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Carbohydrate and lignin partitioning in switchgrass (*Panicum virgatum* L.) biomass as a bioenergy feedstock

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Abstract

Approaching switchgrass (*Panicum virgatum* L.) as a multifunctional energy plant, it is important to comprehensively study the composition and partitioning of organic substances in the biomass. The character of carbohydrates and lignin concentration variation was assessed in switchgrass biomass cut at two maturity stages (heading and seed filling) in the first and second harvest years. Quality components partitioning in the biomass of aboveground plant parts was examined in leaves, stems and panicles of the most productive switchgrass accessions cut at seed filling. The concentrations of lignocellulose (NDF), cellulose (Cel), sum of structural carbohydrates (holocellulose – HoCel), sum of nonstructural and structural carbohydrates (ΣCH_2O) and lignin in switchgrass biomass of both plant development stages in the second harvest year were significantly higher, whereas an average hemicellulose (HCel) concentration was significantly lower compared with the respective parameters in the first harvest year. The concentrations of nonstructural carbohydrates (NSC) and their individual fractions (water soluble carbohydrates (WSC) and starch) in biomass were similar both in the first and second harvest years. The concentrations of NDF, Cel, HoCel and ΣCH_2O and particularly lignin at seed filling were significantly higher compared with the respective data at heading in both harvest years. High lignin concentration (105 g kg^{-1} dry matter (DM)) in switchgrass biomass at seed filling in the second harvest year showed its great suitability for solid biofuel production. Considerable amount of ΣCH_2O (693–742 g kg^{-1} DM) indicated that switchgrass biomass at this stage fits for the second-generation bioethanol production. At heading, switchgrass in the second harvest year produced quite a high NSC yield (an average 28.4 g $plant^{-1}$) and low lignin output (an average 19.3 g $plant^{-1}$), which is a favourable feature of feedstock for biogas production, biomass at seed filling is less suitable for that than at heading. Switchgrass plant part significantly ($P < 0.01$) affected the concentration of all biomass quality attributes tested, but did not affect HCel concentration. Accessions' DM yield correlated positively with NDF ($r = 0.781, P < 0.05$), Cel ($r = 0.882, P < 0.01$) and lignin ($r = 0.517$) and negatively with WSC and NSC ($r = -0.982, -0.959; P < 0.01$).

Key words: aboveground plant parts, biomass, carbohydrates, energy plants, lignin, *Panicum virgatum*.

Introduction

Switchgrass, a perennial C4 type warm-season grass native to the prairies of North America, has been identified by the U.S. Department of Energy as its main species of emphasis for development into a herbaceous biomass fuel crop (Vogel, Jung, 2000). The species is able to adapt to growth in different latitudes (Fike et al., 2006). It has become one of the potential new crops in the European countries with Mediterranean climate in the South (Greece, Italy) and oceanic climate of the Western Europe (Germany, The Netherlands and United Kingdom) (Switchgrass, 2012). Biomass from switchgrass could be used as a multi-purpose bioenergy feedstock for biogas, bioethanol of the second generation, direct combustion. Different use of feedstock from switchgrass biomass (methanisation, liquid and solid bio-fuels) demands particular requirements of chemical composition of the raw material for optimization of the respective process parameters. Ones of the main indicators are carbohydrates, their fractions and lignin. For direct combustion, higher concentration of lignin in biomass is desirable (Demirbaş, 2003). For methane production high concentration of NSC is very important (Nizami et al., 2009). For bioethanol fermentation, lignocellulose as well as NSC yield plays a significant role (Sluiter et al., 2010).

The energy in herbaceous plant biomass is largely concentrated in plant cell walls. The most important factor, affecting biomass yield and its quality, including cell-wall chemical composition, is grass maturity or harvesting time. Cell walls account for 40% to 80% of the biomass in herbaceous plants, depending on species and maturity of the plant material (Vogel, Jung, 2000). Cellulose and hemicellulose are the major polysaccharides of plant cell walls. Lignin (a polyphenolic polymer) comprises a substantial portion (~20%) of the grass secondary cell wall and essentially fills the pores between the polysaccharides

