Seasonal Changes in Shoot and Root Nitrogen Distribution in Switchgrass (*Panicum virgatum*)

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Abstract Switchgrass is a promising bioenergy source that is perennial, productive, native to a broad geographic region, and can grow on marginal, nitrogen (N)-poor soils. Understanding N dynamics in switchgrass is critical to predicting productivity, conserving N, and optimizing the timing of harvest. We examined seasonal changes in N distribution in above- and belowground tissues in switchgrass to quantify N retranslocation rates. Above- and belowground biomass from three sites (two in PA and one in NE) were collected and analyzed for biomass growth and N concentrations at 30-day intervals from June through October. Total living plant mass ranged from 10.3± 2.4 standard error (SE) to 14.9±2.5 SE Mg ha^{-1}. Belowground mass comprised 52–57 % of total mass. Blades had the highest N concentration during summer, ranging from 6 to 22 g kg^{-1} N. Aboveground N concentrations decreased from September until autumn senescence, whereas belowground N concentration increased from August until senescence. Across the sites, total N retranslocated from aboveground to belowground components between September and October averaged 16.5±7.1 (SE)kg ha^{-1} N representing 26.7 % of the average maximum N content of aboveground biomass. Based on N fertilizer costs, delayed harvest would conserve some N and provide financial savings on fertilizer ($9 ha^{-1}) if harvest occurs after senescence but before overwinter biomass loss. However, biomass losses of even 10 % will negate potential economic savings accrued from N retention. To maximize environmental and economic savings from N retranslocation and to simultaneously minimize harvest losses, it would be optimal to harvest switchgrass as soon as possible after complete senescence.

Keywords Bioenergy · Biofuel · Harvest · Nitrogen retranslocation · *Panicum virgatum* · Switchgrass

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Introduction

Biomass is a promising alternative energy source because it is renewable, nearly carbon neutral, and has the potential to reduce energy-related greenhouse gas emissions [1–4]. Switchgrass (*Panicum virgatum* L.) is a warm-season perennial grass that is productive and nutrient-use efficient on land that is marginally productive for annual row crops [1, 3, 5]. On-farm research has demonstrated that switchgrass is more energy efficient than corn for ethanol production and that switchgrass has 94 % lower greenhouse gas emissions than gasoline [2]. On non-irrigated marginal soils using similar fertilizer rates, switchgrass had greater potential ethanol yield than corn [7]. Switchgrass is projected to compete favorably with anticipated increases in prices of natural gas and crude oil [8] and can provide socioeconomic benefits especially in rural areas [9].

As a biofuel, switchgrass offers several environmental benefits. It is favorable to wildlife if habitat diversity and appropriate harvest strategies are employed [10]. The extensive root system [11, 12] of switchgrass reduces erosion [13–15] and can sequester more than 1 Mg ha^{-1} of soil carbon annually [16–21]. Switchgrass stores up to 80 % of its mass belowground in the perennial root systems [22, 23].

Switchgrass has low nitrogen (N) needs but responds to N fertilizer with increased biomass yields [5, 24, 25]. Annual removal of switchgrass requires nutrient replacement through fertilizer application. However, because N application is expensive and has the potential for increasing N emissions and

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contaminating surface and groundwater, inputs need to be managed closely [26, 27]. In a multistate study with an average N application of 74 kg ha^{-1}, fertilization accounted for 10 % of total production costs [28]. Additionally, energy used in fertilizer manufacture and application is a major driver in the life cycle assessment of switchgrass [6, 29].

Switchgrass N demands are met through uptake from soil, but also from recovery of some of its aboveground N through the process of retranslocation or the movement of N from aboveground tissues to belowground tissues prior to autumnal senescence [30–32]. Although studies quantifying N retranslocation in switchgrass are limited, aboveground biomass N can be retranslocated and made available for the next growing season [30, 33]. Recent work on switchgrass grown in Illinois [33] showed that belowground biomass N stocks nearly doubled from late summer to early autumn, illustrating substantial conservation of N within the plant. Depending on when retranslocation occurs, the timing of harvest may determine how much N is removed from the site. For example, Reynolds et al. [30] reported Cave-in-Rock switchgrass harvested in summer contained about 7.5 g kg^{-1} N in harvested biomass, whereas autumn-harvested switchgrass contained only 3.8 g kg^{-1} N. If switchgrass is harvested before N retranslocation is maximized, then N removal due to harvest will be greater and subsequent crops will require greater fertilizer inputs [34, 35]. Harvesting when senescence is complete allows for maximum N retranslocation [4]. Other benefits may accrue from harvesting at a later time as well, including reduced ash and moisture content [36] as well as habitat protection for birds of management concern [37].

Nitrogen retranslocation is often cited as a benefit of delaying switchgrass harvest, but quantified N retranslocation is limited. Understanding seasonal changes in aboveground and belowground N concentrations will help quantify the ecological importance of N retranslocation and can enhance management plans and decisions. Our objectives were to (1) quantify the amount of switchgrass N retranslocation in several environments, (2) estimate the economic value of N retention due to N retranslocation, and (3) evaluate economic trade-offs of N retranslocation to potential crop losses incurred due to delayed harvest.

