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Prairies Thrive Where Row Crops Drown: A Comparison of Yields in Upland and Lowland Topographies in the Upper Midwest US

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Abstract: Cellulosic biofuel production is expected to increase in the US, and the targeted establishment of biofuel agriculture in marginal lands would reduce competition between biofuels and food crops. While poorly drained, seasonally saturated lowland landscape positions are marginal for production of row crops and switchgrass (*Panicum virgatum* L.), it is unclear whether species-diverse tallgrass prairie yield would suffer similarly in saturated lowlands. Prairie yields typically increase as graminoids become more dominant, but it is uncertain whether this trend is due to greater aboveground net primary productivity (ANPP) or higher harvest efficiency in graminoids compared to forbs. Belowground biomass, a factor that is important to ecosystem service provisioning, is reduced when switchgrass is grown in saturated lowlands, but it is not known whether the same is true in species-diverse prairie. Our objectives were to assess the effect of topography on yields and live belowground biomass in row crops and prairie, and to determine the mechanisms by which relative graminoid abundance influences tallgrass prairie yield. We measured yield, harvest efficiency, and live belowground biomass in upland and lowland landscape positions within maize silage (*Zea mays* L.), winter wheat (*Triticum aestivum* L.), and restored tallgrass prairie. Maize and winter wheat yields were reduced by more than 60% in poorly drained lowlands relative to well-drained uplands, but diverse prairie yields were equivalent in both topographic settings. Prairie yields increased by approximately 45% as the relative abundance of graminoids increased from 5% to 95%. However, this trend was due to higher harvest efficiency of graminoids rather than greater ANPP compared to forbs. In both row crops and prairie, live belowground biomass was similar between upland and lowland locations, indicating consistent biomass nutrient sequestration potential and soil organic matter inputs between topographic positions. While poorly drained, lowland landscape positions are marginal lands for row crops, they appear prime for the cultivation of species-diverse tallgrass prairie for cellulosic biofuel.

Keywords: cellulosic biofuels; corn; harvest efficiency; maize; root biomass; perennial grasslands; wheat

1. Introduction

Concerns of energy security and climate change have spurred a movement towards large-scale production of liquid transportation biofuel in the United States. The 2007 US Energy Independence and Security Act requires 136 billion liters of annual renewable fuel production by 2022 [1]. While the

majority of liquid biofuel production is currently derived from maize grain, most of the future increase in renewable fuel is expected to come from cellulosic sources [1]. However, there is also concern that cellulosic biofuels will displace food agriculture, thereby raising food prices and creating food shortages [2]. If cellulosic biofuels can be produced efficiently on lands marginal for the production of row crops, then competition between biofuels and food agriculture would be reduced [3].

Marginal lands are defined as those that are prone to degradation or are simply unproductive due to climate or edaphic conditions [4]. Row crop productivity in relation to edaphic conditions has been well studied, and topographically-defined patterns of soil moisture often account for nearly half of the field-scale yield variability [5]. When water is a limiting factor, yields are usually greater in relatively moist, lowland topographic locations [5,6]. This relationship has been observed in many of the crop systems common to the US Corn Belt including maize, soybeans, and wheat [7–9]. However, when water is excessive, anaerobic stress reduces plant productivity [10,11], and row crop yields in poorly drained lowlands may be substantially reduced compared to well-drained uplands [12]. Yield in row crop systems is further complicated by the effects of soil moisture on establishment of annual crops [13]. The marginality of lowlands for row crop production is therefore dependent on whether water is limiting in the uplands or excessive in the lowlands, both during establishment and growth.

Compared to row crops, the effect of topography and soil moisture on perennial grassland yield has been less thoroughly studied. When water availability is a limiting factor, diverse perennial grassland biomass production is greatest in moist, lowland landscape positions [14,15]. In contrast, when moisture is excessive, perennial grassland yields are substantially reduced in poorly drained lowlands, at least in monoculture switchgrass (*Panicum virgatum* L.) systems [12,16]. However, in polyculture grasslands, soil hydrology plays an important role in structuring plant species assemblages, and plant species with adaptations to anaerobic stress are more likely to occur in inundated soils [17,18]. Therefore, it is not clear whether more diverse perennial grasslands would suffer yield losses similar to monoculture grasslands in poorly drained locations. If row crop yields suffer when exposed to excess moisture, but diverse perennial grassland yields do not, then poorly drained lowland landscape positions would be ideal for diverse grassland biofuel crops.

