TITLE: Distribution of switchgrass (*Panicum virgatum* L.) aboveground biomass in response to nitrogen addition and across harvest dates

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ABSTRACT

Decisions about the harvest timing for switchgrass (*Panicum virgatum* L.) crops has important implications for economic and environmental objectives because there may be a significant trade-off between harvestable yield, bioenergy crop quality, and environmental cost or benefit. We investigated the effects of harvest timing and nitrogen (N) addition on switchgrass crops established in Wisconsin, USA to investigate the causes of biomass loss over time and to identify plant components that contribute to N loss or retention at each harvest date. We found that harvestable yield decreased over successive harvest dates, as a result of the physical loss of leaves and inflorescence biomass. Although N addition increased total aboveground biomass, it

also increased the proportion of biomass occurring as leaves and inflorescence. Leaf and inflorescence biomass decreased over time and during harvest operations; however, this biomass became incorporated into the litter pool and increased on-site N retention. We conclude that although adding N to switchgrass is unlikely to increase harvestable yield when harvests are conducted after plant senescence, retention of high-N plant components will help maintain long-term site productivity and ecosystem function of bioenergy cropping systems, especially for sites targeted for low-input management.

KEYWORDS: Bioenergy crop, sustainability, reconstructed grassland, crop residue, Wisconsin

ABBREVIATIONS: GCWF: Grant County working farms, AARS: Arlington Agricultural Research Station

1. INTRODUCTION

Perennial native grasses such as switchgrass (*Panicum virgatum* L.) have been identified as significant sources of feedstock for cellulosic biofuels [1]. High-yielding and efficient nutrient-use attributes [2] give perennial grasses potential to provide environmental, economic, and societal benefits as bioenergy sources, if managed properly [3]. Environmental benefits provided by switchgrass crops include providing habitat for wildlife [4–9], sequestering carbon and increasing soil organic matter [10–12], decreasing erosion via extensive root systems [13–15], and retaining nitrogen (N) on site [16]. Proper timing of fertilization and harvest are key to sustainable management [17], as these factors affect nutrient dynamics [18], biomass quality and quantity [19,20], and ecosystem processes [5,21].

Nitrogen (N) addition is recommended to increase and maintain switchgrass yields [1], however, highly variable responses have been reported [13,22–24] and the response to N is uncertain for many perennial grass bioenergy crops [25]. Because exogenous N is a major source of agricultural pollution [26,27], N conservation should be a primary sustainability concern for bioenergy production. Understanding retranslocation processes for nutrient and carbohydrate recycling during senescence of perennial grasses [28–30] is important for making informed nutrient management choices, and timing crop harvests to maximize nutrient retranslocation may decrease need for future inputs. However, trade-offs among yield, crop quality, and environmental cost or benefit are inherent in decisions about the timing of switchgrass harvest, with economic and environmental implications. Although delaying harvest maximizes nutrient retranslocation, delays also reduce yield [24,30–35] and can result in significant economic loss for farmers [16].

Seed and leaf shatter through litterfall, carbohydrate and nutrient retranslocation, and herbivory can all contribute to biomass loss over time, as can biomass loss from

1 mechanical/harvest inefficiencies during field operations. The baling process for a lowland
2 switchgrass variety in Texas resulted in 1 to 5% yield loss [36], whereas 21% and 40% yield loss
3 was observed in autumn and spring switchgrass harvest in Pennsylvania, respectively [35]. These
4 examples illustrate that yield loss occurs when balers leave plant residues in the field, and that
5 the loss increases with time when harvest is delayed. Unharvested litter may equal up to 50% of
6 harvested biomass [30,35,37], and between 5 to 25% of total biomass [30,35,38]. The factors that
7 contribute to the accumulation of biomass residue on the ground surface are not well understood.

8 Retranslocation of mineral nutrients and carbohydrates to belowground tissues for storage
9 overwinter also contributes to yield loss [39–43]. Carbohydrate retranslocation can decrease
10 switchgrass yield by 15% over a two-month period [44]. Similarly, 20 to 60% of peak N is
11 retranslocated in switchgrass [16,24,31,45]; however, fertilization decreases N retranslocation,
12 suggesting that N addition may compromise the N conservation strategies of perennial grasses
13 [24]. However, much more information is needed to understand the effects of environmental and
14 fertility factors on the timing and rates of retranslocation in switchgrass [46,47].