Methods

Site Description

This study was conducted on three managed switchgrass fields (Table 1) to evaluate N retranslocation in a range of environments. The Pennsylvania (PA) study sites were within a temperate deciduous forest region with about 50 % agricultural land cover. Average temperature at the two PA sites (which are approximately 3 km apart), is 20.8 °C in July and −4.4 °C in January. Precipitation is generally greater in summer (June, 11.5 cm) than winter (January, 7.2 cm). Each PA site was a 10-ha switchgrass seed production field. Soils at the PA sites are Alfisols (38). The PA-1 site was planted to Cave-in-Rock in 2000 and contains Frenchtown (Typic Fragiaqualf) and Venango (Aeric Fragiaqualf) silt loam soils. The PA-2 site was planted to Shawnee in 2000 and contains Cambridge (mesic Oxyaquic Fragiudalfs) silt loam soils derived from glacial till. Both PA sites received 45 kg ha^{-1} $year^{-1}$ of slow-release N (encapsulated urea) in spring. Herbicides (Paramount® (3,7-dichloro-8-quinolinecarboxylic acid)) and Stinger ® (3,6-dichloro-2-pyridinecarboxylic acid, monoethanolamine salt) were applied as needed to control weeds at planting. Switchgrass at the PA sites was mildly infected with smut (*Tilletia maclaganii*).

The Nebraska (NE) site was a 23-ha bioenergy research field planted to Shawnee in 2006 and managed for biomass production. The site received 50 kg N ha^{-1} as sulfur-coated urea applied as a single spring application in 2007 and 2008. Herbicides were applied post-planting (560 g a.i. ha^{-1} Quinclorac (3,7-dichloro-8-quinolinecarboxylic acid)) and in July (2 kg a.i. ha^{-1} 2,4-D(2,4-dichlorophenoxy) acetic acid) in 2006 to control weeds during establishment. Average temperature is 25.4 °C in July and −5.4 °C in January. Precipitation has a distinct seasonal pattern, with higher monthly precipitation in summer (June, 10.8 cm) than winter (January, 1.4 cm). Soil is a very deep, moderately well-drained, Sharpsburg (Typic Argiudoll) silty clay loam.

Sampling Methods

Biomass

Biomass was estimated from three 1-m^2 plots sampled from each field during autumn 2008. The PA sites were sampled in September and the NE site was sampled in early November. Each field was divided into thirds and one plot was sampled randomly from each third. In each plot, standing biomass was divided into two categories, biofuel, which was that material >10 cm above the soil surface, and residual biomass, or that material 0–10 cm above the soil surface. Plant litter (fallen leaves and stems) on the soil surface was collected separately. Plant material was dried at 105 °C for 48 h.

Belowground biomass was not quantified at the NE site. In the PA sites, belowground biomass was measured to a soil depth of 115 cm in the 1-m^2 plots used for aboveground biomass estimation. For the AP horizon, soil surrounding the 1-m^2 plots was removed to a depth of 50 cm using shovels and a backhoe and the exposed soil faces were cleaned manually to clearly identify the boundary between the AP horizon (~15 cm in depth) and the B horizon. The entire AP horizon was extracted using a backhoe and shovels.

Table 1 Description of switchgrass sampling sites in PA and NE

Site	Location	Elevation (m)	Soils [38]	Stand age (year)	Study area (m)	Precipitation (mm year^{-1}) [39, 40]	Fertilizer kg ha^{-1} year^{-1} N
PA-1	41°34′N 80°10′W	427	Alfisol: Venango series and Frenchtown series silt loams	10–12	200×75	1,120	45
PA-2	41°33′N 80°8′W	427	Alfisol: Cambridge series silt loams	10–12	300×75	1,120	45
NE	41.15°N 96.40°W	366	Argiudoll: Sharpsburg series silty clay loam	3	30×30	700	0 after est.

Roots in the B horizon were collected separately in September and October 2009; three plots were chosen within 10 m of the location where the AP horizons had been removed in the previous year. The AP horizon was removed first using a backhoe and hand shovels, after which a tarp with a 51-cm diameter hole was placed atop the B horizon. Using a hydraulic soil auger (Bobcat, Inc.) attached to a skid steer loader, a 51-cm diameter hole was excavated through the tarp opening to a depth of 100 cm below the surface of the B horizon. Soil was extracted from the hole and sieved in a 0.64-cm sieve to separate the roots, which were washed to remove attached soil particles and dried at 105 °C for 48 h.

