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Return of aboveground nutrients by switchgrass into the surrounding soil during senescence

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Roland Ahouelete Yaovi Holou^{*1,2}, Gene Stevens¹ & Valentin Kindomihou³

Background: Switchgrass (*Panicum virgatum* L.) is a crop that holds promise for cellulosic biofuel production. To minimize fertilizer costs, farmers prefer to reduce crop removal of nutrients from the soil when biomass is harvested. The objective of this study was to monitor, from May 2008–November 2009 at Portageville (MO, USA), the nutrient concentration in the soil, switchgrass roots and rhizomes in a 20-year-old switchgrass field. Soil and tissue samples were collected to determine the sink of the nutrients lost in the aboveground biomass during senescence of the plant. **Results:** Nutrient concentration in switchgrass biomass decreased from July to the end of the season. In general, as switchgrass senesced, the nutrient concentration of the roots did not significantly change, whereas that of the rhizomes increased. Soil test results varied depending on where samples were collected relative to switchgrass root clumps. Generally, soil samples collected from the clump showed the highest evidence of nutrients returning to the soil from the aboveground biomass; however, some of this could be due to root breakage during sampling. Soil ammonium acetate extracted K in the clumps and averaged 218 kg K kg⁻¹ soil in October, compared with 302 mg K kg⁻¹ soil in November. Soil NO₃-N content in the clumps in November was 5.5 mg kg⁻¹ soil, compared with 1.5 mg kg⁻¹ soil in October. **Conclusion:** This study provided evidence of nutrient recycling in the field by switchgrass plants and supports the concept of a reverse flow of nutrients to soil at the end of the season. The harvest of switchgrass late in November will help minimize the nutrient removal and maximize biomass yield.

Switchgrass (*Panicum virgatum* L.) is a plant native to North America. It is used to protect from soil erosion or to stabilize levees, provide a suitable ecological niche for wildlife, revegetate highly degraded ecosystems, phytoremediate the environment [1], prevent runoff or reduce the effects of raindrops on soil [2], reduce the effects of the wind on soil erosion [3], ornament the landscape [4], make paper for industry [5] and make antioxidants for the pharmaceutical industry [6]. In addition, switchgrass is being investigated to produce cellulosic bioethanol in many countries [1,7–12]. Cellulosic ethanol produced from switchgrass can cause less pollution to the environment by displacing fossil fuel and sequestering CO₂ as carbon in the switchgrass [13]. Switchgrass can also grow well on agriculturally marginal soils [8].

Lowland ecotype switchgrass usually produces more biomass than highland cultivars, while the former are more generally adapted to growing conditions in the southeast USA [14–16]. In the Midwest USA, the optimum harvest periods for biomass yields occurred at the maturity stages R3–R5 (panicle fully emerged from boot to postanthesis) [17].

Usually, when switchgrass is grown for biofuel purposes, having minimal minerals in the biomass is desired, as it improves processing into biofuel [1,10,18,19]. The high content of certain minerals in biomass reduces the fermentation and the ethanol yield [7]. N is critical for a high biomass production by switchgrass [1,20,21]; however, upon oxidation, N that is not utilized by plants can form nitrous oxides, which pollute the environment,

¹University of Missouri, PO Box 160, Portageville, MO 63873, USA

²Monsanto Company, 800 N. Lindbergh Blvd, Mail Zone Q4B/Q420E-A, St Louis, MO 63167, USA

³Laboratory of Applied Ecology, Faculty of Agronomic Sciences, University of Abomey-Calavi, 01 BP 526 Cotonou, Benin

*Author for correspondence: Tel.: +1 574 349 5642; E-mail: rayholou@yahoo.fr

Key terms

NH₃ volatilization: The loss of NH₃ gas to the atmosphere from soil and plants.

Rubisco: Ribulose-1,5-bisphosphate carboxylase oxygenase; an important enzyme involved in carbon fixation reactions.

as the ability of nitrous oxide to contribute to global warming is 300-times greater than CO₂ [22,23].

In an attempt to determine the best time to harvest switchgrass, in order to maximize aboveground biomass while minimizing nutrient removal in that material, we

previously observed that as switchgrass was senescing the nutrient uptake in the biomass decreased [24]. In this study we reported that the maximum and the end-of-season (November) nutrient uptake was 488.9 and 130.9 kg N ha⁻¹, 21.9 and 5.7 kg P ha⁻¹, 369.7 and 60.4 kg K ha⁻¹, 80.3 and 3.5 kg Ca ha⁻¹, 39.4 and 17.5 kg Mg ha⁻¹, 3.4 and 0.6 kg Zn ha⁻¹, 16.2 and 3.5 kg Fe ha⁻¹, 2.7 and 1.7 Mn ha⁻¹, and 0.5 and 0.3 kg Cu ha⁻¹ (Table 1) [24]. Other scientists have also observed that nutrient uptake by switchgrass decreases as the plant is senescing [25]. A decrease of the leaf N content in switchgrass was also obtained between the middle and the end of the growing season [26]. Similarly, Madakadze *et al.* recorded that the N content in switchgrass in Canada decreased from 25 g kg⁻¹ in the spring to 5 g kg⁻¹ at the end of the season [27]. However, a highly important yet unanswered question is where the switchgrass nutrients went when the plant was senescing.

Seasonal fluctuations of soil acidity and P and K levels are common in fields in the central USA [28]. In corn fields, soil pH was lowest in summer months and increased in the fall and winter [29]. According to these authors, soil P and K test levels were lowest in the fall and highest in the spring. Many scientists speculated that at the end of the growing season, some plants remobilize their N into the belowground biomass [30,31]. Drought

can also induce nutrient translocation [32]. In the case of switchgrass, many authors hypothesized that during its senescence, aboveground biomass nutrients return to roots [1,7,22]. However, to our knowledge, very few scientists have designed an experiment to prove where these nutrients really went. The decrease of nutrient concentration in the aboveground biomass is not sufficient to claim that they returned to the roots. For instance, as soybeans senesced, the N mostly moved from the leaves to the seeds [33]. Similarly, in *Arabidopsis*, N was remobilized towards the seeds during senescence [34]. Moreover, during the senescence of wheat, N can be lost through the leaves by NH₃ volatilization [35]. During the senescence of most cereals, Rubisco breaks down and consequently N moved out of the chloroplast [36,37]. Finally, some perennial or hay grasses can remobilize and store assimilates in the crown area of the plant and uses them for growth the next spring.

Several papers claimed that native grasses actively retranslocate nutrients belowground during senescence [1,7,22,30–32], but given the switchgrass/biofuel possibilities, more data quantifying these trends would be a useful addition to the literature.

In this research, we hypothesized that the nutrients remobilized from the switchgrass aboveground biomass [24] went back to the belowground biomass and surrounding soil. To test our hypothesis, we monitored the nutrient accumulation not only in the above- and below-ground biomass, but also in the soil surrounding the switchgrass roots and rhizomes. The monitoring of those nutrients will help to locate the sink of the nutrients that declined in the aboveground biomass over time. The understanding of the nutrient sink can give additional information on the best time to harvest

Table 1. Mean separation of nutrient uptake by date for Alamo switchgrass grown at Portageville (MO, USA) in 2008–2009.