In addition to topography, the functional composition of species within diverse, perennial grasslands may have a considerable impact on yield. For example, at the stand scale, monoculture grasses typically have greater yield than forbs and mixtures of graminoids and forbs [19,20]. Similarly, at the regional scale, greater abundance of C4 grasses in diverse perennial grasslands increases overall yields [21]. However, it is not known whether these patterns result from greater aboveground net primary productivity (ANPP) in graminoids compared to forbs, greater harvest efficiency in graminoids (*i.e.*, the ratio of yield to ANPP), or a combination of both factors. A better mechanistic understanding of this effect could help to inform decisions regarding perennial grassland seed mixtures and harvest methods.

While yield is a primary objective of bioenergy agroecosystems, ecosystem services such as carbon sequestration and water quality regulation are also priorities [22]. Perennial grasslands can quickly accrue large stores of C in belowground biomass [23], and high belowground productivity accelerates soil organic matter formation [24]. However, belowground biomass and productivity is reduced in monoculture switchgrass stands when established in lowland landscape positions [25], thereby decreasing nutrient storage in belowground biomass and reducing the potential for soil organic matter formation. However, it is not clear whether a similar reduction in belowground biomass occurs from upland prairies to lowland prairies, where plant species may turnover in response to soil moisture.

Our broad objective was to evaluate the use of poorly drained, lowland landscape positions for the production of cellulosic biofuel biomass. Our specific objectives were (1) to quantify the effect of excess moisture on yields in row crops and diverse tallgrass prairies; (2) to evaluate the effect of graminoid dominance on overall prairie yield, ANPP, and harvest efficiency; and (3) to quantify the effects of excess moisture on live belowground biomass. We expected that row crops would suffer productivity losses in wet, lowland landscape positions, but that diverse, perennial grasslands would

be unaffected by saturated soil moisture conditions. Additionally, we expected greater ANPP and yields when graminoids were relatively more dominant. Finally, we anticipated that live belowground biomass would be reduced in lowland compared to upland row crops, but would remain similar between topographic positions in prairie. We evaluated our hypotheses in maize (*Zea mays* L.), winter wheat (*Triticum aestivum* L.), and restored tallgrass prairie systems in Northeast Wisconsin, USA.

2. Materials and Methods

2.1. Site Details

In 2009, we established six research plots in row crop production systems in Oneida, Wisconsin, USA (44.4660° N, 88.1804° W) and six plots in restored tallgrass prairie in Green Bay, Wisconsin, USA (44.5277° N, 87.9264° W). Although the sites are separated by 21 km, all research plots were located on the Kewaunee-Manawa soil series association. Both soil types are formed in deep, clayey till and are similar in terms of texture and horizonation [26]. Kewaunee soils are classified as fine, mixed, active, mesic Typic Hapludalfs and Manawa soils are fine, mixed, active, mesic Aquollic Hapludalfs [26]. Thus, Kewaunee soils are typically well-drained, upland soils, whereas Manawa soils are somewhat poorly drained, lowland soils [26,27]. At each site, we established three pairs of research plots in three separate fields, with one upland and one lowland plot per field. In order to conform to the sizes of lowland swales, plots were 15 m × 10 m and 15 m × 5 m in the row crop and prairie fields, respectively. Within each field, the upland and lowland plots were separated by an average of 45 m, ranging from 25 to 75 m. The row crop production fields were collectively owned and administered by the Oneida Nation of Wisconsin, but each field was managed independently in terms of crop selection and fertilizer application. Similarly, the tallgrass prairie restorations were collectively administered by the Cofrin Center for Biodiversity at the University of Wisconsin-Green Bay, but each field was restored independently and was typically managed separately. Average annual temperature is 6.9 °C and average total precipitation is 740 mm.