(Vogel, 2008). As plants mature, wall composition shifts from almost no lignin to its substantial amounts (20–30%) (Vogel, Jung, 2000). High content of lignin is especially undesirable in the biomass used as bioenergy feedstock for methane and lignocellulosic bioethanol production. Multiple cross-linking in cell wall limits accessibility of hydrolytic enzymes; consequently, lignin restricts the degradation of structural polysaccharides, thereby limiting the bioconversion of biomass into liquid fuels or biogas (Vogel, Jung, 2001). Regression analysis using a two-parameter (ethanol yield – lignin in stem) linear model ($r = -0.681$) indicated that less than half of the total variation among the genotypes was due to differences in stem lignin concentration (Sarath et al., 2011). On the other hand, lignin is the most valuable substance in the cell walls, when the biomass is referred to as a source for solid biofuel. Because lignin is less oxidized than the structural polysaccharides, it has higher energy content than cellulose or hemicellulose. Theoretically, cellulose has a higher heating value nearly 18.6 MJ kg^{-1} and higher heating value of lignin varies in a range of 23.3–25.6 MJ kg^{-1} (Sheng, Azevedo, 2005).

Plant maturity is not the only factor affecting variation in content of non-structural carbohydrates and structural components of cell wall and their relationship. Sink-source dynamics within the plant direct how much, where, and when carbohydrates are allocated, as well as determine the harvestable tissue (Slewinski, 2012). Plant morphology has a major impact on C-containing compounds, cell-wall concentration and composition of herbaceous plants due to differences between leaves and stems ratio (Vogel, Jung, 2000). Results of many researches show, that cell walls of grass stems do tend to be more lignified than leaves (Mann et al., 2009 and others); however, there exists the opposite data also (Hu et al., 2010). Understanding the physical and chemical properties of switchgrass is an important issue for future utilization of biomass for biofuels and is essential for optimizing pre-treatment technologies for this bioresource (Hu et al., 2010). The objectives of the present study were to assess the character of carbohydrates and lignin concentration at the different switchgrass plants' developmental stages of the first and second year of herbage use. Moreover, we included the analysis of chemical components' allocation in leaves, stems and panicles at seed filling stage of the most productive accessions.

Material and methods

Plant material and trial conditions. Experimental collection was set up using the seedlings grown in a greenhouse. Seeds for the germplasm collections of switchgrass were obtained from the Plant Genetic Resources Conservation Unit (PGRCU) of the United States Department of Agriculture and Agricultural Research Service. The part of collection set up in 2011 was qualified as germplasm collection of the first harvest year and the part set up in 2010 – as germplasm collection of the second harvest year. The tested accessions included 8 varieties and 32 wild ecotypes. Each accession consisted of 32 plants spaced 0.5 m apart with 8 plants per row, two rows per replication, and two replications per treatment. Reed canary grass variety 'Chiefton' was established according to the same design.

The soil of the experimental site is *Endocalcari-Epihypogleyic Cambisol* (*CMg-p-w-can*) with the following characteristics of the plough layer (0–25 cm): pH 6.52, humus content 1.82. Simulating the species management under commercial cultivation conditions, the grass was cut twice per season at the beginning of anthesis (20 July) and after re-growth of aftermath (11 September) as feedstock for biogas in the first treatment. In the second treatment, the grass was cut once at seed ripening stage as feedstock for bioethanol of the second generation and for solid biofuel.

Plants were sampled at two stages: heading and seed filling. Dry matter yield was measured in 500 g herbage samples dried to a constant moisture content. The biomass of the SFS-sampled plants was separated into leaves (blades + sheaths), stems, and panicles and the percentage of each fraction, based on their dry mass, was determined. The data discussed in the paper concern only those accessions that proved to be promising by complex agrobiolocal traits, i.e. five switchgrass accessions in the first harvest year and seven switchgrass accessions in the second harvest year (Table 1).

Table 1. The catalogue number of the switchgrass accessions discussed in the paper

2010 yr collection (the 2nd harvest year)		2011 yr collection (the 1st harvest year)	
PGRCU catalogue No.	Lithuanian catalogue No.	PGRCU catalogue No.	Lithuanian catalogue No.
642295	46	642198	67
642296	47	642200	69
642300	51	642208	74
642306	57	537588	77
642309	60	477003	79
642191	62		
642194	64		

PGRCU – Plant Genetic Resources Conservation Unit

The weather conditions favoured herbage growth and development during the whole vegetation period in 2012. The winter conditions of 2011–2012 were similar to long term average and were conducive to overwintering of perennial grasses.