15 Retranslocation, leaf shatter, and harvest inefficiencies can also influence the quality of
16 harvested biomass and crop residues. Chemical composition differs between the plant
17 components that make up the litter pool versus harvested biomass [48,49], and leaf shatter
18 contributes to an increase in leaf biomass in the litter pool during senescence, with a concurrent
19 decrease in leaf-to-stem ratios on standing biomass [32]. Because litter quality and quantity
20 affects nutrient cycling, decomposition rates and plant community composition [50–52], litter
21 chemical composition directly affects ecosystem functioning [53]. Thus, management decisions
22 can affect the interplay among agronomic, ecological and economic parameters of a perennial
23 bioenergy cropping system.

Our objectives were to characterize yield and N retention in switchgrass with delayed harvests under N addition and contrasting environmental conditions. First, we compared mechanical versus hand-harvesting of switchgrass to estimate yield loss associated with field operations. We then asked how biomass and N allocation in different plant parts change through senescence across time using 1) three levels of N addition and 2) four farm locations in hand-harvested plots. Results from this study provide benefit to ongoing efforts to develop economically and environmentally sustainable biofuel systems by quantifying differences between potential and harvestable yield, and by characterizing the effect of N addition on harvestable yield at contrasting harvest dates.

[Note to editor: insert Figure 1 and Table 1 near this location]

2. METHODS

2.1 Site description

This research was part of two larger studies at the University of Wisconsin-Madison (Figure 1). One study site was located on working farms in Grant County, WI (hereafter, GCWF; 42.734° N, 90.479° W, elev 303 m asl) and was designed to evaluate the effectiveness of weed management methods for switchgrass (*var.* Cave-in-Rock) establishment [54]. Here we focus on three of six original farms (hereafter DS, SC, and WO). The average temperature and total precipitation for the April to October growing season in 2010 was 17.8 °C and 579 mm, respectively, with annual mean temperature and total precipitation 9.4 °C and 633 mm, respectively, for the nearby town of Platteville, WI [55]. Fields were established in 2008 and treated with a mixture of glyphosate (140 g ha⁻¹ acid equivalent) and imazapic (70 g ha⁻¹ acid equivalent) before switchgrass emergence to control weed competition. We established five 3 ×

30 m experimental blocks at each farm, each with four plots to which we randomly assigned harvest timing (late August, late September, and early November in 2010, and mid-April 2011, hereafter AUG, SEP, NOV, APR). One of the farms (WO) was mechanically harvested after the NOV experimental harvest, therefore the APR data we present represents two farms only (DS, SC).

The second study site was located at the Arlington Agricultural Research Station (AARS) in Columbia County, WI (43.301° N, 89.347° W, elevation 320 m asl). The average temperature and total precipitation for the April to October growing season in 2010 was 17.2 °C and 830 mm, respectively, with annual mean temperature and total precipitation 9.4 °C and 962 mm, respectively [56]. We overlaid our sampling on a pre-existing study designed to evaluate switchgrass yield response (*var.* Hiawatha) to ammonium nitrate (0 kg ha⁻¹, 56 kg ha⁻¹, and 112 kg ha⁻¹) [57]. This site was seeded in 2007 using seeds that resulted from a second-selection cycle [58] and was harvested in 2008 and 2009 prior to the initiation of our study. Nitrogen treatments were randomly assigned within blocks to 1.5 m × 8 m plots, each of which was divided into nine 0.9 m × 1.5 m subplots. We selected five block × plot combinations to obtain five replicates of each fertilization level, and randomly assigned harvest timing (AUG, SEP, and NOV). Soil characteristics at GCWF and AARS are given in Table 1.

2.2 Field and laboratory methods

We used a 0.5-m² sampling frame for GCWF, and a 0.13-m² sampling frame for AARS. We hand-clipped all standing biomass to 15 cm stubble height, collected litter (i.e., unattached biomass on the ground surface, hereafter “residual biomass”) and then collected the stubble by clipping to the ground surface. We separated standing biomass into stem, leaf and inflorescence

components. We separated inflorescences at the base of the lowest-most panicle branch, and leaves at the base of the leaf blade. We dried samples to constant mass at 60° C before weighing, ground subsamples in a Wiley mill to pass a <1 mm screen, then pulverized samples to fine powder in a ball mill before analyzing for C and N concentrations (mass fraction) using a Flash EA 1112 CN Automatic Elemental Analyzer (Thermo Finnigan, Milan, Italy).