2.2. Field History and Management

Based on aerial photographs, row crop fields had been in crop production since at least 1938 (71 years). In the year prior to our study, maize (*Zea mays* L.) for grain was planted in all three crop fields. The fields were chisel plowed following the harvest in fall of 2008. In spring 2009, the soil was prepared with two passes by a field cultivator, and maize for silage (Dairyland HiF-3007-6) was planted in 76 cm rows. Liquid starter fertilizer was applied at planting at a rate of 9 kg$\cdot$N$\cdot$ha^{-1}, 27 kg$\cdot$P$_2$O$_5\cdot$ha^{-1}, and 6 kg$\cdot$K$_2$O$\cdot$ha^{-1}. Based on soil nutrient tests, urea N (Environmentally Smart Nitrogen, ESN) was applied at 148 kg$\cdot$N$\cdot$ha^{-1} on two of the maize fields and at 124 kg$\cdot$N$\cdot$ha^{-1} in the third field. All three maize fields received 135 kg$\cdot$K$_2$O$\cdot$ha^{-1}. Maize fields were sprayed with pre-emergence herbicides acetochlor, atrazine, and dichlormid at 2.03 L active ingredient (AI) ha^{-1}, 760 mL$\cdot$AI$\cdot$ha^{-1}, and 330 mL$\cdot$AI$\cdot$ha^{-1}, respectively. Maize fields were also sprayed with broadleaf herbicides clopyralid and flumetsulam at 130 mL$\cdot$AI$\cdot$ha^{-1} and 40 mL$\cdot$AI$\cdot$ha^{-1}, respectively. Following harvest of maize silage in September 2009, winter wheat (*Triticum aestivum* L.) was planted in 20 cm rows using a no-till grain drill. N fertilizer was applied as ESN, ammonium sulfate, and monoammonium phosphate at 49 kg$\cdot$N$\cdot$ha^{-1}, 24 kg$\cdot$N$\cdot$ha^{-1}, 12 kg$\cdot$N$\cdot$ha^{-1}, respectively. Potash was applied at 84 kg$\cdot$K$_2$O$\cdot$ha^{-1}, and P was applied at 58 kg$\cdot$P$_2$O$_5\cdot$ha^{-1} as monoammonium phosphate. Wheat fields were sprayed with the pre-emergence herbicide glyphosate and the broad-spectrum fungicide propiconazole at 960 mL$\cdot$AI$\cdot$ha^{-1} and 120 mL$\cdot$AI$\cdot$ha^{-1}, respectively. Wheat fields were also sprayed with the broadleaf herbicides pyrasulfotole, bromoxynil octanoate, and bromoxynil heptanoate at 30 mL$\cdot$AI$\cdot$ha^{-1}, 120 mL$\cdot$AI$\cdot$ha^{-1}, and 110 mL$\cdot$AI$\cdot$ha^{-1}, respectively. Winter wheat was harvested in July 2010.

Prior to restoration, all three of the prairie fields were in row crop production. Two of the prairie fields were in row crop production since at least 1938, while the third field entered crop production

sometime between 1938 and 1960. The three fields were converted to prairie in 1973, 1978, and 1982, 27 to 36 years prior to the onset of this study [28]. Since restoration, the prairies have been burned every few years to reduce woody plant encroachment. One of the prairie fields was burned in spring 2009, while the other two fields were burned three and five years earlier, respectively [28]. The fields have not been fertilized since prairie establishment. Mean species richness is 14.6 species m^{-2} among the prairies, and prairie species composition changes in response to soil moisture [29]. We previously documented 77 plant species present in the prairie plots [29], and a table of the most common species is available in Reference [29].

2.3. Plant and Soil Sampling

We estimated crop and prairie yield in six quadrats per plot. We collected row crop yield samples in September 2009 (maize) and July 2010 (winter wheat), just prior to field-scale mechanical harvest. We used 0.76 m × 0.80 m quadrats in order to conform to crop row spacing. To simulate mechanical harvest, we hand-clipped maize and wheat at 20 cm and 10 cm above the soil surface, respectively. We also collected the remaining stubble and weeds separately in order to estimate unharvested biomass (residue). For wheat, we separated the yield biomass into stalks and seedheads, and we further divided the seedheads into grain and chaff components. We considered the chaff to be unharvested residue.

For prairie, we collected yield samples following the first killing frost, which occurred in late October 2009 and early November 2010. Using 0.5 m × 1.0 m quadrats, we hand-clipped erect biomass at 10 cm above the soil surface in order to mimic mechanical harvest yield. We also collected the remaining stubble, but not the previous years' litter, in order to estimate unharvested biomass. In order to calculate harvest efficiency (yield/ANPP × 100), we measured prairie ANPP and yield in August and October 2011, respectively. ANPP was collected in the same fashion as yield, except that biomass was clipped at the soil surface in order to account for all aboveground biomass production. All biomass samples were dried for 48 h at 65 °C and weighed.