Seasonal N Changes

To examine seasonal changes in tissue N concentrations, aboveground (AG) and belowground (BG) biomass was collected each month at each site. At the NE site, a 50×50 m sampling area of the field that was not harvested during field-scale biomass harvest was divided into four quadrants. At the PA-1 site, a 300×75 m section of the field was selected for sampling; at the PA-2 site, the sampled section was 200×75 m. On the fifteenth (±2 days) of each month, from June through October 2009, four randomly selected 30×30 cm samples of switchgrass were collected at each site. Each 30×30 cm sample typically represented a portion of one switchgrass plant. The aboveground biomass was harvested by hand using pruning shears (PA) or a rice knife (NE). After AG harvest, soil and roots were excavated to a depth of 15 cm. Standing AG biomass sampling in the PA sites ended in October.

Belowground biomass was washed thoroughly by hand with water to remove all attached soil, dried to a constant weight at 105 °C, and sorted into three categories: rhizomes, crown material, and roots. AG biomass was separated into four categories: stems, blades and sheaths, seedheads, and residual (the 10 cm of stem that remains aboveground after commercial harvesting operations). The AG biomass was dried to a constant weight at 105 °C. These monthly data were used to characterize the growth pattern over the growing season but were not used to quantify biomass at the field scale. Biomass data are more representative of yield per plant because switchgrass produces dense clumps of approximately the size as the sample area. For N analyses, subsamples were ground in a Thomas Scientific Wiley Mini-Mill to pass a 0.85-mm screen and analyzed using a Leco CNS-2000 Determinator (St. Joseph, MI, USA).

To track N concentration in total AG and total BG biomass in the 30×30 cm samples, we aggregated the individual components to obtain total N for AG and BG components. Dividing the total biomass for AG and BG components by the total AG and BG N contents yielded average weighted N concentrations for total AG and BG biomass tissues, respectively, from June through October. To obtain site-level biomass nitrogen estimates, total AG and BG biomass from the 1-m^2 (2008) plots was multiplied by either the AG or BG weighted N concentrations, respectively. Net N retranslocation was calculated as the change in total aboveground N between September and October.

Economic Value of N Retention

To estimate the economic value of N retranslocation, we calculated the economic value of N retained on the site using an N fertilizer value of \$0.55 kg^{-1} N. Fertilizer application costs were not included in the value of retranslocated N because we assumed that these were fixed costs not influenced strongly by N rate. To estimate the net economic tradeoff of delaying harvest to maximize N gains from retranslocation, we first calculated the economic value of N savings on site due to N retranslocation and from the retention of N in biomass that fell upon and remained on site. These savings were then compared to the economic losses resulting from a 10 % loss of harvestable material that might occur if aboveground switchgrass could not be recovered after delayed harvest. To estimate the value of switchgrass biomass, we used a recent sales value of \$88 Mg^{-1}.

Statistical Analysis

Statistical analyses were conducted using SigmaPlot 12.5. One- or two-way analyses of variance (ANOVA) were used

for parametric data (evaluated via a Shapiro–Wilk normality test) and Kruskal–Wallis ANOVAs on Ranks were used for nonparametric data. Data of unequal variances (tested via an equal variance test) were ln-transformed to produce equal variance. Post hoc analyses were the Holm–Sidak post hoc method for parametric analyses and Dunn's method for nonparametric analyses.

Results

Biomass

Aboveground biofuel ranged from 9.10±2.24 to 13.31±2.32 Mg ha^{-1} (Table 2) with seasonal changes over the growing season ($p<0.001$), and peak biomass (Fig. 1) was greater in September ($p<0.001$) or October ($p=0.002$) than in June (Holm–Sidak method). For belowground biomass in the PA sites, 12.4±1.8 and 15.8±2.9 Mg ha^{-1}, most of the roots (89.4 and 96.7 %, respectively) occurred in the AP horizon. Belowground biomass showed no seasonal changes. Litter mass atop this soil surface was similar at the two PA locations, with 3.7 Mg ha^{-1} at PA-1 and 4.1 Mg ha^{-1} at PA-2.

All three sites had similar biomass distributions (Fig. 2) in September with stems, blades, and rhizomes generally comprising the majority of the biomass. In aboveground biomass, blades and stems comprised similar proportions of total biomass. In belowground biomass, rhizomes comprised the greatest proportion of biomass for all three environments in September representing 20–31 % of total biomass. Seedheads and residual biomass comprised the smallest biomass components.

Biomass N Concentration

Nitrogen concentration (Fig. 3) differed significantly among aboveground tissue components ($p<0.001$). Blades and seedheads were not different from one another but were higher ($p<0.001$) than the other tissues, which were not different from one another. N concentrations decreased over the sampling season ($p<0.001$) with highest values in June in most tissues