Year	Date of biomass harvest	Nutrient uptake in aboveground biomass (kg ha ⁻¹)†								
		N	P	K	Ca	Mg	Zn	Fe	Mn	Cu
2008	28 May 2008	75.3 d	7.9 de	98 ef	80.3 a	7.1 c	0.3 b	1.1 b	0.4 e	0.3 cd
	19 June 2008	186.1 bcd	14.1 bcd	234.1 bc	11.2 d	20.7 abc	0.9 b	2.3 b	0.7 de	0.4 bc
	21 July 2008	488.9 a	10.5 cde	174.8 cd	2.9 d	27.1 ab	1.1 b	7.8 ab	1.5 c	0.5 b
	4 October 2008	391.7 abc	19.6 ab	160.3 de	3 d	37.1 a	1.4 ab	4 b	2 abc	0.1 d
	24 November 2008	130.9 cd	5.7 e	60.4 f	3.5 d	21.6 abc	1.3 b	7 ab	1.7 bc	0.3 bc
2009	28 May 2009	174.2 bcd	11 cde	243.1 b	2.5 d	15.2 bc	0.2 b	2.2 b	0.6 e	0.1 cd
	24 June 2009	459.5 a	15 abc	369.7 a	5.4 d	36.1 a	0.6 b	3.3 b	1.5 c	0.4 bc
	21 July 2009	317.5 abcd	21.9 a	354.2 a	46.1 b	39.4 a	3.4 a	6.8 ab	2.7 a	0.4 bc
	2 October 2009	412.7 ab	14.9 abcd	241.1 bc	23.3 c	37.7 a	0.6 b	16.2 a	2.4 ab	0.5 b
	23 November 2009	374.1 abc	11.3 cde	103.6 ef	13.1 cd	17.5 bc	0.6 b	3.5 b	2 abc	0.9 a

†Numbers followed by different letters are statistically different at p = 0.05 within the same column and for the same year. Harvesting the biomass late will significantly reduce the nutrients removal. Data taken from [24].

switchgrass biomass while minimizing the economical and environmental effects associated with nutrient removal. For instance, if the nutrients are returned to the soil, roots or rhizomes, they may be used by the plant in the following years. In contrast, if they volatilize, they will not only constitute a big loss, but they will also create environmental problems. If the nutrients retranslocate to the soil, harvesting the biomass late in the season would be a good practice. However, all other things being equal (e.g., biomass process systems), if these nutrients volatilize, it would be better to harvest the plant early to avoid any eventual air pollution. Other factors to consider for the early harvest are: nutrient balance, harvest costs and impact on the future plant productivity, and the ability to capture and recycle the nutrients. In this paper, we predominantly focused on the translocation of nutrients toward other organs or toward the soil. Our objectives were to:

- Monitor the soil characteristics (pH, neutralizable acidity [NA] and nutrient concentration) at different dates, soil depths and locations in the field;
- Determine the location in the soil where these characteristics significantly change;
- Determine the progression of the nutrient concentration in the roots and the rhizomes.

A systemic comparison of the changes observed in the aboveground biomass with that in the belowground biomass and in the soil will determine whether the nutrients that translocated from the aboveground biomass ended up in the roots, and/or the rhizomes, and/or the soil. A reduced nutrient concentration in vegetation can also be due to reduced uptake. Net concentration in the vegetation is a balance between uptake and remobilization. The comparison of the changes at different soil depths and locations in conjunction with the changes in the aboveground biomass will help determine at which soil depth the nutrient sink is as the plant senesces, and will help better understand the relationship between decline in uptake and increased remobilization.

The answer to these questions will help decide whether later harvesting of switchgrass will return a significant amount of nutrients back to the soil or whether it would be better to have earlier harvests.

Methods

▪ Growth & harvest of switchgrass

In 1990, Alamo cv. switchgrass was drill planted in 6 m wide strips (east to west), spaced parallel 100 m apart and 450 m long by a cotton field near Portageville (MO, USA; 36.4253°N, 89.6994°W). The main soil in the field was a Bosket fine sandy loam (bosket, fine loamy,

mixed active, thermic, mollic, hapludales) soil. The field was located in the upper Mississippi River Delta region where the topography is nearly flat and southwest winds in May and June sometimes cause damage to young crops. The farmer planted the switchgrass as a wind break to minimize blowing sand injury to cotton seedlings. An added benefit of the strips is habitat for birds and rabbits. The field is burned every 4 years in April and mowed annually in September or October, and switchgrass strips have not received any lime, pesticides, N, P or K since establishment in 1990.

In 2008 and 2009, switchgrass biomass was harvested in monthly intervals from May to November. For each sampling date, four plots in the field were evaluated. The biomass was harvested from the center of the strips by hand in a floristically homogenous subplot of 1.67 m² using a hay sickle mower. After harvest, the total fresh biomass weight within each subplot was taken. A sample of that biomass was separated into leaves, stem and head. The fresh weight of each category was recorded in the field and those samples were later dried in an oven until their weight became constant. Switchgrass biomass was determined by extrapolation from the biomass obtained in the 1.67 m² subplot.

Details about the experiment design and how the switchgrass was grown and harvested can be found in a previous study [24]; switchgrass biomass yield is summarized in [Table 1](#).

▪ Digging of switchgrass clumps & soil sampling

At the beginning of the growing season, the average diameter of the switchgrass clumps was determined using a ruler. Based on that preliminary investigation, a switchgrass clump with a diameter of approximately 35 cm was dug each time the biomass was harvested. Before digging a clump, its aboveground biomass was harvested and weighed in the field. A biomass was sampled and dried in oven until constant weight.

In each of the four plots, one clump was carefully dug using a shovel and a pickaxe. A 50 cm × 50 cm square was made around the clump so that the clump itself was located in the middle of the square. The clump was dug and all the soil in that square was removed up to 25 cm deep. After the clump was dug, it was put in a sack. The final volume of soil removed was 62,500 cm³ (50 × 50 × 25 cm³); all the soil that came out of the hole was added to the clump in the sack for later manipulation in a laboratory. Then, using a soil sampler, soil samples were taken beneath the 62,500 cm³ hole, at two depths: 0–15 cm and 15–30 cm, labeled 'under 0–15' and 'under 15–30', respectively ([Figures 1 & 2A](#)). Three other soil samples were taken outside the clump in a region where no switchgrass grew, but the leaves overlaid and covered the soil ([Figure 2B](#)). Usually the

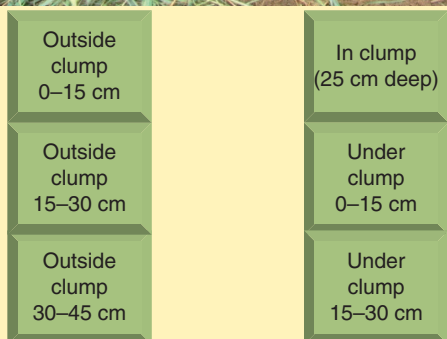


Figure 1. Switchgrass root harvest and soil sampling at Portageville (MO, USA) in 2008–2009. Four clumps were dug each month from May to November.