After hand-harvesting, we conducted field-scale mechanical harvesting at GCWF by mowing to 15 cm and baling harvested biomass into round bales using conventional farm equipment. We measured bale weights in the field and collected a subsample of wet biomass which was dried at 60 °C to constant mass to calculate dry mass equivalent of mechanically-harvested biomass. We added the dry mass of hand-harvested plots to field-scale weights to determine total mechanical yield.

2.3 Statistical methods

We performed all statistical analyses with SAS 9.3 (SAS Institute, Carey, NC). To evaluate differences in biomass and N removal from harvest timing and differences among farms within Grant County, we used linear mixed models (PROC MIXED) with harvest month, farm and their interaction as fixed effects, and experimental block $\times$ farm as a random effect. Because one of the three farms was harvested before the APR sampling period, we limited among-month statistical comparisons to AUG, SEP and NOV. To meet model assumptions, we log-transformed (litter biomass, C:N ratio, and C mass; inflorescence N mass fraction) or ranked (litter N mass; stem C:N ratio) data before analysis. To evaluate N fertilization effects on biomass and N removal by harvest date at AARS, we used harvest month, fertilization level and their interaction term as fixed effects, and block and block $\times$ fertilization level as random effects. To meet model

assumptions, we log-transformed (total harvestable biomass N mass; litter mass and C mass; stem biomass and C mass; leaf N mass) or ranked (total aboveground biomass N mass; litter N mass; inflorescence N mass fraction; stem C and N mass fractions and N mass; leaf C mass fraction and C:N ratio) data before analysis. Significant fixed effects were followed with means separation tests using Tukey's adjustment for multiple comparisons. We determined statistical significance at $p < 0.05$.

3. RESULTS

3.1 Harvested and total aboveground biomass

Averaged across site at GCWF, field-scale mechanical harvest of the switchgrass crop in November yielded $4.19 \pm 0.99 \text{ Mg ha}^{-1}$, whereas hand-harvesting yielded $53\% \pm 2\%$ more biomass. Greater fragmentation and dispersal of plant fragments occurred during field-scale mechanical harvests than during plot-scale manual harvests (personal observation). The results presented below identify the plant components that become more susceptible to physical separation over time. At GCWF, harvested (i.e., to 15 cm stubble height) and total aboveground biomass was greater in SEP than in AUG or NOV, and there were no differences among farms within months (Figure 2a, 2b, Table 2). Averaged across farms, 87.3% of total aboveground biomass was removed by harvesting in AUG, 90.4% in SEP, 89.8% in NOV, and 63.2% in APR.

[Note to editor: insert Figure 2, Table 2 and Table 3 near this location]

At AARS, N addition increased harvested and total aboveground biomass across months (Table 3). Harvested biomass decreased in NOV relative to AUG and SEP (Figure 3a), whereas the overall effect of month was not significant (across all fertility levels) for total aboveground

biomass (Figure 3b). The percentage of total aboveground biomass removed by harvesting peaked in SEP for the unfertilized treatment (84.1%, 86.9%, and 80.5% for AUG, SEP, and NOV, respectively), whereas it decreased at each harvest time for the 112 kg ha⁻¹ treatment (91.1%, 88.3%, and 75.1% for AUG, SEP, and NOV, respectively) and remained relatively constant for the 56 kg ha⁻¹ treatment (86.8%, 86.9% and 84.1% for AUG, SEP, and NOV, respectively).3.2 *Within-plant distribution of biomass*

Plant stems contributed the majority of harvested biomass at all harvest periods for both study sites, and the stem proportion of harvested biomass increased over time, whereas the leaf and inflorescence proportions decreased (Figures 3, 4). Averaged across farms, the inflorescence proportion of harvested biomass at GCWF decreased over time, from 8.0% in AUG to 2.3% in APR (Figure 4a); in contrast, the litter proportion of total aboveground biomass at GCWF increased dramatically over the study period, from <4.0% in AUG and SEP to 5.1% in NOV and 26.2% in APR (Figure 4b). The proportion of total aboveground biomass attributed to residual biomass ranged between 12 and 43% across sites and harvest periods, and was greatest at the April harvest for GCWF.