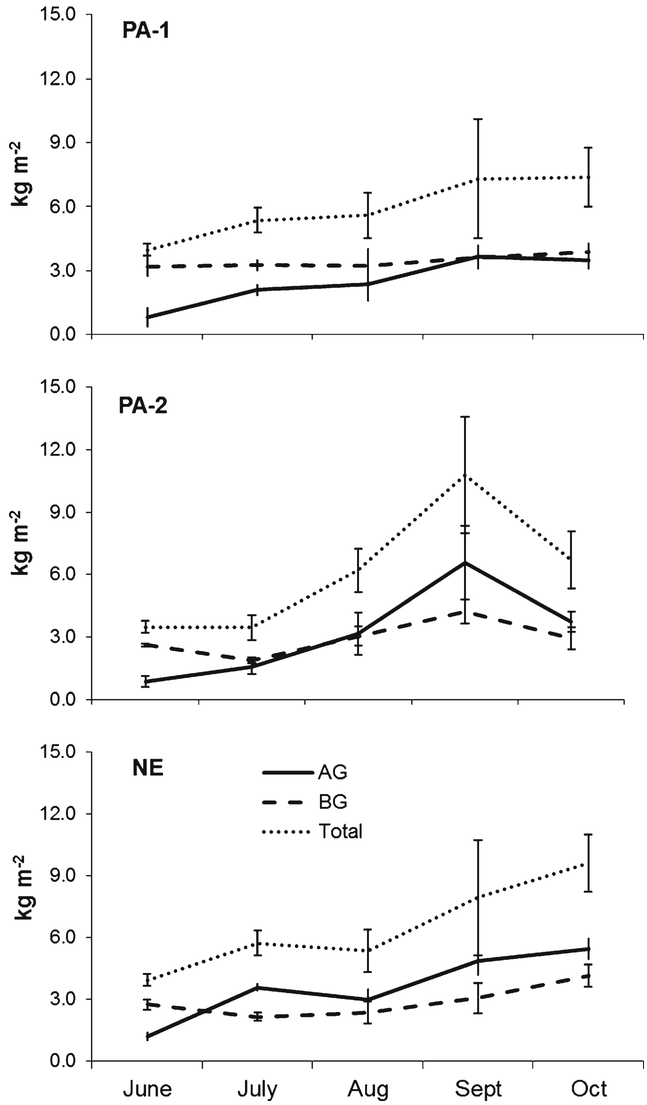

Fig. 1 Aboveground (AG) and belowground (BG) biomass in 30×30 cm samples collected from three switchgrass fields in Pennsylvania (*PA*) and Nebraska (*NE*) in June through October 2009 (*bars* standard errors)

Table 2 Late summer biomass (MT ha^{-1}) for switchgrass sites in PA and NE (*SE*, standard error)

		Aboveground (AG) living mass (MT ha^{-1})			Surface litter (MT ha^{-1})	Belowground (BG) living mass (MT ha^{-1})			AG+BG living biomass (MT ha^{-1})
Site		Biofuel	Residual	Total		AP—horizon roots	B—horizon roots	Total roots	
PA-1	x	13.31	1.56	14.89	3.69	15.77	0.52	16.29	31.17
	SE	2.32	0.21	2.53	1.14	2.92	0.10	3.01	4.67
PA-2	x	9.10	1.18	10.28	4.14	12.40	1.25	13.66	23.93
	SE	2.24	0.16	2.40	0.61	1.81	0.02	1.77	3.81
NE	x	10.40	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	SE	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