Photo reproduced with permission from Roland Holou, Portageville, MO, USA (2008).

‘outside the clump’ region was located 50 cm from the clump. Soil samples outside the clump were taken at three depths: 0–15, 15–30 and 30–45 cm, labeled ‘outside 0–15’, ‘outside 15–30’ and ‘outside 30–45’, respectively (Figures 1 & 2B). At each depth, the soil that was sampled was put in a different paper sack. The samples were taken at each of the four plots every time the biomass was harvested. After all the soil samples were harvested, the hole was filled with soil collected from the surrounding area. We did not sample in the same soil depth increments outside the clumps as inside the clumps because of the size of the clumps and the need to sample soil under them. At each sampling date, four soil samples were also taken in the cotton field near the switchgrass strips to monitor the changes in its nutrient contents. In that field, the soil was collected 0–15 cm depth between the cotton plants.

Key term

Necromass: Dead plant material on the soil surface or in standing senesced plants.

■ Handling of clump & soil in the laboratory

In the laboratory, the soil was shaken from the root ball (Figure 2C), following which a sample of that soil was taken after it was mixed homogeneously. During the whole process the soil at the base of the plant was avoided. All the remaining necromass and biomass (leaf, stem and root) were then removed from that soil sample, the soil sample was sieved, and was labeled ‘in clump’. Each clump was separated into the individual plants that constituted the clump. The roots and the rhizomes (Figure 2D) were well shaken to remove all soil. Unfortunately, the shaking may have caused damage to the roots.

Fresh weight was taken immediately. A sample of the roots and rhizomes was quickly washed with de-ionized water, mostly to remove dirt and contamination from microorganisms. These samples were called ‘root washed’, and ‘rhizome washed’. After soaking water from these wet samples with paper towels, they were dried in an oven until their weight became constant. The belowground biomass samples (roots and rhizomes) and the soil samples were also dried in oven at 100°C until their weight became constant.

The transportation of the clumps from the field to the laboratory and their processing could have caused root breakage and the leakage of their content into the soil. Therefore, the method we used to sample and process the samples may partially explain some of our results. The quick washing and soaking of the roots with paper was done to remove most of the microorganisms while trying to minimize biasing the results.

To recapitulate, seven soil samples were taken in each switchgrass block: in clump; under clump 0–15 cm; under clump 15–30 cm; outside clump 0–15 cm; outside clump 15–30 cm; outside clump 30–45 cm; and cotton field 0–15 cm (Figure 1).

■ Nutrients analysis

Soils samples were oven dried and analyzed for their nutrient content (N, P, K, Ca, Mg, S, Zn, S, Mn, B, Cu, NO_3^- and NH_4^+), organic matter (OM), pH and NA. Soil OM content was measured by the loss on ignition method [38]. Soil pH_{salt} was measured with a glass electrode in 0.01 M CaCl_2 salt solution and NA was measured in Woodruff buffer solution [39,40]. K, Ca and Mg were extracted in 1-N ammonium acetate and measured on the atomic absorption spectrophotometer [41]. P was measured colorimetrically using Bray-1 extraction solution [42]. Nitrate was determined using a 0.025-M aluminum sulfate extraction and ion-specific electrode. Ammonium was measured with a 2-M KCl extraction idophenole blue colorimetric determination. Zn, Fe, Mn and Cu were extracted using the nonequilibrium extraction method with diethylene

triamine pentaacetic acid [43] and measured on the atomic absorption spectrophotometer. Sulfate sulfur was extracted with 2-M acetic acid solution and then measured with a BaSO_4 turbid metric system [39].

The dried biomass samples at each harvest were digested with $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ with a Hach Digesdahl® (Loveland, CO, USA) and then analyzed for their N, P, K, Ca, Mg, Fe, Cu, Zn and Mn content, using the same methods as soil. The cations were analyzed by atomic absorbance spectrophotometer, whereas the N was analyzed by idophenol blue.

Statistical analysis

The data were analyzed using the linear mixed model in SAS® 9.2 (SAS Institute Inc., Cary, NC, USA). Significant differences were assumed for $p \leq 0.05$. The year of the study, the soil depth and the date of biomass harvest were considered the main fixed factors, whereas the plot was classified as a random variable. For the linear mixed model, the estimation method was the restricted maximum likelihood. Means were separated and grouped by letter by using the macro developed by Saxton [44].

Results

Weather summary

The weather conditions in the study area during the course of this experiment were detailed in our previous study [24]. The annual precipitation in 2009 was 1313 mm compared with 1095 mm in 2008. The temperatures during both years were similar (maximum air temperature: 20.2°C for both years; minimum air temperature: 9.4°C in 2008 and 9.9°C in 2009; average air temperature: 14.7°C in 2008 and 14.8°C in 2009). The total solar radiation was 13.9 MJ M^{-2} in 2008 compared with 13.4 MJ M^{-2} in 2009. The average monthly vapor pressure (1.4 kPa) and

vapor pressure deficit (0.6 kPa) did not change during the course of the study.



Figure 2. Digging and handling of switchgrass roots. (A) Taking soil samples under switchgrass clump. (B) Taking soil samples outside a switchgrass clump. (C) Switchgrass clump dug, and ready to be taken into the laboratory for more root work. (D) Switchgrass rhizomes (right) and roots (left).

Photo reproduced with permission from Roland Holou, Portageville, MO, USA (2008).

Soil pH, NA, cation exchange capacity & OM

The pH of the soil depended on the year of the study ($p = 0.0002$) and the time of biomass harvest ($p < 0.0001$) (Table 2). In general, the pH outside the clump did not change during the year. In contrast, the pH of the soil taken at the other places (in clump, under clump 0–15 cm, under clump 15–30 cm and cotton field 0–15 cm) was highly affected by the date ($p < 0.0001$) and it fluctuated along the dates. The pH of the soil varied between 4.6 and 5.7, with the highest value recorded in the clump.

NA was affected by the year of study, the month and the date of biomass harvest (Table 2). Generally, it was only in and under the clump that the NA significantly changed along the year. The NA decreased from the beginning of the growing season until October, after which it picked up, suggesting that towards the end of the season the soil NA (meq/100 g) drastically changed (Table 3).