Nitrogen inputs at AARS increased biomass allocation to the inflorescence, and this pattern was evident at all harvest timings in harvested biomass (Figure 5a) and in total aboveground biomass (Figure 5b). The inflorescence contributed 17 to 28% of harvested biomass in AUG and only 4 to 10% in NOV. The greatest increase in the proportion of total aboveground biomass present as residual biomass that occurred was observed in the 112 kg ha⁻¹ N addition treatment (Figure 5b), whereas the proportion at AARS in NOV was 23%, 18% and 35% for the 0 kg ha⁻¹, 56 kg ha⁻¹ and 112 kg ha⁻¹ N addition levels, respectively.

1 *[Note to editor: insert Figure 3 and Figure 4 near this location]*

3 *3.3 Nitrogen pools in harvested and residual biomass at each harvest period*

4 Differences in N mass across the study period at GCWF followed a pattern similar to
5 biomass, with greatest N mass in SEP for harvested biomass (Figure 2c) and total aboveground
6 biomass (Figure 2d) and no significant differences in N mass between AUG and NOV. Leaves
7 contributed the greatest proportion of total aboveground N mass in AUG through NOV harvests
8 at GCWF (3d), and in the 0 kg ha⁻¹ N treatments at AARS (Figure 5d). Our results from GCWF
9 showed that delaying harvest until spring leaves >40% of N in plant biomass on site as litter and
10 stubble. A much greater proportion of total aboveground N occurred in litter and stubble in APR,
11 and this followed the pattern we observed for litter and stubble contributions to total
12 aboveground biomass (Figure 4d). Nearly 50% of N mass remained on site at GCWF following
13 the APR harvest (Figure 4b, 4d).

14 We observed a trend of decreasing N mass in harvested and total aboveground biomass
15 over time at AARS, although only NOV was significantly less than AUG and SEP, across
16 fertility levels (Figure 3c, 3d). Much less N was removed in NOV harvest than in AUG or SEP
17 harvest. Nitrogen addition increased N in the inflorescence in AUG and NOV. Leaves
18 contributed the majority of N mass in the 0 kg ha⁻¹ N treatment in NOV, whereas the majority of
19 N in harvested biomass in the 112 kg ha⁻¹ N treatment was present in plant stems (Figure 5c).
20 Although there was a trend towards increased harvestable biomass with N addition level (Figure
21 3a), 25.6% of the biomass in the 112 kg ha⁻¹ N treatment in AUG occurred as inflorescence
22 (Figure 5a), and the 112 kg ha⁻¹ N treatment also resulted in the greatest proportion of total
23 aboveground biomass present as litter in NOV (Figure 5b). This treatment also supported the
24 greatest proportion of biomass N in residual (litter and stubble) biomass (Figure 5d). Harvesting

in AUG removed >90% of total plant N in biomass, whereas harvesting in NOV removed only 60% to 80% of biomass N meaning NOV harvests retained more N on site relative to AUG or SEP harvests (Figure 5d).

[Note to editor: insert Figure 5 near this location]

3.4 Harvest timing effects on residual biomass quality

Litter quality (indicated by C:N ratio, where smaller ratios indicate greater litter quality) differed among GCWF farms (SC > DS, WO), whereas there was no effect of harvest timing (Figure 6a, Table 2). In contrast, stubble C:N differed among months and farms, with a significant month × farm interaction (Figure 6b, Table 2). Lower stubble quality occurred in NOV than AUG or SEP, and this effect was evident even when there were differences in quality among farms (Figure 6b, Table 2). Litter C:N ratios at AARS were greater in AUG than SEP, and intermediate in NOV across N treatments (Figure 6c, Table 3). Across months, both levels of N treatment decreased litter C:N ratio relative to the unfertilized control (Figure 6c, Table 3), whereas the stubble C:N ratio was greater in the 0 kg ha⁻¹ and 50 kg ha⁻¹ N treatments than the 112 kg ha⁻¹ N treatment, with no differences among dates (Figure 6d, Table 4).