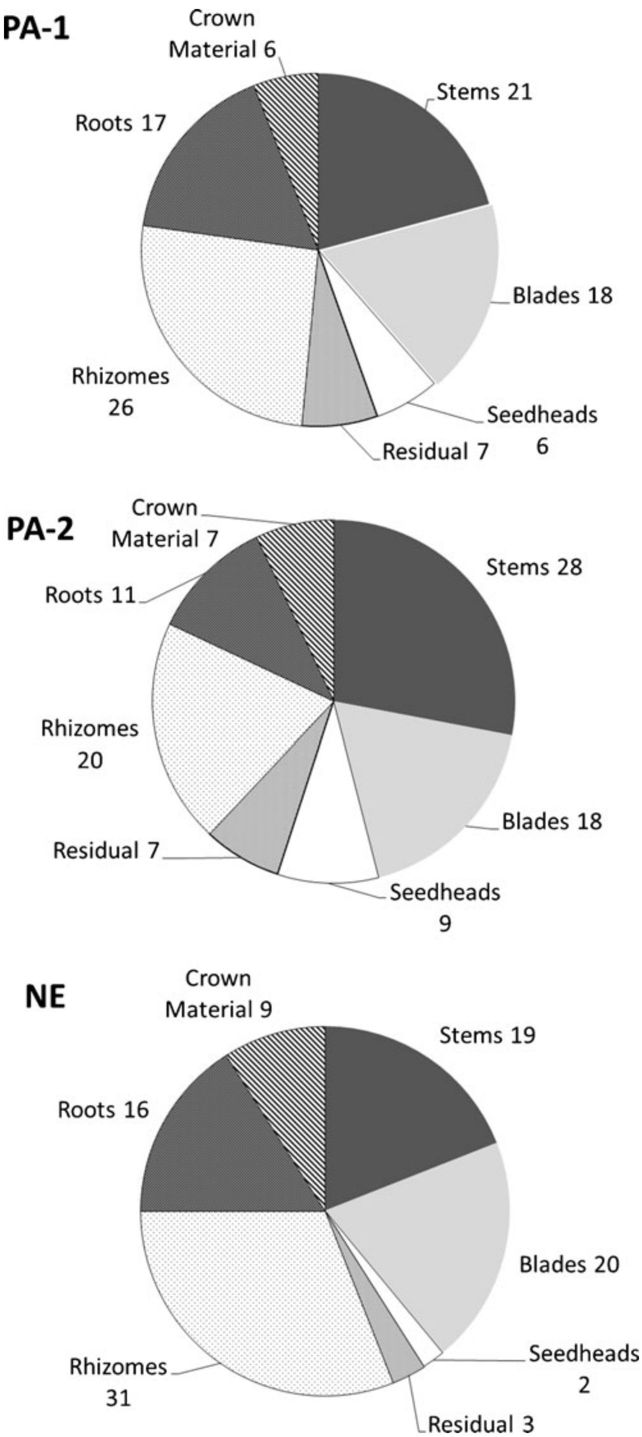

Fig. 2 Mean biomass distribution in three switchgrass fields in Pennsylvania (*PA*) and Nebraska (*NE*) in September

decreasing until the postfrost sampling in November. For example, the N concentration in blades in PA-1 was 21.8 g N kg^{-1} in June declining to 6.8 g N kg^{-1} in November, a 69 % decrease. Stem N concentrations decreased 77–82 % among the sites between June and August, after which time little change occurred. Seedheads did not appear at the sites until July; in the PA sites, seedheads were harvested and removed in late October; hence, there are no data for the PA seedheads for November.

Nitrogen concentrations (Fig. 3) differed among the belowground tissues ($p<0.001$) and were higher in belowground stems than roots or rhizomes, which were not different from one another. Nitrogen concentration differed among sampling dates ($p<0.001$). Averaged across the three sites, rhizomes had N concentrations of 3.8 g N kg^{-1} in June and 7.1 g N kg^{-1} after the frost in late October.

Weighted N concentrations in AG tissue (Fig. 4) differed across the season ($p<0.001$). Across all sites, the aboveground weighted N concentration was 15.2±2.5 SE g N kg^{-1} in June, declining to 4.8±1.2 SE g N kg^{-1} in October. Belowground weighted N concentrations differed seasonally ($p<0.001$); concentrations were fairly constant in June and July but increased after August. The weighted N concentration was 4.2±0.3 SE g N kg^{-1} in June increasing to 7.1±1.3 SE g N kg^{-1} in October.

Both aboveground and belowground tissue N concentrations showed strong and predictable trends over the season. Aboveground N concentrations of individual tissues were predicted strongly by month, with r^2 values of blades and seedheads ranging from 0.48 to 0.83. Relationships between concentration and month were somewhat less predictable in stems and residual material, with r^2 ranging from 0.13 to 0.93. For belowground tissues, most r^2 values exceeded 0.50. Overall, weighted N concentrations of AG and BG tissue were highly correlated with month, with r^2 values ranging from 0.82 to 0.89 for aboveground tissues and 0.84 to 0.97 for belowground tissues.

Biomass Nitrogen Content and Retranslocation

Total aboveground N (Fig. 4) in the 30×30 cm samples differed seasonally ($p<0.001$) with values across the sites averaging 0.83±0.03 kg m^{-2} N in June to 4.23±0.63 kg m^{-2} N in October. The NE site had the greatest decrease (42 %) of N in AG tissues from September to October decreasing from 51 to 30 kg ha^{-1} (Table 3). PA-1 had the least change in N in AG tissues from September to October decreasing from 94 to 89 kg ha^{-1}. Total BG N was not significantly different over the season. Based on net changes in aboveground N between September and October, the amount of N retranslocated at the sites ranged from 2.7 to 26.5 kg ha^{-1} N. Across the three sites, N retranslocation averaged 16.5±7.1 SE kg ha^{-1} N.

Economic Value of N Retention

The mean value of switchgrass biomass among the sites (\$962.1 ha^{-1}) was 2 orders of magnitude greater than the value (\$9.6 ha^{-1}) of the total amount of retranslocated N (Table 4). If harvesting is delayed to assure maximum rates