Concurrent with crop and prairie yield sampling, we took six soil cores per plot to measure live belowground biomass and soil properties. The cores were 6.2 cm in diameter, taken to a depth of 40 cm, and cut into 10 cm segments. The soil was air dried and sieved to 2 mm. A subsample of the soil was saved for chemical analysis, while the remaining soil was washed with DI water, and live belowground biomass was collected on a 500-μm sieve [30]. Belowground biomass was dried for 48 h at 65 °C and weighed. Soil texture was measured with the hydrometer method [31], and soil pH was determined in a 1:1 mixture of soil and water [32]. Soil organic C was measured on a Shimadzu SSM-5000A (Shimadzu Corp., Kyoto, Japan), and Bray P was measured on a Lachat Quikchem 8500 using the orthophosphate in Bray extract method (Hach Company, Loveland, CO, USA). Volumetric soil moisture (0–6 cm; *n* = 6 per plot) was measured approximately biweekly during the 2010 growing season (May–November) using a Delta-T ML2x ThetaProbe (Delta-T Devices Ltd., Cambridge, UK). A summary of soil properties is presented in Table 1.

Table 1. Soil properties in upland and lowland row crops and prairies (mean with standard error).

Property	Row Crop		Prairie	
Topographic position	Upland	Lowland	Upland	Lowland
Volumetric moisture (m$^3 \cdot$m^{-3})	29.5 (1)	38.2 (1)	33.5 (1)	44.4 (3)
Sand (%)	47.9 (6)	32.4 (12)	55.1 (10)	40.5 (1)
Silt (%)	35.1 (6)	36.6 (1)	31.1 (4)	34.3 (2)
Clay (%)	17.0 (2)	30.9 (11)	13.9 (7)	25.3 (2)
pH	6.8 (0.3)	7.5 (0.1)	6.1 (0.1)	7.3 (0.2)
SOC (%)	1.13 (0.2)	1.30 (0.2)	1.16 (0.1)	1.98 (0.7)
Bray P (ppm)	32.1 (16)	26.8 (6)	51.7 (20)	20.3 (6)

All properties are 0–40 cm averages, except for volumetric moisture, which is 0–6 cm.

2.4. Statistical Analyses

We used linear mixed models to evaluate the effect of topography on yield, unharvested biomass, and live belowground biomass. Since the crop and prairie sites were geographically separated, and because we were not interested in directly juxtaposing crop and prairie, we analyzed the effect of topography separately for row crops and prairie. We treated each field as a random block effect because each field was managed independently and upland and lowland plots were paired within a field. We used a repeated measures analysis to account for replicated sampling of the same plots in multiple years. To test the effect of graminoid abundance on prairie yield, we used a linear mixed model with yield as the response variable, percent graminoid (as determined from fall yield) as the independent variable, and a repeated term to account for three years of prairie yield measurements. Additionally, we used linear regression to test the effect of relative graminoid dominance (as determined in summer) on ANPP, yield, and the ratio of yield to ANPP. We used a significance level of 0.05 in all statistical tests. All statistical analyses were performed in SAS 9.4 (SAS Institute Inc., Cary, NC, USA).

3. Results

The primary portion of our study encompassed two divergent years in terms of temperature and precipitation. In 2009, mean annual temperature was 6.4 °C and precipitation totaled 700 mm, resulting in a slightly cooler and drier than normal year. In contrast, 2010 was warmer than average and was the second wettest year on record to date, with an average temperature of 8.3 °C and 970 mm of total precipitation. A secondary portion of our study was conducted in 2011, when mean temperature was 7.5 °C and total precipitation was 960 mm. Growing season volumetric soil moisture content was higher in lowlands compared to uplands by 29% and 33% in row crop and prairie, respectively (Table 1).