[Note to editor: insert Figure 6 near this location]

4. DISCUSSION

4.1 Delayed harvest and N addition alters biomass distribution among plant parts

Over time during fall and into spring, an increasing proportion of plant biomass becomes incorporated into the litter pool. Litter and stubble are the major plant components that are

unharvestable by conventional farm equipment, and this residual biomass left on site contributes to the pool of potentially available nutrients that become incorporated into soil as dead plant material decays. The composition of plant components that comprise litter changed across harvest dates and was influenced by N addition level. Nitrogen addition increased the biomass of plant components that are most easily lost during senescence and mechanical harvest, such as inflorescence and leaves [16,35], indicating that high levels of N addition may be ineffective for increasing harvestable biomass. The N addition benefit to switchgrass productivity was transient as seed shatter and physical breakage contributes to the loss of inflorescence biomass; thus, N addition did not increase post-senescence yield. Our results agree with previous studies reporting loss in yield over time as harvest is delayed, although site characteristics, switchgrass variety, and time since crop establishment contribute to variability in the proportion of total aboveground biomass that exists as residual biomass. Similar to our results, other researchers have shown that the transfer of leaves and inflorescences from plant stems into the litter pool contributes to major losses in harvestable biomass [16,35]. However, the increase in dominance by stem biomass over time may translate to improved quality of biomass for bioenergy via greater fiber content [48] and lower N concentration (mass fraction) in stems, which is desirable for both combustion and fermentation technologies [19].

Over-winter losses in harvested biomass in this study were much smaller than the 40% loss reported between autumn (Oct-Nov) and spring (Apr-May) harvests of switchgrass in Pennsylvania, which was attributed to the inability of the baler to pick up approximately 20% of biomass in autumn and 40% in spring [35]. In contrast, evaluating changes in total aboveground biomass illustrates biophysical influences on switchgrass biomass loss, such as carbohydrate loss, herbivory, and/or fragmentation and wind-dispersal of biomass. Retranslocation of non-

1 structural carbohydrates to roots can account for a significant aboveground mass loss from
2 summer to fall [44,59,60], whereas more limited estimates available to date show that biomass
3 loss to insect herbivory is small relative to inherent yield variation, as insecticide treatments only
4 marginally increase yield [57]. Finally, some biomass is lost via wind-dispersal and litter
5 components not recoverable in our sampling (i.e., dropped seeds, which were not collectable in
6 our litter sampling). The mass loss we observed is within range of what others have attributed to
7 carbohydrate retranslocation [44,59,60]. We assume that the majority of unaccounted mass loss
8 in our study resulted from carbohydrate retranslocation.

9 Our method of hand-harvesting biomass plots likely explains the relatively small
10 decrease in harvestable biomass we observed over time compared to studies that involved
11 mechanical harvest [35,36], however, we emphasize that our approach was designed to identify
12 changes in the relative contribution of specific plant components to harvested and total
13 aboveground biomass. Other authors have reported a 36% yield loss for mechanical harvests
14 compared to hand harvesting, attributed to both uncut stems missed by the mower as well as
15 biomass missed by the baler [61]; our loss estimate was much greater, which suggests that
16 biomass, within-plant distribution of biomass components, region and harvest efficiency
17 influence perennial bioenergy crop yield.

18 19 *4.2 C and N response to harvest timing and N addition*

20 Our results showed that N addition and harvest timing affect residual C and N pools,
21 which together are likely to influence site productivity and ecosystem function over the longer
22 term. Although the overall effect of N addition increased harvestable biomass relative to the
23 control, N addition also contributed to greater plant biomass – and consequently N mass – being

1 retained on site as residual biomass. Retaining plant biomass on site helps maintain and/or
2 increase soil organic matter content [62], which in turn benefits soil structure and nutrient supply
3 and retention. Our study showed among-farm differences in litter quality at GCWF, and
4 decreased C:N ratios with high N addition at AARS relative to the control. The type of plant
5 tissue incorporated into soil is important for microbial processes, as greater N mineralization
6 occurs from leaf biomass than from stem biomass, and soil respiration rates increase with the
7 mass fraction of N in biomass N [21]. Thus, harvest timing, N addition, and environmental
8 conditions can each influence not only the quantity, but also the quality of residual biomass.

9 Nitrogen retained on site in residual biomass provides an important pool of potentially
10 cycling N that will contribute to longer-term site productivity. In our study, delaying harvest
11 timing increased both total residual biomass and N mass. Although N addition may contribute to
12 greater site productivity over the longer term via the accumulation of organic matter, in some
13 situations no changes in soil organic matter content occur over time in switchgrass
14 monocultures[63]. The effects of N addition on decomposition may have variable effects on C
15 retention, depending on the soil organic matter fraction and soil texture [64].