Sample preparation and chemical analyses. Fresh samples chopped into particles of 3–5 cm, were fixed at 105°C for 15 min, dried at 65 ± 5°C and ground in a cyclonic mill with 1 mm sieve. Samples of the accessions were analysed according to the standard methods as follows: for dry matter (DM) concentration the samples were dried at 105°C, for the cell wall components analyses: acid detergent fibre (ADF), and neutral detergent fibre (NDF) and acid detergent lignin (ADL) using cell wall detergent fractionation method according to Van Soest (Faithfull, 2002). NDF and ADF extraction was done on an ANKOM220 Fibre Analyzer (ANKOM Technology, USA) using F57 filter bags (25 µm porosity). Sodium sulphite was added to the neutral-detergent solution and data of NDF are presented as ash-free. Contents of cell wall structural carbohydrates cellulose (Cel) and hemicellulose (HCel) were calculated as the following differences: Cel = ADF − ADL and HCel = NDF − ADF (Hindrichsen et al., 2006), HoCel was calculated as the sum of structural carbohydrates Cel and HCel. Concentrations of water soluble carbohydrates (WSC) in water extracts of dried samples were measured photocolorimetrically using the anthrone reagent (Yemm, Willis, 1954). Starch, a water-insoluble component of nonstructural carbohydrates (NSC) was determined in plant biomass residue after WSC washing with ethanol and water. It was solubilized and hydrolysed to glucose using enzymes α-amylase and amyloglucosidase and released glucose was assayed following the general procedures described by Zhao et al. (2010). Total NSC content was calculated as the sum of WSC and starch.

Statistical analysis was done using the software *ANOVA* and *STAT* from the package *SELEKCIJA* (Tarakanovas, Raudonius, 2003).

Results and discussion

Knowledge of the distribution patterns of carbohydrates in herbage biomass could support harvest management decisions and herbage conversion to energy technology. Carbohydrates composition as well as lignin concentration in DM of biomass depended both on plant development stage and harvest year (Tables 2 and 3). Carbohydrates in switchgrass, cut at heading stage in the first harvest year (HS1) averaged and ranged: Cel 339; 325–347 g kg^{-1} DM, HCel 262; 228–284 g kg^{-1} DM, WSC 43.9; 37.7–56.8 g kg^{-1} DM, and starch 38.9; 31.6–55.4 g kg^{-1} DM (Table 2). The ΣCH_2O concentration ranged from 665 to 701 g kg^{-1} DM. Grass for anaerobic digestion is grown in the same way as high-quality grass for animal feed as, in both cases, the aim is to maximise metabolisable energy by harvesting the grass as long as it is in a leafy, non-lignified stage (Murphy et al., 2013). Hence, in the current study switchgrass at heading stage was cut while simulating the biomass use as the feedstock for biogas production. Lignin is one of the factors limiting high biogas output. An average switchgrass accumulation of this microbe recalcitrant biopolyphenol was higher in the plants of the second harvest year (HS2) than in that of the first harvest year (59.0 and 48.8 g kg^{-1} DM, respectively).

Table 2. Pattern of the variation in lignocellulose, carbohydrates fractions and lignin in biomass dry matter (DM) of switchgrass (SWG) cut at heading stage as influenced by herbage age

Quality attribute	SWG HS1		SWG HS2	
	Mean ± SD	Range	Mean ± SD	Range
	g kg^{-1} DM			
Lignocellulose (NDF)	650 ± 29.0	608–679	704 ± 20.5	661–727
Cellulose (Cel)	339 ± 9.0	325–347	392 ± 11.1	364–407
Hemicellulose (HCel)	262 ± 23.3	228–284	253 ± 14.3	229–277
Holocellulose (HoCel)	601 ± 31.7	552–630	645 ± 18.4	611–668
Water soluble carbohydrates (WSC)	43.9 ± 7.8	37.7–56.8	45.5 ± 8.45	26.6–67.8
Starch	38.9 ± 9.52	31.6–55.4	39.8 ± 6.47	30.3–55.9
Nonstructural carbohydrates (NSC)	82.8 ± 17.0	71.0–112	87.3 ± 13.8	63.1–124
Sum of carbohydrates (ΣCH_2O)	684 ± 16.0	665–701	733 ± 19.7	703–762
Acid detergent lignin (ADL)	48.8 ± 8.29	39.7–58.7	59.0 ± 7.56	48.0–82.7

HS1 – at heading stage, 1st harvest year, HS2 – at heading stage, 2nd harvest year; SD and Range – data for values in all samples, including replications