The soil OM in the switchgrass field depended on the soil depth and varied from 0.5 to 2.4% (Table 3). The

highest values were recorded in the soil taken from the clump. Although changes in the OM occurred everywhere in the soil, it was only in the soil taken from the clump that the OM significantly depended on the date ($p \leq 0.035$) (Tables 2 & 3). Indeed, toward the end of the season, OM accumulated in the soil taken from the clumps. The increase in OM in the clump could indicate that there was more root breakage at the last sampling date; however, the same sampling procedure was used throughout the study. This data suggested that the most significant change of OM happened mostly in the clump. In both years, the OM in the clump significantly increased from October to November (Table 3).

Macronutrients

Both the time of biomass harvest and the soil depth significantly affected the $\text{NO}_3\text{-N}$ content of the soil (Tables 2 & 3). The $\text{NO}_3\text{-N}$ in the soil in November was lower under the clump than in any other locations in the soil sampled, whereas the highest values were recorded in the soil taken from the clump.

Table 2. Impact of the year and the harvest time on the nutrient content of the soil on which the switchgrass cv. Alamo was grown at Portageville (MO, USA) in 2008–2009[†].

Variable	Year of study	Effect for all data combined			Impact of the date of harvest						
		Year of study	Date of biomass harvest	Soil depth (cm)	Cotton field (0–15 cm)	In clump (0–25 cm)	Outside (cm)			Under (cm)	
							0–15	15–30	30–45	0–15	15–30
pH	2008					**	NS	NS	NS	NS	NS
	2009	***	****	****	NS	NS	NS	*	**	*	*
Neutralizable acidity (meq/100 g)	2008			**		***	NS	NS	NS	NS	*
	2009	***	****	**	NS	**	NS	NS	NS	**	NS
Organic matter (%)	2008			****		*	NS	NS	NS	NS	NS
	2009	NS	NS		NS	*	NS	NS	NS	NS	NS
P Bray I (mg kg ⁻¹)	2008			****		**	NS	*	NS	NS	NS
	2009	NS	***		NS	**	NS	NS	*	NS	**
Ca (mg kg ⁻¹)	2008			****		NS	NS	NS	*	NS	NS
	2009	***	NS		NS	NS	NS	NS	*	*	NS
Mg (mg kg ⁻¹)	2008			****		*	NS	NS	NS	NS	NS
	2009	**	*		NS	NS	NS	NS	NS	NS	NS
K (mg kg ⁻¹)	2008			****		**	NS	*	NS	NS	NS
	2009	NS	**		NS	*	NS	NS	NS	NS	NS
SO ₄ -S (mg kg ⁻¹)	2009		****	NS	*	NS	NS	***	*	*	NS
Zn (mg kg ⁻¹)	2009		****	****	NS	NS	NS	NS	NS	NS	NS
Fe (mg kg ⁻¹)	2009		****	**	NS	NS	NS	**	NS	NS	NS
Mn (mg kg ⁻¹)	2009		****	*	NS	NS	NS	NS	*	NS	NS
Cu (mg kg ⁻¹)	2009		****	**	*	*	*	*	NS	NS	NS
NO ₃ -N (mg kg ⁻¹)	2009		****	*	***	NS	**	***	NS	***	****
B (mg kg ⁻¹)	2009		****	**	*	NS	***	**	**	*	**

[†]Soil samples were monthly taken at six soil depth from May to November. For each field, four blocks were considered. Soil was analyzed as described in the 'Methods' section. The most significant changes occurred in the clump.

**** $p < 0.0001$; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; NS: $p > 0.05$.

NS: Nonsignificant.

Table 3. Impact of the harvesting time and the soil sampling depth on the neutralizable acidity, organic matter and NO₃-N of switchgrass cv. Alamo's soil at Portageville (MO, USA) in 2008–2009.

Soil characteristic	Sample location/ soil depth (cm)	Year of study	Nutrient concentration in soil ^a				
			May	June	July	October	November
Neutralizable acidity (meq/100 g)	Cotton field (0–15)	2009	1.6	1.8	3.3	0.3	2.5
		In clump	2008	3.4 a	2.5 bc	2.8 b	1.8 d
	2009		3.9 a	2.0 b	1.8 b	1.1 b	1.8 b
	Outside (0–15)	2008	2.5	2.4	2.9	1.8	2.5
		2009	2.8	2.6	1.3	1.3	2.4
	Outside (15–30)	2008		2.8	3.6		3.1
		2009	3.0	2.4	1.8	1.9	2.1
	Outside (30–45)	2008		3.0	3.1		2.8
		2009	2.9	2.5	1.8	2.1	2.6
	Under (0–15)	2008	3.1	3.5	3.3		2.9
		2009	3.6 a	2.4 b	2.2 bc	1.4 c	2.5 b
	Under (15–30)	2008		3.0 a	3.3 a		2.5 b
2009		3.8	2.1	2.2	2.5	3.0	
Organic matter (%)	Cotton field (0–15)	2009	0.9	0.6	0.9	0.9	0.6
		In clump	2008	1.1 c	1.9 a	1.8 ab	1.2 bc
	2009		1.8 ab	1.2 b	1.1 b	1.5 a	2.4 a
	Outside (0–15)	2008	0.9	1.5	0.8	1.8	1.5
		2009	1.3	0.9	0.9	1.7	1.1
	Outside (15–30)	2008		0.7	0.6		0.9
		2009	0.6	0.5	0.9	0.7	0.5
	Outside (30–45)	2008		1.2	0.8		0.6
		2009	0.9	0.7	1.0	0.9	0.8
	Under (0–15)	2008	0.8	0.9	0.7		0.7
		2009	1.1	0.7	1.4	0.9	0.5
	Under (15–30)	2008		1.2	1.1		1.1
2009		0.9	0.4	0.9	0.10	0.9	
NO ₃ -N (mg kg ⁻¹)	Cotton field (0–15)	2009	9.8 b	19.5 a	6.9 bc	0.8 c	2.6 c
		In clump	2008		5.3	2.8	2.0
	2009		3.4 b	9.1 a	5.4 ab	1.0 b	4.3 ab
	Outside (0–15)	2008		1.9	8.1	2.4	4.5
		2009	2.8 bc	10.1 a	5.8 ab	0.8 c	3.4 bc
	Outside (15–30)	2008		1.9	2.8		3.9
		2009	2.5 bc	7.3 a	3.3 b	0.7 c	1.0 bc
	Outside (30–45)	2008		2.1	4.4		3.4
		2009	2.5	18.2	2.4	1.9	0.6
	Under (0–15)	2008		1.9	3.2		3.3
		2009	3.8 b	5.5 a	3.0 bc	1.5 cd	0.9 d
	Under (15–30)	2008		1.9	2.9		3.3
2009		3.3 b	5.1 a	2.1 c	1.6 cd	0.7 d	

^aMean separation was done only for the data that showed significant difference between harvest date. Within the same row, number followed by same letter are not statistically different at $p = 0.05$. Results showed that nutrients are moving from the belowground biomass to the soil.