17 *4.3 Agronomic, environmental and economic implications*

18 Management of perennial bioenergy cropping systems will dictate many of the
19 agronomic, ecological and economic trade-offs that exist among management scenarios. Some
20 authors report an economic advantage to harvest as close to senescence as possible [16], and
21 others conclude that the cost of delaying harvest to spring is offset by the savings in P and K
22 fertilizers (and no change in N fertilizer savings) [34]. However, nutrient conservation may not
23 always be economically valuable to a farmer depending on fertilizer prices. Often the economic

1 risk of under-applying fertilizer contributes to farmer over-application for risk management [65].
2 Further, economic trade-offs between yield and nutrient conservation may differ considerably by
3 site and year, depending on the severity of winter weather conditions [35]. Removing all
4 standing biomass may decrease the value of perennial grassland sites for wildlife, but late-season
5 harvests can lessen impacts on wildlife (such as grassland birds) habitat [4], but can translate into
6 yield and economic loss. Ultimately, land management decisions will be largely driven by the
7 attitudes and priorities of the land managers, which are affected by numerous socioeconomic
8 factors such as farmer knowledge of production practices, attitudes toward profit or
9 environmental sustainability, and market conditions [66]. Policy incentives may be needed to
10 alleviate the opportunity costs of managing for ecosystem services such as C and N retention or
11 wildlife habitat , and to encourage producers to plant switchgrass [67]. Understanding the causes
12 and pathways of biomass loss with delayed harvests may help lessen the trade-offs farmers face.

14 *4.4 Conclusions*

15 Our study showed that although adding N to switchgrass is unlikely to increase
16 harvestable yield when harvests are conducted after plant senescence, retention of high-N plant
17 components will help maintain long-term site productivity and ecosystem function of bioenergy
18 cropping systems. Thus, initial or periodic N amendments are likely to support sustained
19 productivity of sites targeted for low-input management by increasing the residual biomass and
20 the stock of N retained on site in decomposing organic materials. Where N amendment is
21 economically undesirable, initial or periodic spring harvest has potential to provide similar N
22 retention in unharvestable residual biomass.

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Tables

Table 1. Soil classification and 0-10 cm texture and nutrient concentrations at the Grant County working farms (GCWF) and the Arlington Agricultural Research Station (AARS). Values for GCWF represent composited samples and values for AARS represent mean (s.e.) of 20 samples within site.

Study	Location	Soil map unit	Sand (%)	Silt (%)	Clay (%)	C (g kg ⁻¹)	N (g kg ⁻¹)	C:N
GCWF	DS	Fayette silt loam	7	72	21	16.26	1.70	9.11
	SC	Hixton loam	19	68	13	18.00	1.84	9.79
	WO	Dubuque silt loam	9	78	13	29.05	3.05	9.52
AARS	--	Plano silt loam	9 (0.5)	66 (0.5)	25 (0.3)	18.6 (2.3)	1.9 (0.7)	11.1 (0.6)

Table 2. ANOVA results for comparisons of switchgrass biomass for each plant component over time at Grant County working farms (GCWF). Shown are F and p values for switchgrass biomass (Mg ha⁻¹), C and N mass fraction (%), C:N ratio, and C and N stock (kg ha⁻¹) for biomass harvested to 15 cm stubble height, total aboveground biomass, and each component of aboveground biomass. Fixed effects significant at p<0.05 are indicated in bold text.