NDF, Cel, HoCel and ΣCH_2O contents in switchgrass HS2 biomass were higher, and average HCel concentration was lower than in switchgrass HS1 biomass. The concentrations of NSC and their separated fractions (WSC and starch) were similar in the grass biomass of the both harvest years. In contrast to C3 (plants in which captured atmospheric CO_2 in the first step of the Calvin cycle reacts with ribulose 1,5-biphosphate to form two 3-carbon molecules of 3-phosphoglycerate), C4 (these plants have the 4-carbon molecule of oxaloacetate as the first CO_2 fixation product) plants accumulate starch as their storage carbohydrate (Longland, Byrd, 2006), i.e. NSC fraction of switchgrass is composed of both WSC and starch. NSC is an important attribute to consider when herbage biomass is evaluated as a bioenergy feedstock, whose conversion into energy mechanisms includes anaerobic digestion and fermentation procedures because fermentation primarily converts NSC. However, switchgrass biomass was poor both in WSC and starch. WSC, and even NSC concentrations in switchgrass at heading stage were lower than WSC concentrations in C3 energy grass (cocksfoot and tall fescue), which WSC accumulated at this stage in average 128 and 165 g kg^{-1} DM (Butkutė et al., 2011). Whereas WSC concentration in reed canary grass variety 'Palaton' (84 g kg^{-1} DM) (Butkutė et al., 2011) was approximate to the average NSC concentration in switchgrass biomass at heading stage in the current study (Table 2).

On the other hand, application of the biological pre-treatment of feedstock such as the use of cellulase enzymes can result in an increased degradation of cell walls and the breakdown of structural carbohydrates Cel and HCel, in the following way improving the potential of methane production (Murphy et al., 2013). In that case switchgrass at heading stage could be a promising feedstock for anaerobic digestion. There is relatively little data on the switchgrass biomass as an energy source to produce methane. El-Mashad (2013) reported that the methane yield of switchgrass was 126.69 and 166.71 ml g^{-1} of volatile solids at mesophilic and thermophilic temperatures, respectively. There it should be noted that in the aforesaid study switchgrass was harvested in the post killing frost stage and air dried and authors indicated that another N-rich feedstock is needed to increase the yield of methane production from switchgrass. Massé et al. (2011) pointed out that the average specific methane yield from reed canary grass-seeded plots was less than from switchgrass-seeded plots. In our opinion, switchgrass cultivation for biogas production should be a relevant object for further complex studies and debates.

While simulating the biomass use as the feedstock for lignocellulosic ethanol or solid biofuel production, switchgrass was cut at seed filling stage in the current study. Table 3 shows the lignocellulose, carbohydrates fraction and lignin content in biomass samples harvested at this stage from plots of the first and second harvest years. Our research results confirmed the well known regularity that the amount of NDF and all its structural components (Cel, HCel and ADL) increases during grass maturing. As for plant age, the similar trends were determined at seed filling stage to those at the heading stage: NDF, Cel, HoCel, ΣCH_2O and ADL concentrations in average were higher in the grass biomass of the 2nd harvest year than in that of the 1st year (respectively 742, 413, 636, 756 and 106 *vs.* 675, 355, 596, 722 and 78.6 g kg^{-1} DM). Hemicellulose amount was lower than in switchgrass SFS1 biomass (223 *vs.* 241 g kg^{-1} DM) and average NSC, WSC and starch concentrations were similar in the grass biomass of the both harvest years.

Table 3. Pattern of the variation in lignocellulose, carbohydrates fractions and lignin in biomass dry matter (DM) of switchgrass (SWG) cut at seed filling stage as influenced by different herbage age