NO₃-N content of the soil collected from the clumps in November was 4.6 mg N kg⁻¹ higher than that of October. These results suggested that harvesting the switchgrass in November will help return significant amount of NO₃-N to the soil. As switchgrass was senescing, no significant increase in N content was found in the roots as opposed to the rhizomes (Figure 3A). At the same

time, the N content of the leaves decreased, suggesting a translocation toward the soil, toward other organs, or a volatilization.

P content of the soil depended on the date of biomass harvest ($p = 0.0003$) and the soil depth ($p < 0.0001$) (Table 2), and ranged from 11 to 51 mg kg⁻¹ (Table 4). From July to the end of the season, the P content of

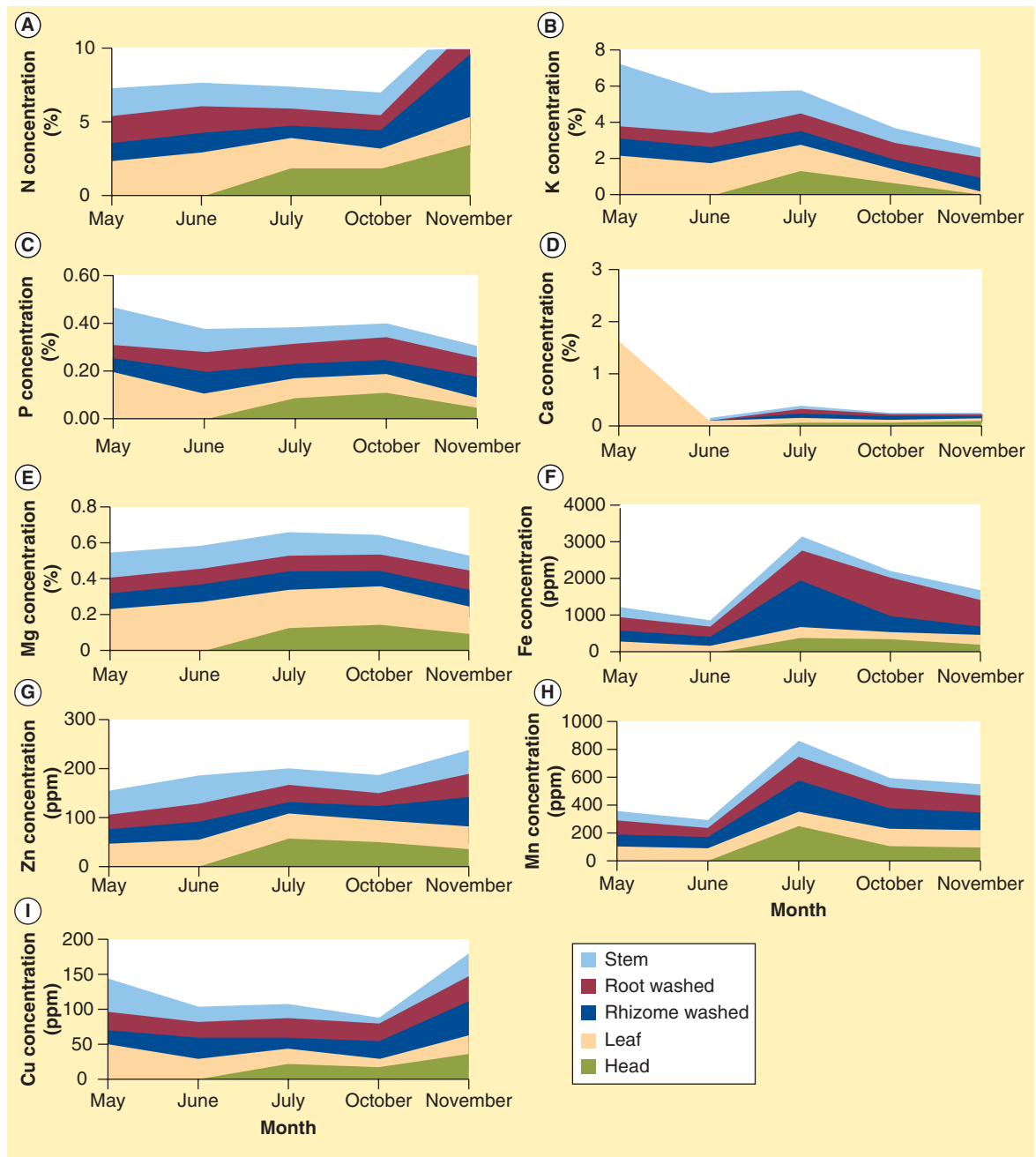


Figure 3. Seasonal progression of nutrients concentration in the aboveground and the belowground biomass of Alamo switchgrass (MO, USA) 2008–2009. Generally, as switchgrass was senescing, the nutrient uptake in the aboveground biomass decreased [24], whereas some nutrients accumulated in the roots/rhizomes tissues. These results in conjunction with those on soil (Tables 2–5) suggested that the nutrients increase in the soil was due to their translocation from the aboveground biomass to the soil. During senescence: (A) N concentration decreased in the leaves, but increased in the rhizomes; (B) K decreased in most organs from July to the end of the growing season; (C) P decreased in leaf and stem. (D) Ca content in the biomass was very high at the beginning of the season and then stabilized at a basal level in all organs. (E) Mg content did not increase in roots or rhizomes toward end of season. (F) Fe content of roots and rhizomes was higher than that of the aboveground biomass. In all organs, it increased after June. (G) Zn content in belowground biomass increased toward the end of the season. (H) Generally, once Mn content reached its peak in July, it did not change until the end of the season. (I) From May to July, Cu in the aboveground biomass decreased, and then increased in the biomass during senescence.

the soil augmented at every location that was explored in the soil (Table 4). Soil P content in clumps was the same in October and November 2008. In November 2009, the P content of the soil increased from 19 mg P kg⁻¹ soil to 26 mg P kg⁻¹ soil. The highest increase was recorded under the clump (15–30 cm) and outside the clump (30–45 cm) (Table 4). The most significant

change was always recorded in the clump ($p \leq 0.008$) (Table 2), suggesting that although the P levels changed in all parts of the soil, the most significant variation occurred in the environment near the roots (in the clump and under the clump). In general, the P content of the aboveground and belowground biomass was similar (Figure 3C).

Table 4. Impact of the harvesting time and the soil sampling depth on the P, Ca, Mg and K concentration of the switchgrass cv. Alamo's soil at Portageville (MO, USA) in 2008–2009.