	Biomass		Mass fraction C		Mass fraction N		C:N ratio		C stock		N stock	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Harvested to 15 cm												
<i>Month</i>	12.50	<0.001	-	-	-	-	-	-	12.20	<0.001	19.23	<0.0001
<i>Farm</i>	0.23	0.798	-	-	-	-	-	-	0.27	0.769	4.55	0.034
<i>Month x Farm</i>	1.66	0.193	-	-	-	-	-	-	1.62	0.202	2.23	0.096
Total Aboveground												
<i>Month</i>	12.33	<0.001	-	-	-	-	-	-	11.89	<0.001	18.76	<0.0001
<i>Farm</i>	0.52	0.609	-	-	-	-	-	-	0.56	0.588	9.87	0.003
<i>Month x Farm</i>	2.60	0.061	-	-	-	-	-	-	2.49	0.070	2.26	0.093
Inflorescence												
<i>Month</i>	20.23	<0.0001	7.45	0.003	34.86	<0.0001	38.73	<0.0001	19.45	<0.0001	29.59	<0.0001
<i>Farm</i>	1.26	0.319	0.61	0.561	9.01	0.001	8.79	0.001	1.25	0.321	1.01	0.392
<i>Month x Farm</i>	3.12	0.034	1.58	0.211	4.12	0.008	5.06	0.002	3.13	0.033	2.33	0.085
Stem												
<i>Month</i>	12.49	<0.001	7.51	0.002	0.81	0.452	0.68	0.511	12.31	<0.001	5.85	0.009
<i>Farm</i>	0.61	0.560	4.16	0.024	48.65	<0.0001	50.82	<0.0001	0.62	0.553	22.39	<0.0001
<i>Month x Farm</i>	2.22	0.097	0.89	0.479	3.47	0.017	3.64	0.014	2.16	0.105	3.24	0.029
Leaves												
<i>Month</i>	10.88	<0.001	0.95	0.401	44.44	<0.0001	95.91	<0.0001	10.60	<0.001	24.55	<0.0001
<i>Farm</i>	1.59	0.243	3.06	0.085	16.15	<0.001	48.00	<0.0001	1.64	0.234	0.07	0.931
<i>Month x Farm</i>	1.04	0.410	1.51	0.232	8.25	<0.001	25.28	<0.0001	1.03	0.410	0.89	0.484
Litter												
<i>Month</i>	17.95	<0.0001	2.43	0.103	0.60	0.557	1.64	0.215	16.27	<0.0001	25.33	<0.0001
<i>Farm</i>	55.89	<0.0001	4.01	0.027	22.31	<0.0001	15.87	<0.001	55.89	<0.0001	108.30	<0.0001
<i>Month x Farm</i>	10.46	<0.0001	2.37	0.071	1.51	0.231	1.80	0.162	10.34	<0.0001	10.15	<0.0001
Stubble												
<i>Month</i>	7.16	<0.001	15.69	<0.0001	0.32	0.727	7.29	0.002	6.15	0.005	4.43	0.019
<i>Farm</i>	20.40	<0.0001	2.35	0.110	140.25	<0.0001	187.18	<0.0001	19.01	<0.0001	89.69	<0.0001
<i>Month x Farm</i>	6.43	<0.001	4.74	0.004	4.77	0.003	10.13	<0.0001	5.99	0.001	3.76	0.012

Table 3. ANOVA results for comparisons of switchgrass biomass for each plant component over time at Arlington Agricultural Research Station (AARS). Shown are F and p values for switchgrass biomass (Mg ha⁻¹), C and N mass fraction (%), C:N ratio, and C and N stock (kg ha⁻¹) harvested to 15 cm stubble height, total aboveground biomass, and each component of aboveground biomass. Fixed effects significant at p<0.05 are indicated in bold text.

	Biomass		Mass fraction C		Mass fraction N		C:N ratio		C stock		N stock	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Harvested to 15 cm												
<i>Month</i>	6.46	0.006	-	-	-	-	-	-	5.41	0.012	30.37	<0.0001
<i>N level</i>	6.79	0.011	-	-	-	-	-	-	6.78	0.011	11.67	0.002
<i>Month x N level</i>	1.27	0.308	-	-	-	-	-	-	1.24	0.321	2.45	0.074
Total Aboveground												
<i>Month</i>	3.89	0.035	-	-	-	-	-	-	3.54	0.045	17.29	<0.0001
<i>N level</i>	8.29	0.006	-	-	-	-	-	-	7.78	0.007	16.14	<0.001
<i>Month x N level</i>	0.72	0.588	-	-	-	-	-	-	0.82	0.525	0.94	0.458
Inflorescence												
<i>Month</i>	16.00	<0.0001	5.06	0.012	28.80	<0.0001	33.31	<0.0001	15.65	<0.0001	29.99	<0.0001
<i>N level</i>	8.97	0.009	6.38	0.005	0.00	0.995	0.13	0.88	9.06	0.009	6.32	0.023
<i>Month x N level</i>	2.55	0.065	0.29	0.884	1.23	0.326	0.69	0.61	2.54	0.066	0.45	0.772
Stem												
<i>Month</i>	1.61	0.220	10.83	0.000	65.82	<0.0001	70.03	<0.0001	1.38	0.271	12.52	<0.001
<i>N level</i>	8.39	0.005	1.35	0.312	16.58	<0.0001	12.24	<0.001	8.31	0.005	19.48	<0.001
<i>Month x N level</i>	0.64	0.636	0.10	0.981	1.02	0.411	0.60	0.663	0.63	0.648	1.00	0.426
Leaves												
<i>Month</i>	22.46	<0.0001	3.86	0.035	10.12	<0.001	13.86	<0.0001	18.09	<0.0001	29.45	<0.0001
<i>N level</i>	1.53	0.255	1.99	0.200	24.73	<0.0001	24.15	<0.0001	1.94	0.186	2.58	0.117
<i>Month x N level</i>	3.28	0.028	0.29	0.884	1.11	0.37	1.12	0.367	3.22	0.030	4.26	0.010
Litter												
<i>Month</i>	19.17	<0.0001	1.53	0.232	9.26	0.001	4.73	0.016	18.92	<0.0001	13.65	<0.001
<i>N level</i>	6.65	0.011	0.31	0.735	14.93	0.002	13.55	<0.0001	6.69	0.004	9.71	0.003
<i>Month x N level</i>	1.24	0.320	1.77	0.160	1.63	0.200	0.17	0.954	1.00	0.422	2.17	0.103
Stubble												
<i>Month</i>	0.92	0.411	2.84	0.079	0.89	0.425	0.63	0.541	1.59	0.225	0.83	0.449
<i>N level</i>	1.37	0.308	0.44	0.656	10.58	0.002	7.57	0.008	1.61	0.258	3.47	0.082
<i>Month x N level</i>	0.71	0.594	1.2	0.339	0.71	0.594	0.25	0.905	0.50	0.737	0.72	0.588