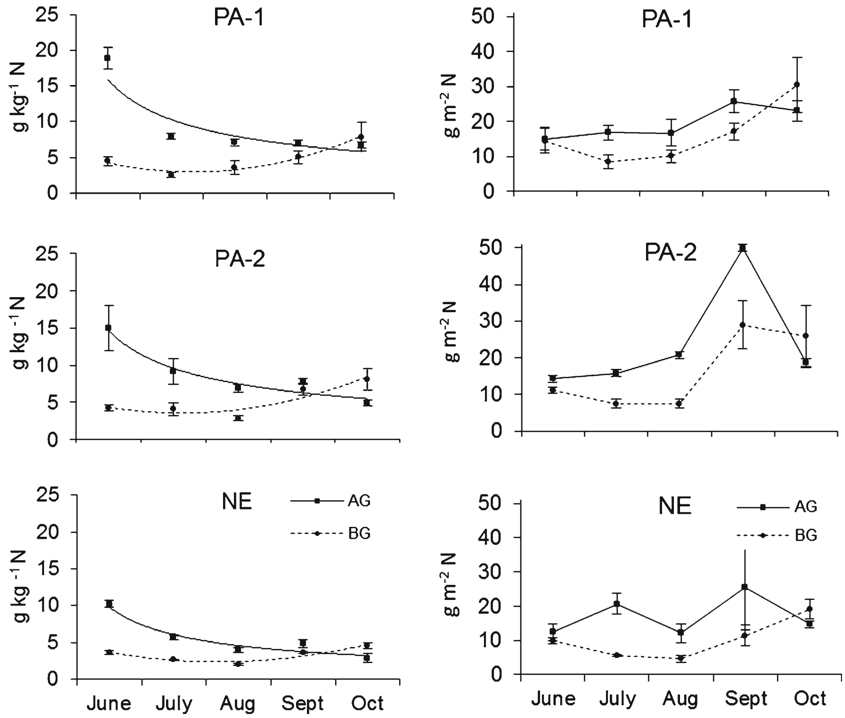

Fig. 3 Nitrogen concentrations of belowground tissues (rhizomes, roots, and crown material) and aboveground tissues (seedheads, stems, blades, residual) in three switchgrass fields in PA and NE sampled from June through November (*bars* standard errors). BG tissue: *PA-1* rhizome [N]= $0.314x^2-0.750x+3.802$, $r^2=0.88$; root [N]=$0.306x^2-1.405x+4.632$, $r^2=0.93$; crown material [N]=$0.723x^2-3.847x+9.41$, $r^2=0.87$. *PA-2* rhizome [N]=$-0.370x^3+3.776x^2-10.133x+10.991$, $r^2=0.75$; root [N]= $-0.165x^3+1.889x^2-5.869x+8.520$, $r^2=0.96$; crown material [N]= $-0.499x^3+5.195x^2-15.061x+17.502$, $r^2=0.85$. *NE* rhizome [N]= $0.125x^2-0.245x+3.198$, $r^2=0.70$. Root [N]=$0.149x^2-0.812x+3.867$, $r^2=0.545$; crown material [N]=$0.053x^2+0.086x+3.382$, $r^2=0.38$. AG tissue: *PA-1* stem [N]=$9.053x^{-0.767}$, $r^2=0.59$; blade [N]=$20.404x^{-0.519}$, $r^2=0.83$. Seedhead [N]=$12.122x^{-0.121}$, $r^2=0.133$; residual [N]= $6.7944x^{-0.438}$, $r^2=0.27$. *PA-2* stem [N]=$9.508x^{-0.843}$, $r^2=0.77$; blade [N]=$20.592x^{-0.677}$, $r^2=0.66$; seedhead [N]=$18.162x^{-0.317}$, $r^2=0.93$; residual [N]=$7.3x^{-0.476}$, $r^2=0.52$. *NE* stem [N]=$4.479x^{-0.639}$, $r^2=0.49$; blade[N]=$13.78x^{-0.617}$, $r^2=0.58$; seedhead [N]=$22.006x^{-0.816}$, $r^2=0.63$; residual [N]=$3.220x^{-0.24}$, $r^2=0.21$. *x* month

of N retranslocation and that delay results in a 10 % harvest loss due to senescing material, then economic gains are offset by a loss of \$96.2 ha^{-1} in the value of material that falls to the ground and is not harvestable. The economic gains include the value of N that is retranslocated, plus N in the 10 % of biomass that is not removed in harvest. The loss includes the economic value of biomass that is not harvested. The economic loss in biomass is nearly sevenfold greater than the gains due to N retranslocation and N retention combined resulting in a net loss of \$83.9 ha^{-1}.

Discussion

Biomass and Biomass N Concentrations

Aboveground tissue comprised about 45 % of total biomass and AG blade mass was 33–49 % of total AG biomass. This is consistent with results for Alamo switchgrass in Arkansas [41] where blades represented about one third of total harvested AG biomass.

Total BG biomass at the PA sites averaged 55 % of the total living biomass with the majority of the root mass concentrated at the soil surface. These results are comparable to those found in other studies. Berdahl et al. [22] found that root biomass was 27 % of the total plant biomass increasing to 84 % when crown tissue (material remaining after roots and aboveground tissue was removed) was included with root biomass. In slight contrast to Berdahl et al. [22], who found that root biomass in the upper 30 cm of soil comprised 46–49 % of total root mass, we found that most roots were concentrated in the AP horizon, which extends to approximately 15 cm. Although we did not partition soil samples by depth within the B horizon, we observed few roots below the surface of the B horizon. Soils at the PA sites have a high bulk density, particularly below the AP horizon, which likely hinders root extension into deeper soil.

