditions than maize, but seedling germination in both species was much less tolerant of anoxia than rice (*Oryza sativa* L.), which is known for its high tolerance to anoxia (Crawford, 2003). For any sorghum or maize seeds that germinated before ponding occurred, the prolonged oxygen deprivation resulting from waterlogging likely led to high pre-emergence seedling mortality (Cobb et al., 1995). Although we are unable to deduce the specific mechanisms hindering post-ponding establishment in our study, our evidence supports the notion that sorghum is generally more resistant to pre-emergence ponding than maize.

Replanting is a common remedy for annual crops that fail at the pre-emergence stage, but replanting necessitates additional monetary and environmental costs that would ideally be avoided (Benson, 1990), particularly in the case of biofuel feedstocks. To reduce the need for replanting, pre-emergence ponding tolerance may be improved through breeding and selection programs that explicitly evaluate germination and emergence responses to waterlogging (e.g., Liu et al., 2010). For example, Khosravi and Anderson (1990) demonstrated a wide efficacy of seed germination among 20 inbred maize lines under anoxic conditions, with germination rates ranging from 42 to 85% after 144 h of exposure to anoxia. Similarly, Thseng and Hou (1993) reported that seed germination rates ranged from 0 to 100% among 635 sorghum lines that were submerged in water for 144 h, with 40% of tested lines showing >50% germination efficacy. While other genotypic characteristics such as yield potential and days to maturity are undoubtedly important considerations for growers, in areas where ephemeral waterlogging is common, increased emphasis on excess water tolerance may help to improve crop establishment in lieu of replanting (Pancaldi & Trindade, 2020). Future studies investigating the anoxia tolerance of modern maize and bioenergy sorghum varieties would allow farmers to better select crops for areas that experience ephemeral waterlogging (e.g., Zaidi et al., 2004; Zhou, 2010).

4.2 | Plant growth and yield

Despite relatively poor establishment in waterlogged areas, sorghum yield (i.e., late-season LAI) exceeded expectations based on establishment, whereas maize yields were congruent with establishment rates. Although we did not explicitly quantify maize grain yield, waterlogging has been shown to have negligible to slightly negative effects on grain harvest index (Meyer et al., 1987; Ren et al., 2013), and thus we expect waterlogging could have resulted in some degree of grain yield reductions. The fact that sorghum relative yields exceeded relative establishment in poorly drained locations illustrates phenotypic plasticity that permitted the sorghum plants in low-establishment areas to take advantage of increased light availability and thus largely rebound from suboptimal establishment. Specifically, sorghum plants exhibited greater tillering (i.e., stems plant^{-1}) in the poorly drained, low-establishment areas compared to the drier areas with optimal establishment. Although minimal maize tillering occurred in areas of low plant density, the tillers were small and sporadic, and thus there was no overall trend across the transects. Whereas tillering in many modern maize hybrids has been reduced through selective breeding (Hake & Ross-Ibarra, 2015; Rotili et al., 2021), sorghum tillering is known to be strongly related to water stress and light availability (Alam et al., 2017). In terms of water stress, early-season soil waterlogging often reduces sorghum tillering, whereas late-season soil waterlogging increases tillering (Orchard & Jessop, 1984). Given that soil waterlogging occurred during the early growing season in our study, and that early-season sorghum LAI was lower than expected based on establishment, it is likely that the observed tillering response in sorghum was a result of increased light availability rather than a direct consequence of soil waterlogging.

Even though there were more sorghum tillers plant^{-1} on the wetter side of the transects, the total stem density and subsequent late-season LAI were still greater on the drier side, and thus LAI may have exceeded the optimal value in the drier locations (e.g., Anten et al., 1995). If the optimal LAI was exceeded on the drier side, canopy-level photosynthesis would have been reduced via self-shading, which would have slowed plant growth and subsequent biomass increment. In agreement with this, Snider et al. (2012) reported that sorghum biomass yields in two locations plateaued or decreased with increasing planting density for a photoperiod-sensitive sorghum variety. Thus, similar or greater yields may have been achieved with lower seeding densities on the drier sides of our transects. However, lower seeding densities would have also resulted in lower absolute establishment rates and thus lower yields in the waterlogged areas, where only about 25% of the planted sorghum seeds emerged. This illustrates a spatially dependent tradeoff between planting density and yields that must be considered when planting sorghum fields with spatially heterogeneous soil moisture conditions.

Although other studies have demonstrated that N limitations to plant growth can occur concurrently with soil waterlogging (e.g., Orchard et al., 1986; Tian et al., 2020), we did not find evidence to suggest that this occurred in this study. If N limitation were present, we would have expected chlorophyll content to decrease from drier to wetter areas of our transects (e.g., Tian et al., 2020), but we did not observe a monotonic spatial trend in chlorophyll content in either cropping system. Moreover, if N or other nutrients were limited waterlogged locations, we would have anticipated late-season LAI plant^{-1} to decrease from drier to waterlogged areas (e.g., Orchard & Jessop, 1984), but we observed no spatial trend in maize and the opposite trend in sorghum. Because there was not an identifiable confounding nutrient limitation in our study, it is likely that early season soil water dynamics were the proximal driver of plant biomass production along our transects.

5 | CONCLUSIONS

As early-season precipitation events continue to rise in the midwestern United States, it will be increasingly important to consider the impacts of ponding and soil waterlogging in annual bioenergy cropping systems during the early growing season. To mitigate yield losses while avoiding the economic and environmental costs associated with replanting, land managers will need to select annual crops that maintain reasonable establishment and growth in poorly drained areas. Photoperiod-sensitive sorghum appears better adapted than maize to pre-emergence soil waterlogging because of its higher seedling emergence rates and increased tillering in areas with low seedling establishment. However, additional studies are needed to better understand the effects of early-season soil waterlogging in other sorghum and maize varieties. Breeding and selection programs that consider post-anoxia seed germination rates and light-induced tillering propensity may help to improve the yield compensation in sorghum and maize exposed to ephemeral soil waterlogging. In the meantime, photoperiod-sensitive bioenergy sorghum is a seemingly better choice than maize for land managers seeking to grow an annual cellulosic feedstock in areas that are prone to seasonal soil waterlogging.

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AUTHOR CONTRIBUTIONS

Adam C von Haden: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Visualization; Writing-original draft. Mark Burnham: Conceptualization; Formal analysis; Investigation; Methodology; Writing-original draft. Wendy Yang: Funding acquisition; Project administration; Resources; Supervision; Writing-review & editing. Evan DeLucia: Funding acquisition; Project administration; Resources; Supervision; Writing-review & editing

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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