Nutrient	Sample location/ soil depth (cm)	Year of study	Nutrient concentration in soil (mg kg ⁻¹) [†]				
			May	June	July	October	November
P Bray I	Cotton field (0–15)	2009	37.9	36.8	29.0	27.5	38.4
		In clump	2008	24.0 b	32.6 a	23.5 b	35.8 a
	Outside (0–15)	2009	33.1a	33.4 a	26.0 ab	19.4 b	25.8 b
		2008	23.8	32.5	27.8	27.9	37.3
	Outside (15–30)	2009	24.0	26.4	23.2	25.1	33.1
		2008		18.8 b	17.4 b		23.5 a
	Outside (30–45)	2009	17.5	13.9	13.5	23.9	20.6
		2008		19.0	23.4		17.83
	Under (0–15)	2009	25.4 ab	12.5 c	12.3 bc	14.9 bc	29.5 a
		2008	24.0	15.0	17.1		23.4
	Under (15–30)	2009	22.9	11.0	18.5	19.8	25.3
		2008		20.8	20.0		20.8
Ca	Cotton field (0–15)	2009	728	666	679	774	619
		In clump	2008	4708	680	509	592
	Outside (0–15)	2009	607	564	616	632	587
		2008	550	595	485	672	556
	Outside (15–30)	2009	507	536	599	6703	644
		2008		5345	473		462
	Outside (30–45)	2009	555	538	847	457	574
		2008		1150.5 a	806 ab		578 b
	Under (0–15)	2009	922 b	959 b	1009 b	887 b	1458 a
		2008	620	844	669		521
	Under (15–30)	2009	1404 a	909 b	808 b	633 b	896 b
		2008		1443	1021		1012
Mg	Cotton field (0–15)	2009	163	178	162	208	121
		In clump	2008	116 b	213 a	161 ab	200 a
	Outside (0–15)	2009	180	176	194	186	194
		2008	153	171	143	207	157
	Outside (15–30)	2009	149	177	193	187	154
		2008		149	112		133
	Outside (30–45)	2009	125	146	160	163	141
		2008		164	116		124
	Under (0–15)	2009	154	154	165	175	190
		2008	108	134	107		113
	Under (15–30)	2009	194	146	133	124	154
		2008		164	120		158
		2009	225	173	167	221	228

[†]Mean separation is shown for data that showed significant difference for the same soil depth. Number followed by same letter are not statistically different at $p = 0.05$ within the same row.

Table 4. Impact of the harvesting time and the soil sampling depth on the P, Ca, Mg and K concentration of the switchgrass cv. Alamo's soil at Portageville (MO, USA) in 2008–2009 (cont.).

Nutrient	Sample location/ soil depth (cm)	Year of study	Nutrient concentration in soil (mg kg ⁻¹) [†]					
			May	June	July	October	November	
K	Cotton field (0–15)	2009	149	206	113	153	112	
		In clump	2008	152 c	136 c	199 bc	274 ab	311 a
			2009	234 ab	159 b	298 a	163 b	293 a
	Outside (0–15)	2008	125	126	165	154	182	
		2009	133	164	147	181	122	
	Outside (15–30)	2008		109 b	116 b		138 a	
		2009	126	123	94	219	91	
	Outside (30–45)	2008		96	110		119	
		2009	128	97	72	118	143	
	Under (0–15)	2008	119	99	92		115	
		2009	112	133	80	116	131	
	Under (15–30)	2008		88	75		116	
		2009	92	131	71	160	136	

[†]Mean separation is shown for data that showed significant difference for the same soil depth. Number followed by same letter are not statistically different at $p = 0.05$ within the same row.

While P concentration in the aboveground biomass was decreasing, the belowground biomass did not encounter a significant increase (Figure 3C). This suggested that as the P returned back to the roots and the rhizomes, it did not stay in them before ending up in the neighboring soil.

Ca concentration in the soil mostly depended on the year of the study ($p = 0.001$) and the soil depth ($p < 0.0001$), ranging from 457 to 1738 mg kg⁻¹ (Table 4). Although toward the end of the season, the Ca concentration in the clump did not significantly increase, under the clump (0–15 cm) and outside the clump (30–45 cm) it did. In general, the Ca content in the biomass was very high at the beginning of the season and then stabilized at a basal level in all organs (Figure 3D).

Over the course of this study, the most significant impact of the time of biomass harvest on the magnesium content of the soil happened in the clump ($p = 0.0142$) (Table 2). From July to November, Mg content increased under the clump (0–15 cm) (Table 4). Although a decrease in the Mg content in the leaves and the stalk occurred toward the end of the season, no increase was found in the roots or the rhizomes (Figure 3E). This suggested that Mg returned directly to the soil as they reached the belowground biomass, which is reflected in the higher Mg content of the soil as the plant was senescing. Some Mg likely leached out of the plant tissue – thus going directly from plant to soil. In real field conditions, it will be very difficult to quantify this phenomenon.

Potassium content of the soil varied between 71 and 311 mg kg⁻¹, with the highest value obtained at the end of the season in the clump. In general, K was more concentrated in the soil removed from the clump. On average,

the K content of the soil in the clump in November was 302 mg K kg⁻¹ soil compared with 218 mg K kg⁻¹ soil in October (Table 4). Additionally, under the clump, the K content in the soil from October to November increased up to 21% (Table 4). From July to November, the K content of the soil beneath the clump increased up to 198% according to the year (Table 4). The K content of the root and the rhizome was more than half that of either the leaves or the stem. After July, the K content of the stem and the leaves significantly decreased, whereas no significant increase was found in the belowground biomass, suggesting that the K return to the soil (Figure 3B).

Sulfur content reached its lowest level in October, after which it significantly increased until the end of November (Table 5). On average, the sulfur content of the soil in November was three- to 11-times that of October (Table 5).

▪ Micronutrients

Although the Zn content of the soil increased in most of the sampled soils, the highest significant change occurred in the clump ($p = 0.067$) (Table 5). The Zn content of the soil in November was up to 5.6-times that of October. The highest increase was observed outside the clump (15–30 cm) (Table 5). At any date, the highest Zn content was recorded in the clump.

In general, the Zn content of both the roots and the rhizomes increased toward the end of the season (Figure 3G), suggesting that Zn accumulated in the belowground biomass as the plant was senescing. In addition, Zn content of the soil in November was up to four-times that of October.

Iron content of the soil increased from October to November outside the clump, whereas it decreased in and

Table 5. Impact of the harvesting time and the soil sampling depth on sulfur and the micronutrient concentration of the switchgrass cv. Alamo's soil at Portageville (MO, USA) in 2009.