In both 2009 and 2010, row crop yields were significantly lower in lowland than upland topographic positions ($p = 0.001$), and there was no effect of year ($p = 0.130$) nor a significant interaction ($p = 0.228$; Table 2). In lowland areas, total maize silage and winter wheat yields were reduced by 71% and 64%, respectively (Figure 1a). Both wheat grain and wheat straw yields were 64% lower in lowlands than uplands. Topography did not affect prairie yield ($p = 0.117$), prairie yields did not vary between years ($p = 0.546$), and the interaction was not significant ($p = 0.635$; Table 2). In 2009 and 2010, the prairies yielded an average of 3.7 Mg dry matter (DM) ha^{-1}, with graminoids accounting for 39% of the yield (Figure 1b).
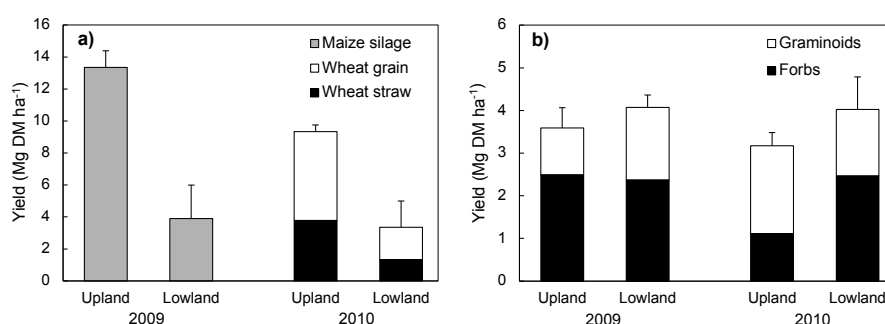

Figure 1. Upland and lowland yields in (**a**) row crops; (**b**) prairie. Error bars show the standard error of total yield. Note the differences in scale between panels.

There was a significant relationship between the percent of fall graminoid biomass and total fall yield in the prairie ($p = 0.020$; Figure 2), and the relationship did not vary by year ($p = 0.664$). The slope of the relationship indicated that for every 10 percentage point increase in the relative dominance of fall graminoid biomass, yields are expected to increase by 0.17 Mg·DM·ha^{-1} (Figure 2). Thus, yields increased by 45% as relative graminoid dominance increased from 5% to 95% (Figure 2). The relationship between percent summer graminoid biomass and fall yield, as measured in 2011, was also significant (Figure 3a). However, a higher percentage of summer graminoid biomass did not lead

to greater ANPP (Figure 3b). Rather, a greater percentage of summer graminoids was associated with higher harvest efficiency (Figure 3c), and thus higher yield (Figure 3a).
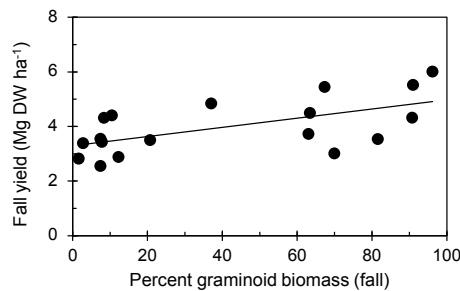

Figure 2. The relationship between the percent of fall graminoid biomass and fall prairie yield combined among 2009, 2010, and 2011. The effect of percent graminoid biomass was significant ($p = 0.020$), but the effect of year was not significant. Full model R^2 was 0.37.
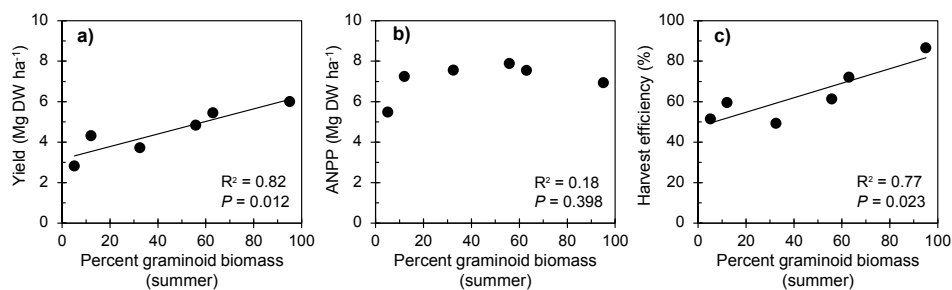

Figure 3. The relationship between graminoid biomass, as measured in at peak standing biomass in summer 2011, and (**a**) yield; (**b**) aboveground net primary productivity (ANPP); (**c**) harvest efficiency.