Figure Captions

Figure 1. Location map and photos of study sites. Left panels show location of Wisconsin in the upper Midwest region of the United States (lower left panel) and study site locations within Wisconsin (upper left panel corresponds to dashed box in lower left panel). Photos of the study sites are shown in the upper right panel (Arlington Agricultural Research Station, AARS) and lower right panel (Grant County Working Farms, GCWF). Both photos were taken at the November harvest date.

Figure 2. Harvested (a) and total aboveground (b) biomass (Mg ha^{-1}) and nitrogen mass (kg ha^{-1}) in harvested (c) and total aboveground (d) biomass, by harvest date for switchgrass monocultures at GCWF. Capital letters above horizontal dashed lines indicate statistically significant differences among August to November harvest dates (i.e., testing the fixed effect of harvest month in the mixed effects model), across all farms, with different letters indicating statistically significant differences among months, determined at $p < 0.05$. There were no statistically significant differences among individual farm measurements across months. We attribute the NOV to APR increase in total aboveground biomass for the DS farm to over-winter redistribution of litter, likely influenced by animal activity (deer and small mammals).

Figure 3. Harvested (a) and total aboveground (b) biomass (Mg ha^{-1}), and nitrogen mass (kg ha^{-1}) in harvested (c) and total aboveground (d) biomass, by harvest date for switchgrass monocultures at the AARS. Capital letters above horizontal dashed lines indicate statistically significant differences among harvest dates (i.e., testing the fixed effect of harvest month in the

mixed effects model) across nitrogen (N) addition levels, with different capital letters indicating statistically significant differences among months, determined at $p < 0.05$. Lowercase letters above individual bars indicate statistically significant differences among all combinations of month and N addition level. Significant differences among N addition levels across all sample dates are shown in italicized inset text.

Figure 4. Biomass percent of harvested (a) and total aboveground biomass (b), and nitrogen mass fraction of total N mass in harvested (c) and total aboveground biomass (d) by plant component for each harvest period, for switchgrass harvested from three working farms in Grant County, Wisconsin. Values shown are means of N=3 farms for August, September, and November, and N=2 farms for April.

Figure 5. Biomass percent of harvested (a) and total aboveground biomass (b) and nitrogen mass fraction of total N mass in harvested (c) and total aboveground biomass (d) by plant component for each harvest period, for switchgrass harvested from three N addition levels at the Arlington Agricultural Research Station, Arlington, Wisconsin.

Figure 6. Carbon-to-nitrogen ratio (C:N) for GCWF litter (a) and stubble (b) and AARS litter (c) and stubble (d). Capital letters above horizontal dashed lines indicate significant differences among harvest dates across farms (for GCWF) or across N addition level (for AARS). Lowercase letters in panel b indicate differences among all combinations of month and farm; for AARS, significant differences among N addition levels across all sample dates are shown in italicized inset text. Note differences in y-axis scales among panels.