Nutrient	Sample location/ soil depth (cm)	Nutrient concentration in soil (mg kg ⁻¹) ^a				
		May	June	July	October	November
SO ₄ -S	Cotton field (0–15)	20.95 ab	0.98 bc	2.20 abc	0.25 c	4.35 a
	In clump	0.33 b	0.58 b	2.50 ab	0.48 b	3.85 a
	Outside (0–15)	0.93 ab	0.48 ab	3.97 ab	0.33 b	5.75 a
	Outside (15–30)	1.13 b	0.55 b	2.66 a	0.28 b	3.00 a
	Outside (30–45)	0.58 b	1.25 ab	2.76 a	0.80 b	2.85 a
	Under (0–15)	3.03 a	1.05 b	3.8 a	0.35 b	2.13 ab
	Under (15–30)	4.40	1.40	1.53	0.70	2.40
Zn	Cotton field (0–15)	0.48	0.73	1.07	0.70	0.73
	In clump	1.28 b	1.18 b	1.45 ab	0.85 b	2.65 a
	Outside (0–15)	0.83	0.93	0.57	0.93	2.08
	Outside (15–30)	0.50	0.60	0.43	0.25	1.40
	Outside (30–45)	0.43	0.45	0.23	0.18	0.53
	Under (0–15)	0.48	0.35	0.43	0.30	1.40
	Under (15–30)	0.28	0.25	0.17	0.10	0.48
Fe	Cotton field (0–15)	28.9	25.1	38.3	25.9	17.5
	In clump	42.2	34.6	39.8	32.5	28.1
	Outside (0–15)	28	43.4	32.13	32.3	26.93
	Outside (15–30)	29.2 b	31.2 b	44.8 a	22.6 bc	16.8 c
	Outside (30–45)	38.2	39.6	47.3	31.5	35.1
	Under (0–15)	64.2	35.6	44.6	34.8	21.0
	Under (15–30)	53.1	35.3	47.8	40.8	32.3
Mn	Cotton field (0–15)	5.6	10.8	11.0	9.9	4.7
	Outside (0–15)	11.0	10.7	15.2	13.0	11.0
	Outside (15–30)	5.3	9.9	7.2	12.6	7.0
	Outside (30–45)	4.9	9.3	12.1	6.6	4.9
	Under (0–15)	5.4 bc	13.1 a	11.5 ab	8.5 abc	2.2 c
	Under (15–30)	2.8	8.8	11.0	10.8	3.5
	Under 15–30	2.1	10.0	13.4	7.7	2.1
Cu	Cotton field (0–15)	0.37 b	0.55 ab	0.79 a	0.55 ab	0.34 b
	In clump	0.64 b	0.59 b	1.06 a	0.46 b	0.43 b
	Outside (0–15)	0.39 b	0.63 a	0.62 a	0.45 ab	0.40 b
	Outside (15–30)	0.36 b	0.63 b	1.21 a	0.49 b	0.43 b
	Outside (30–45)	0.50 b	1.04 a	1.19 a	0.63 ab	0.50 b
	Under (0–15)	1.13	0.87	1.14	0.70	0.42
	Under (15–30)	0.96	0.66	1.26	0.71	0.49
B	Cotton field (0–15)	0.10 c	0.18 ab	0.22 a	0.13 bc	0.16 abc
	In clump	0.26 a	0.3 a	0.22 a	0.13 a	0.24 a
	Outside (0–15)	0.23 a	0.23 a	0.25 a	0.11 b	0.12 b
	Outside (15–30)	0.24 a	0.14 b	0.22 a	0.10 b	0.09 b
	Outside (30–45)	0.21 a	0.14 b	0.17 ab	0.08 c	0.12 bc
	Under (0–15)	0.17 ab	0.18 ab	0.36 a	0.05 bc	0.10 b
	Under (15–30)	0.07 c	0.14 b	0.21 a	0.07 c	0.16 abc

^aMean separations are shown for data that showed significant difference. Numbers followed by same letter are not statistically different at $p = 0.05$ within the same row.

under the clump. These results suggested that the Fe may have been lost in the leaves by leaching. In most cases, the return of Fe to the soil was not significant (Table 2). These data corroborated with the nutrient removal data.

The belowground biomass was richer in Fe than the aboveground biomass. The Fe content significantly increased in all organs after June, suggesting that the demand was high when the plant entered its active

growth period. During the year, the Fe content of the stem or the leaves did not change (Figure 3F). However, from July a drastic decrease was encountered in the rhizome while a simultaneous increase was found in the roots. This implied that as switchgrass began to senesce, the Fe moved toward the roots. At that time, the Fe content of the roots was almost three-times that of any other organ.

Significant variation in Mn content occurred according to the date of biomass harvest ($p < 0.0001$), but less with the soil depth ($p = 0.054$) (Table 2). Usually, the Mn content of the soil decreased from July to November (Table 5). Mn may have been very important for the growth of switchgrass, and that is why it was retained. The data corroborate that obtained in the aboveground biomass. Indeed, around July the Mn content in most organs (except the stem) increased up to three-times higher than that of June. In most cases, once Mn content reached the maximum in July, it did not change until the end of the season (Figure 3H). From May to July, a significant amount of Cu was recovered everywhere in the soil (Table 5). During that time, Cu content in the aboveground biomass decreased (Figure 3I). In contrast, copper content in the soil decreased from July to November. This data concurred with the nutrient uptake in the biomass as Cu accumulation in the aboveground biomass increased from October to November (Figure 3I).

In 2009, we observed that from October to November, B content in and under the clump doubled (Table 5), with the highest value obtained in the soil taken from clump. From July to October, B content significantly decreased in the soil, suggesting that the plant may have taken up during that time. The small changes in micronutrients could be due to decreases in pH through the season.

Discussion

Our results showed that as switchgrass senesced, the nutrient (e.g., N, P and K) concentration of the soil increased (Tables 3–5) while the amount taken up (in kg ha^{-1}) in the aboveground biomass was decreasing (Table 1). In most cases, the nutrient content of the roots did not significantly change, as opposed to that of the rhizomes. These results suggested that as some nutrients were leaving switchgrass aboveground biomass to return to the roots, some (notably N, Fe, Cu and Zn) were being accumulated in the roots/rhizomes tissues, but once the nutrients reached the roots, some (mostly N, P, K, S and Zn) were in the soil either by leakage or root death from natural causes or damage during sampling.

We observed that switchgrass rhizomes near the soil surface accounted for the majority of the belowground plant material at the depths we explored. That may

explain why most of the increase in the nutrients in the belowground biomass during senescence was encountered in rhizomes. As the aboveground leaves and stems began to senesce in the late summer, much of the roots also stopped growing. Emerging new roots in the spring begin from existing rhizomes and since root age was not directly measured in our study, it was impossible with our methodology to differentiate nutrient content in existing (2 years or older roots) versus new growth.

We also found that the nutrients returned to diverse locations in the soil, but generally in and under the clump. Additionally, our results showed that the movement of nutrients between the soil and the plants was dynamic throughout the year.

In contrast, the nutrient concentration in the soil taken from the clump in November was generally higher than that in October. No change happened with the macronutrient content of the upper level (0–15 cm) of the soil outside the clump. Generally, the soil taken from the clump was the main sink of the nutrients as they returned to the soil. These results indicate that the nutrient increase in the soil may be caused by their movement from the plants to the soil. Some micronutrients probably leached out from the stems and leaves during late summer rainfall, which contributed to their amounts in the outside region (0–15 cm). In general, these results showed that a later switchgrass harvest date could reduce nutrient removal. Although the highest biomass was obtained by October, harvesting the biomass late in October will remove a significant amount of nutrients from the field. However, as the biomass in November was not much different than that of October [24], and knowing that the nutrient concentration in the soil is higher in November than in October, it is clear that the best date to harvest switchgrass in temperate regions such as the USA should be late November. We may even recommend waiting until the plant dries completely before harvesting the biomass. The year effect observed in our study may be explained by the variation in weather conditions.