Mean live belowground biomass in the row crop systems was 2.3 Mg·DM·ha^{-1}, and there was no effect of topography, year, or the interaction (Figure 4a; Table 2). Mean live belowground prairie biomass was 11.5 Mg·DM·ha^{-1}, and belowground biomass was not affected by topography, year, or the interaction of topography and year (Figure 4b; Table 2). In row crop systems, unharvested residue did not vary as a function of topography or year, and there was no interaction between topography and year (Table 2). On average, 2.2 Mg·DM·ha^{-1} was left as residue in row crops (Figure 4a). Weeds accounted for a significant portion of unharvested residue in lowlands, but stubble and chaff accounted for most of the upland unharvested residue for maize and wheat crops, respectively (Figure 4a). Topography did not affect stubble residue in prairie, but there was slightly more residue in 2010 than 2009 (Table 2). On average, 0.89 Mg·DM·ha^{-1} of prairie stubble remained as residue (Figure 4b).
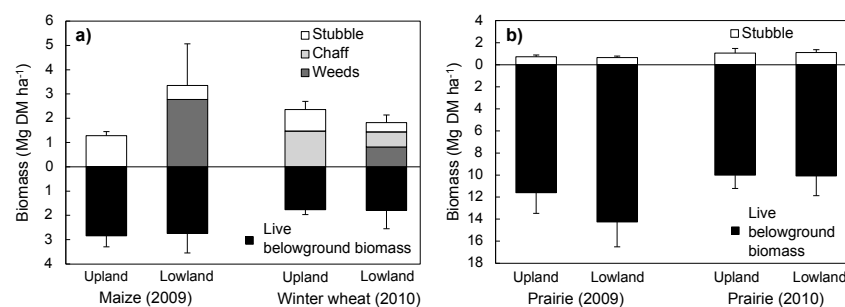

Figure 4. Upland and lowland unharvested biomass and belowground live biomass in (**a**) row crops; (**b**) prairie. Error bars depict the standard error of total above and belowground biomass. Note the differences in scale between panels.

Table 2. ANOVA table summarizing the influence of topography and year on yield, unharvested biomass, and live belowground biomass.

Parameter	System	Effect *p*-Value		
		Topography	Year	Topography × Year
Yield	Row crop	0.001	0.130	0.228
	Prairie	0.117	0.546	0.635
Live belowground biomass	Row crop	0.953	0.143	0.919
	Prairie	0.481	0.164	0.506
Unharvested residue	Row crop	0.405	0.801	0.179
	Prairie	0.957	0.028	0.706

4. Discussion

4.1. Prairie Biomass Production Is Viable in Seasonally Saturated Lowlands

Row crop yields were reduced by 64% to 71% in wet, lowland landscape positions compared to drier upland locations (Figure 1a). Other studies have generally shown smaller crop yield reductions in lowland topographic positions. For example, compared to the summit landscape position, Thelemann *et al.* (2010) demonstrated 26% and 40% yield reduction in maize (grain + stover) within depositional and flat landscape positions, respectively [12]. Yield reductions of 7%–11% have been observed when winter wheat has been subjected to waterlogging at individual growth stages [33]. The larger crop yield reductions found in our study may be a function of greater soil clay content (Table 1) and a subsequent prolonged lack of drainage, as yield reductions have been observed to increase with waterlogging duration [34]. Based on our plot selection process, differences between uplands and lowlands reported here likely represent the maximum yield variability within our fields. In contrast to row crops, we found that prairie yields were statistically equal between seasonally saturated lowland areas and well-drained upland positions (Figure 1b). Relatively few other agronomic studies have examined the effect of landscape position on perennial grassland biomass yield, and most of those studies have examined monoculture grasslands. For example, switchgrass yield reductions of 14% to 54% have been recorded in wet, depositional areas compared to well-drained uplands [12,16,35]. In warmer, drier regions, water is often limiting to prairie production [15], particularly in upland landscape locations [14]. At our site, it is possible that water availability limits upland production, but that excess water limits production in lowlands, thereby leading to similar production in uplands and lowlands. However, considering that our site received 30% above average precipitation in 2010, it seems unlikely that inadequate water supply limited production in the uplands, particularly in that year.

We acknowledge that row crop and prairie yields may show significant inter-annual variability, and thus our two-year study may not be representative of all years. Nonetheless, despite disparate total precipitation in 2009 and 2010, lowland row crop yields were negatively impacted to a similar extent in both years (Figure 1a). One potential explanation for this finding may relate to the strong effects of spring soil moisture conditions on establishment and thus on fall yields. For example, excessive accumulation of soil moisture from spring snow melt or precipitation can negatively impact both seedling germination and growth of annual row crops [10,13]. In contrast to annual row crops, perennial prairie biomass yield was consistently similar among upland and lowland topographic positions (Figure 1b). However, we acknowledge that if water becomes limiting in a drought year, both crop and prairie yields are likely to suffer overall yield reductions, particularly in the uplands [8,14].