Of the four AG biomass components, blades and stems had the highest N concentrations, which is consistent with other studies. Cave-in-Rock grown in Virginia, which had N concentrations of 11.1 g kg^{-1} N in July, declined to 5.4 g kg^{-1} N in November [34]. In Iowa, Cave-in-Rock AG biomass in

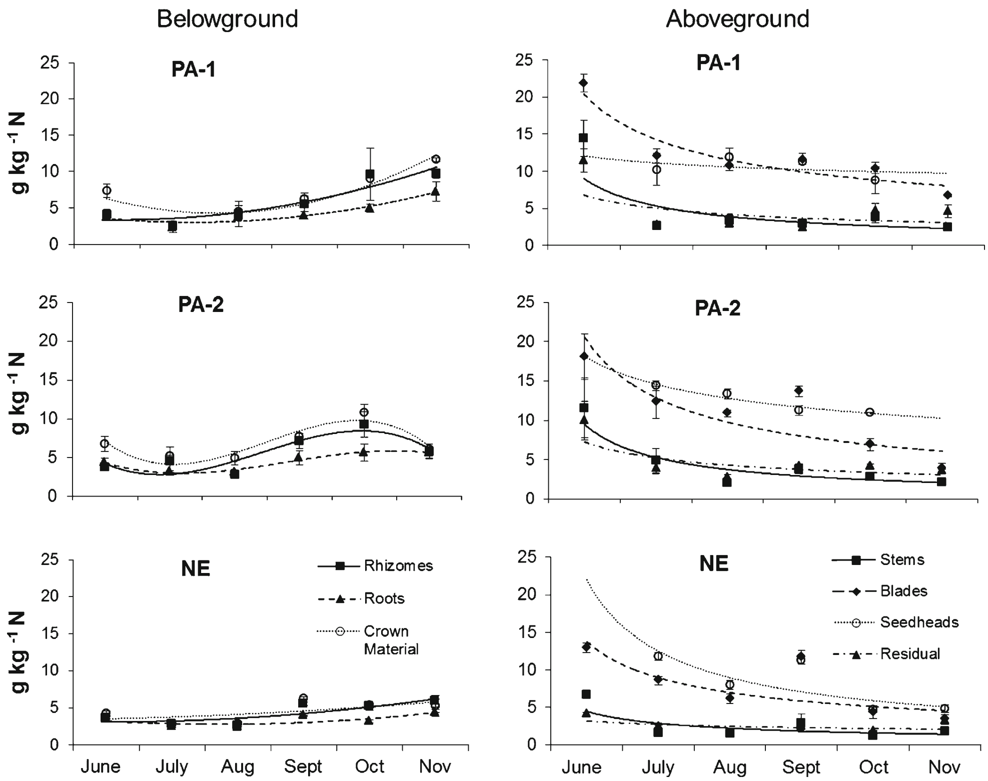

Fig. 4 Average weighted nitrogen concentration (in kilogram per kilogram N) and total N mass (in gram per square meter N) of total aboveground (AG) tissues and total belowground (BG) tissues for three switchgrass fields in PA and NE sampled from 30×30 cm quadrats from June through October (*bars* standard errors). Regression lines are superimposed over the monthly data. *PA-1* AG[N]= $15.879x^{-0.623}$, r^2=0.82; BG[N]= $0.717x^2-3.364x+6.893$, r^2=0.97. *PA-2* AG[N]= $14.640x^{-0.609}$, r^2=0.89; BG[N]= $0.600x^2-2.562x+6.297$, r^2= 0.84. *NE* AG[N]=$9.826x^{-0.698}$, r^2=0.88; BG[N]=$0.447x^2-2.402x+5.584$, r^2=0.88. *x* month

October was 4.2 g kg^{-1} N and BG N concentration was 9.7 g kg^{-1} N [32], comparable to our results. At all three sites, overall AG biomass N concentrations decreased steadily and were highly correlated with the month of collection. Early in summer, high concentrations are likely due to translocation of N from roots into AG tissue, followed by [N] declines as increases in plant biomass dilute N concentrations. Later in summer, as biomass stabilizes, N retranslocation would lead to declines in tissue [N]. Within individual tissue components, the seasonal decrease in N concentration in switchgrass blades and stems in our study may have been due to both N movement from these tissues into the seedheads as plants reached maturity [42, 43] and retranslocation into BG biomass. In contrast to AG tissue, belowground N concentrations increased over the season with the lowest values in early summer and peak concentrations in autumn.

Table 3 Aboveground nitrogen and N retranslocation in switchgrass sites in September and October in PA and NE

Site		kg ha^{-1} N		Retranslocation between September and October	
		x	SE	kg ha^{-1} N	%
PA-1	Sept	93.1	5.2	−2.7	−2.9
	Oct	90.4	5.3		
PA-2	Sept	71.1	3.9	−26.5	−37.2
	Oct	44.6	3.8		
NE	Sept	50.4	4.4	−20.4	−40.5
	Oct	30.0	5.0		

Table 4 Economic trade-offs between nitrogen savings due to N retranslocation and economic losses due to biomass loss in switchgrass sites (nitrogen fertilizer, \$0.55 kg^{-1} N; switchgrass market value, \$88 Mg^{-1})