Switchgrass can return its nutrients to the soil through the apex of its roots, which may be more than 2 m from the base of the plant. At this depth, it would be very difficult to take soil samples. The plant may have lost some nutrients through the stems and leaves. Separating the contribution of nutrient leakage from roots versus leaching from aboveground plant parts by rainfall is not easily done in real field conditions. Therefore, a study in a closed environment would allow studying the release of nutrients by volatilization through the leaves.

Initial soil levels could have affected the movement of nutrients out of the root, if this was the case. If levels were very low to start with because the plots did not receive lime or fertilizer throughout the years, then we would

expect a big nutrient gradient from outside to inside the root and maybe more movement out of the root than would normally occur if there were a smaller gradient. A question of interest would be why the plant needed Cu during senescence while it returned most of the other nutrients back to the soil.

Being a tall, straight grass, some rainfall droplets cling to the outside of switchgrass stems at the top of plants and move vertically to the soil carrying leachable nutrients with them. This would cause some nutrients to accumulate closest to the clump at the base of the stems. For this very reason, we did not consider soil coming directly from the base of the plants. Otherwise, root breakage and stem flow could have influenced our results and, therefore, influenced our conclusions about nutrient flow out of the roots.

Many scientists have observed the nutrient decrease in the aboveground biomass as a plant was senescing [25–27,45]. Those who claimed that the aboveground nutrients returned to the roots may be partially correct if they considered the rhizomes as roots [1,7,22]. Indeed, we found that the increase of the roots nutrient concentration was not significant, but that of the rhizomes was for certain minerals. The breakdown of Rubisco is the main source of N during senescence [36,37]. In soybean and *Arabidopsis*, N moves to the seeds during senescence [33,34]. Switchgrass does not produce many seeds, which may explain why the nutrients might not have gone there. In wheat, N can volatilize and become gaseous as a plant senesces [35]. To our knowledge, none of the previous authors that speculated about nutrients returning to the roots deepened the changes in the soil nutrient concentration. The mechanism of water and nutrient uptake by plants was well established [46,47]. Most of the changes in the leaf mineral composition during senescence were also explained at the physiological and the molecular levels [36,48–50]. In 1929, it was also observed that some plants can return water to the soil through their roots by a mechanism more recently called hydraulic lift [51].

Fine roots are also a nutrient sink [52]. It can be argued that the soil shaken from the clump probably contained some fine roots or root hairs, and that some of the changes in the soil nutrient concentrations may reflect root turnover and decay, rather than nutrient efflux from living roots. However, by sieving the soil before analyzing it, we removed significant amount of biomass (including fine roots). In real field conditions, it will be impossible to remove all fine roots from such a soil. Additionally, the monitoring of the nutrients in soil was not easy as it is hard to work with roots, especially switchgrass roots that clump together. Future studies of nutrient translocation in hydroponic systems will help improve the understanding of the impact of fine roots on nutrient translocation. In future studies, it would also

be important to give a consideration to the input of new plant material (new growth) as nutrient pools may or may not be changing. The concentration of nutrients may be changing, but with more or less material growing or dying, the overall pool might not be altered. A much stronger test of this nutrient retranslocation in the soil can be achieved by using isotope techniques. Additionally the incorporation of the potential role of the plant–mycorrhizae–soil continuum will probably add a value to future investigation on the subject. Nevertheless, our results will advance the field of nutrient translocation in plants, by improving how scientists view nutrient concentration in plants.

Conclusion

Our results showed that when switchgrass is senescing, a significant amount of nutrients return mostly to the rhizomes and to the soil surrounding the roots. Generally, the soil taken from the clump was the main sink as the nutrient returned to the soil. Our results suggest that there is a sink of nutrients translocating from switchgrass aboveground biomass to the roots and soil, therefore providing additional evidence that has been lacking in the field of plant nutrient translocation. We concluded that the harvest of switchgrass late in November will help minimize the nutrient removal and maximize biomass yield. The reverse flow of nutrients may be one possible explanation for our results, but not the only one. More researches are needed in this new field of ‘reverse flow of nutrients to the soil’ to better understand plant biology and harness this strategy for a better ecological, economical management of the environment.

Future perspective

An interesting question that is not answered yet is how or by what mechanism do the nutrients leave the switchgrass to return to the soil? In perennial grasses, some nutrients from roots may return passively to the soil as auxiliary roots from rhizomes that die and decompose each fall and winter. It is also possible that the nutrients returned actively to the soil through the phloem and that maybe, after reaching a certain concentration in the roots, some are released in the soil. As the nutrients move from the aboveground biomass to the roots, they may not be able to remain definitively in the roots without hurting the plants. Indeed, those nutrients can serve as signaling molecules that can induce certain biological reactions. Based on plant physiology, nutrient excess in the roots could damage or disturb their normal physiology [46]. More studies are needed to explore other aspects of the movement of nutrients from the aboveground biomass to the soil. Even in the cotton field, we observed a significant variation in the nutrient concentration of the soil through the year. Hopefully

our results will lead other scientists to study reverse flow of nutrients in perennial grasses to the soil. It would be interesting if future studies explored not only nutrient concentration in soil but also the pool of nutrients by incorporating into the analysis the soil bulk density per soil depth and the samples taken from the rooting zone of the plant. During the processing of the roots and rhizomes (transportation from the field to the laboratory, shaking to remove dirt, washing to remove microorganisms contamination), they would have leaked out some of their contents beforehand. Our methods could have contributed to the response we found. Furthermore, stem flow of rainwater and leached nutrients could have substantially affected our data. Future studies are needed to clarify those questions.

Financial & competing interests disclosure

R Holou is the International Chair of the Sweet Sorghum Ethanol Association and the Chair of the International Service in Agronomy Award Committee. He holds a PhD in Plant, Insect and Microbial Sciences from the University of Missouri (MO, USA) and he is a research scientist at Monsanto. G Stevens is a Faculty at the University of Missouri, and V Kindomihou is a lecturer at the University of Abomey-Calavi (Benin). The Missouri Life Science Research Board and the Missouri Fertilizer and Ag Lime Board funded this research. The authors have no other relevant affiliations or financial involvement with any organization or entity with a financial interest in or financial conflict with the subject matter or materials discussed in the manuscript apart from those disclosed.

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Executive summary

Nutrient translocation

- During switchgrass senescence, nutrients are mobilized from the aboveground biomass to the soil.
- The nutrients are returned to diverse locations in the soil but, generally, soil samples collected from the clump showed the highest evidence of nutrients returning to the soil from the aboveground biomass.

Reverse flow of nutrients

- This study supports the concept of a reverse flow of nutrients to the soil.
- Additionally, our results showed that the movement of nutrients between the soil and the plants was dynamic throughout the year.

Harvest timing

- Harvesting switchgrass late in November will minimize the nutrient removal and maximize biomass yield.

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