The ability of our diverse, perennial grassland to maintain biomass yields across divergent soil moisture conditions was likely in part a function of changing plant species composition from wet to dry landscape locations at our site [29]. Prairie cordgrass (*Spartina pectinata* Bosc ex Link), Culver's root (*Veronicastrum virginicum* (L.) Farw.), and bluejoint grass (*Calamagrostis canadensis* (Michx.) P.Beauv.), all

of which are wet prairie indicator species [36], were found exclusively in lowlands within our prairie. Other wetland species such as lake sedge (*Carex lacustris* Willd.), narrowleaf cattail (*Typha angustifolia* L.), and rushes (*Jucus* spp.) were also found in the wet, lowland topographic positions. The development of aerenchyma and other morphological adaptations allows these plants to thrive in inundated soils [17,37]. While both maize and wheat can form aerenchyma when flooded [38], most row crops are still quite vulnerable to waterlogging, particularly when the plants are young and least able to cope with the anaerobic stress [10]. In our study region, row crops that are planted in the spring are likely to be exposed water-saturated soils [39], thereby increasing the probability of crop yield reduction.

Although the lowland row crop yields were on par with prairie yields (Figure 1a,b), the ecosystem services offered by the prairie may provide the additional motivation necessary to convert lowland row crop areas to diverse prairie. We found no effect of topography on live belowground biomass in prairie or row crops, but live belowground biomass was approximately five times greater in prairie compared to row crops (Figure 4a,b). The lack of a topographic effect on live belowground biomass in row crops may be due to the significant weed growth in lowlands (Figure 4a) which may have compensated for reduced crop-derived belowground biomass. Whereas the live belowground biomass pool is relatively small and temporary in annual row crops, the live belowground biomass pool in prairie represents a large, quickly accruing stock of C, N, and P that will remain stable for as long as the prairies are maintained. Additionally, compared with aboveground biomass, roots contribute proportionally more to stable soil organic matter formation [40]. Anderson-Teixeira (2013) reported a similar difference between maize and prairie belowground biomass, but they also found that belowground biomass was greater in switchgrass than prairie [23]. However, it is important to consider that belowground biomass and production in switchgrass may be substantially reduced if the plants are exposed to excessive soil moisture [25,41]. Thus, when planted in wet, lowland locations, switchgrass and other monoculture perennial grasses may not reap the same benefits as prairie in terms of belowground nutrient sequestration in belowground biomass and soil organic matter formation potential.

4.2. Harvest Efficiency Is Greater in Graminoids Compared to Forbs

In all three years, biomass yields increased significantly as relative summer graminoid dominance increased (Figure 2). However, this trend was not due to intrinsically greater ANPP in graminoid-dominated plots (Figure 3b). Rather, harvest efficiency improved from 51% to 86% as relative summer graminoid dominance increased from 5% to 95% (Figure 3c). Therefore, the relationship between summer graminoid dominance and yield is a result of greater harvest efficiency, not greater ANPP, in graminoids compared to forbs. Forb leaves tend to become brittle following plant senescence, and therefore more pre-harvest litterfall might be expected from forbs compared to graminoids. There is some previous evidence to support our finding. Sanford *et al.* (2016) reported that four-year average harvest efficiency increased from 35% in prairie (a mix of graminoids and forbs) to 61% in monoculture switchgrass [20]. However, at another site, the same study reported a mere one percentage point increase in five-year average harvest efficiency from mixed prairie to switchgrass [20]. Therefore, while harvest efficiency is generally greater in graminoids than forbs, the precise difference in harvest efficiency between graminoids and forbs may depend upon the individual plant species and harvest methods. Earlier harvest may help to improve harvest efficiency, but the yield gain must be weighed against the potential for greater removal of nitrogen in biomass, as plant nitrogen resorption may be incomplete [42]. Additional research is necessary to address this tradeoff in prairie biomass cropping systems.

Although yields were greater when graminoids were more dominant, forbs are nonetheless an important component of species-diverse prairie biomass cropping systems. While leguminous forbs produce relatively little harvestable biomass, they may provide sufficient plant-available nitrogen to maintain high graminoid biomass yields in the absence of nitrogen fertilizer [43]. Grasses provide higher potential ethanol yields per unit biomass [21,44], but forbs offer greater energy content per unit biomass when the biomass is directly combusted or thermochemically converted to other fuels [44].