		Harvest loss rate (%)			
		0		10	
		x	SE	x	SE
Potential biomass harvest	Mg ha^{-1}	10.9	1.2	9.9	1.1
Biomass harvest value	\$ ha^{-1}	962.1	109.2	868.3	98.7
Biomass economic loss	\$ ha^{-1}	0.0	0.0	96.2	10.9
N retranslocated	kg ha^{-1}	16.5	7.1	16.5	7.1
Economic value of retranslocated N	\$ ha^{-1}	9.1	3.9	9.1	3.9
N retained on site in fallen biomass	kg ha^{-1}	0.0	0.0	5.4	1.8
Economic value of N retained in fallen biomass	\$ ha^{-1}	0.0	0.0	3.0	1.0
Total N retained (retranslocation+N in fallen biomass)	kg ha^{-1}	16.5	7.1	21.9	5.6
Value of N retained (retranslocation+N in fallen biomass)	\$ ha^{-1}	9.1	3.9	12.3	3.1
Net economic impact (N retained−biomass loss)	\$ ha^{-1}	9.1	3.9	−83.9	14.1

Biomass N Quantity and Retranslocation

At all the sites, total N in AG tissues increased between August and September; this increase seems to be largely in the blades, which had higher N concentrations than the stems and which comprised a large proportion of the AG biomass (Figs. 2 and 3). Additionally, AG biomass increased between August and September at PA-2 and NE (Fig. 1) suggesting additional N uptake from soil into living tissue. From August to September, blade N concentrations increased indicating that plants were still actively taking up soil N or perhaps that roots were transferring tissue-bound N from distal belowground locations. Given the low amount of root mass below the AP horizon, however, this does not seem likely in PA. Quantifying plant N origin is complicated because plants use N from multiple sources, including both soil and plant tissue storage [25, 30, 32].

Examination of net changes in total AG and BG biomass N reveals movement from AG to BG tissues; AG weighted-average N concentrations among the sites declined between 2.9 and 40.5 % between September and the time of senescence in October. The mean N retranslocation rate across the sites was 16.5 (±7.1 SE)kg ha^{-1} N comparable to rates reported for switchgrass grown in Illinois, where AG biomass declined from 16.5 to 5 g kg^{-1} N between June and December [33]. We observed a tenfold range in rates among our sites from 2.7 kg ha^{-1} N at PA-1 to 26.7 kg ha^{-1} N at the NE site (Table 4). The PA-1 site was more productive than the other sites suggesting a possible correlation between site productivity and movement of AG N to BG tissues at the end of the season, although the relationship between soil N availability and N retranslocation rates is not clear. Reviews of the literature across many tree species [44–47] and grasses [48] show that increased soil N availability reduces retranslocation rates even within the same species. However, those same studies also document that rates of N retranslocation are either independent from or not strongly controlled by rates of N availability. Stand age may play a role in determining rates; however, the NE site, which was 3 years old, and PA-2, at 9 years old, had comparable N retranslocation rates.

Economics of N Retention vs. Harvest Losses

Nitrogen retranslocation, 16.5 (±7.1 SE)kg ha^{-1} N, represented 26.7 % of the average maximum N content of AG biomass and thus provides a substantial source satisfying annual switchgrass N requirements. If biomass harvest is delayed until retranslocation is complete, then this process conserves a large portion of the annual plant needs within the BG tissue. Expressing this N quantity in economic terms, on average, this provides an economic value of \$9.1 ha^{-1} (Table 4). However, if harvesting is delayed such that oncoming winter conditions result in a 10 % loss of total standing biomass, then the economic losses due to lost biomass are more than fourfold greater than the combined value of the economic gains from N retained by retranslocation and in the N contained in biomass that remains upon the site. We have observed that blades and seeds are the first tissue components to fall from the plants in late autumn. These tissues have much higher N concentrations than the stems and together they constitute 49–54 % of the total aboveground biomass. Loss of these tissues can provide an N return to soil due to their high N concentrations, but they are at the greatest risk of being lost from harvestable biomass. Previous work has shown that harvesting an overwintered switchgrass crop in spring resulted in a 20–24 % loss of yield, increasing to 40 % after an especially snowy winter [36]. Long delays in harvesting, however, are not necessary to obtain the benefits related to N retranslocation. Heaton et al. [49] found little change in N removal between an early winter harvest and a late winter harvest in Illinois indicating that harvesting after the AG portion of the plant is no longer physiologically active (usually the first killing frost in cold regions) will allow for the greatest transfer of N from AG to BG tissues.

Timing of biomass harvest is dictated by many factors besides N retranslocation and product loss, including local weather and soil conditions, wildlife habitat requirements, weed pressure, water and ash content, and market conditions. Additionally, biochemical and thermochemical conversion platforms have different optimum feedstock characteristics that may dictate the maturity stage of optimal feedstock harvest [50]. Nonetheless, to maximize N retranslocation and minimize harvest loss, it would be optimal to harvest switchgrass as soon as possible after complete senescence.

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