From an ecosystem services standpoint, lower harvest efficiency in forbs may actually be a desirable trait; analogous to maize stover retention [45], the unharvested forb litterfall may help to increase soil organic matter, reduce erosion, and improve water quality. From a yield standpoint, biofuel plantings may seek to include forbs with grass-like morphologies to reduce shading of grasses by forbs and promote higher end-of-year harvest efficiency. Clearly, these points require further investigation.

4.3. Implications for Regional Biofuel Production

Due to the substantial acreage of non-forested marginal land, Northeast Wisconsin has been identified as a candidate cellulosic biomass production area [4]. Much of the Eastern region is dominated by clayey soils which are subject to frequent water saturation and subsequent limitations to agricultural production [39]. Tile drainage is often necessary to support row crop agriculture, but lowland topographic areas may still experience seasonal saturation [27]. Nonetheless, much of the landscape is cultivated in order to support the large dairy operations in the region [46]. Non-point source phosphorous runoff from agricultural production contributes substantially to the impairment of local water bodies [47,48]. As such, several watersheds within the region are required to reduce phosphorus loading to surface waters by 36% to 77% [49].

If established in lowland agricultural drainage areas and riparian zones, perennial grasslands could help to reduce phosphorous runoff to waterways while reducing the monetary impact to farmers through the sale of biomass for fuel. For example, a modeling study in southern Wisconsin found that the targeted establishment of perennial grasslands in riparian areas that are currently occupied by row crop agriculture would reduce phosphorus runoff by 29% while occupying only 17% of current agricultural land in the watershed [50]. The same study found additional environmental benefits of perennial grassland establishment including higher carbon sequestration, lower nitrous oxide emissions, and greater pollinator abundance. Compared to traditional crops, perennial grassland biomass is a less profitable commodity, but the value of ecosystem services provided by the grasslands likely outweighs the loss of saleable goods [50]. Due to suboptimal biochemical conversion efficiencies, the market for cellulosic ethanol feedstocks is currently limited. However, thermochemical conversion and direct combustion technologies are more efficient [44] and thus are presently more practical options for diverse cellulosic sources.

Compared to switchgrass, the cultivation of wet-mesic prairie species is a relatively new endeavor. Considerable costs and expertise may be required to establish wet-mesic prairies within a timeframe that is compatible with monoculture grassland crop agriculture (*i.e.*, 1–2 years before first harvest). For example, while prairie cordgrass can produce biomass yields on par with switchgrass [51], establishment by seed drilling may be ineffective in inundated conditions, and the use of plant plugs may be necessary for establishment [52]. Additionally, the seed viability of some wetland plant species decreases significantly over the course of a year, and germination rates may approach zero within six months [53]. Thus, very fresh seed may be required for successful establishment. Saturated soils in the Midwestern USA are also susceptible to invasions by aggressive species such as reed canary grass (*Phalaris arundinacea* L.) and common reed (*Phragmites australis* (Cav.) Trin. ex Steud.). For example, Mulhouse and Galatowitsch (2003) found that reed canary grass was present in all 41 of the Midwest restored prairie potholes that they surveyed 12 years after initial restoration [54]. Invasive species may be controlled with herbicides or fire, but such methods are costly and counterproductive to biomass production. Alternatively, if lowland invasive species are harvested for biofuel production, many of the ecosystem services that would have been provided by prairie may still be realized [55,56].

5. Conclusions

We found that row crop yields were reduced by more than 60% in seasonally saturated, lowland landscape positions compared with well-drained uplands, and similar yield reductions were observed in relatively wet and dry years. On the contrary, diverse tallgrass prairies yielded similarly in upland and lowland topographic positions in both wet and dry years. Prairie yields increased as graminoids

became relatively more dominant, an effect due to greater harvest efficiency, not greater ANPP, in graminoids compared to forbs. There was no effect of topography on live belowground biomass or unharvested aboveground biomass (residue) in both row crops and prairie, indicating similar nutrient sequestration potential in both topographic positions. Overall our results indicate that seasonally-saturated, marginal lowlands would be ideal for diverse prairie biomass agriculture, and prairie yields could be enhanced by increasing relative graminoid dominance or by improving forb harvest efficiency.

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Abbreviations

The following abbreviations are used in this manuscript:

AI	Active Ingredient
ANPP	Aboveground Net Primary Productivity
DM	Dry Matter
ESN	Environmentally Smart Nitrogen
SOC	Soil Organic Carbon

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