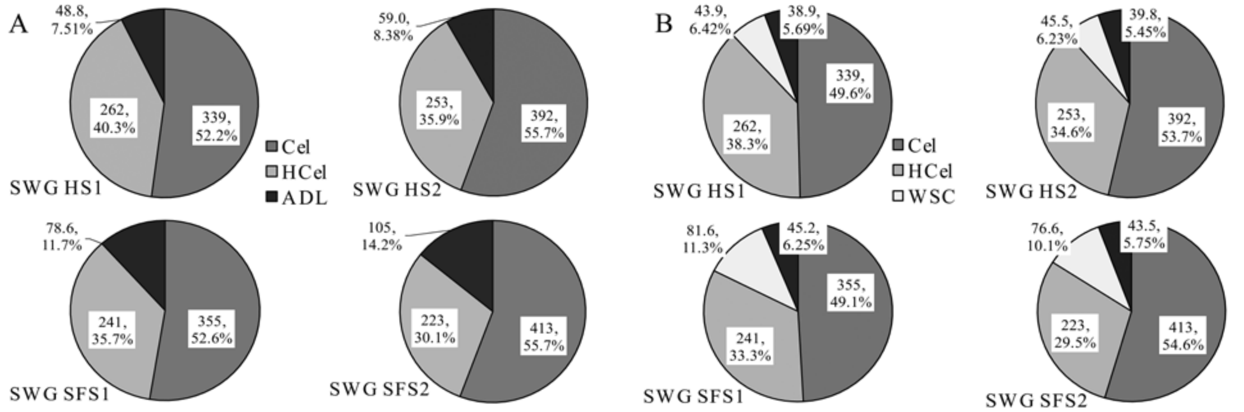
Quality attribute	SWG SFS1		SWG SFS2	
	Mean ± SD	Range	Mean ± SD	Range
	g kg^{-1} DM			
Lignocellulose (NDF)	675 ± 20.2	639–692	742 ± 26.0	692–771
Cellulose (Cel)	355 ± 17.8	329–388	413 ± 13.4	393–438
Hemicellulose (HCel)	241 ± 19.1	211–277	223 ± 17.3	199–257
Holocellulose (HoCel)	596 ± 14.0	576–622	636 ± 22.9	605–676
Water soluble carbohydrates (WSC)	80.8 ± 13.3	63.8–97.2	76.6 ± 16.4	51.7–107
Starch	45.2 ± 6.91	35.3–59.9	43.5 ± 7.30	31.3–58.4
Nonstructural carbohydrates (NSC)	126 ± 19.4	101–157	120 ± 21.3	89.0–161
Sum of carbohydrates (ΣCH_2O)	722 ± 21.5	699–759	756 ± 24.5	707–790
Acid detergent lignin (ADL)	78.6 ± 15.0	59.1–104	106 ± 13.3	86.0–127

SFS1 – at seed filling stage, 1st harvest year, SFS2 – at seed filling stage, 2nd harvest year; SD and Range – data for values in all samples, including replications

Compared to published results (Xue et al., 2011), the whole plant of two switchgrass varieties harvested during the second week of September after the grasses reached maturity stage, contained amounts of NDF, carbohydrates Cel and HCel and lignin, falling within the value ranges for respective component of switchgrass at SFS in our study (Table 3). According to biomass quality data, switchgrass biomass at the seed filling stage in the 2nd harvest year shows higher energy potential both for bioethanol and direct combustion. While usual fermentation (e.g., production of bioethanol of first generation) converts mostly starches and sugars, fermentation processes that include cellulosic materials would be better candidates to become a large scale energy conversion pathway (Hermann et al., 2005). Current systems use acid hydrolysis to convert cellulosic biomass to easily fermentable sugars by breaking up of lignocellulose to Cel and HCel, then finally into glucose and pentoses (mainly xylose) (Hermann et al., 2005; Hu et al., 2010). Structural components of cell wall Cel, HCel, and lignin are differently oxygenated which means the higher heating value of lignin is much higher than that of structural carbohydrates (Sheng, Azevedo, 2005). Demirbaş (2003) statistically proved that the higher heating values of lignocellulosic fuels are highly correlated with lignin content. Consequently, the fairly high lignin concentration (106 g kg^{-1} DM) in switchgrass biomass of SFS2 showed its great suitability for solid biofuel production.

Figure 1A presents the data of summarised lignocellulose composition of switchgrass at two maturity stages and in two harvest years, structural carbohydrate and lignin contents are shown as concentrations g kg^{-1} DM and as percentage shares in NDF. It is evident that despite an increase of Cel concentration in DM of biomass during plant maturity its share in cell wall (or lignocellulose) remains unchanged from heading to seed filling stage. Such trend was subsistent in switchgrass both in the first and second harvest years. Moreover, Cel contribution to the ΣCH_2O depended more on grass age (harvest year) than on grass development stage (Fig. 1B). Switchgrass accumulated more NSC (both WSC and starch) at late stage of maturity than at heading stage both in the first and second harvest years. Such observation is in accordance with that of Smith (1975), who found that plants harvested at late maturity before frost killing contain the highest amount of readily fermentable nonstructural carbohydrates. The HCel contribution rate both to NDF and to ΣCH_2O composition decreased by approximately 5 percentage points from plant heading to seed filling irrespective of herbage age (Fig. 1A and B).

Processing of the non-food material containing high amount of lignocellulose is one of the most perspective technologies of the second-generation biofuels production. Theoretical bioethanol output from switchgrass, depending on yield, ranges from 2000–4000 (Schmer et al., 2008) to 5000–6000 t ha^{-1} (Parrish, Fike, 2005). However, McKendry (2002) indicated that due to complicated pentoses fermentation to ethanol, for its production, a biomass feedstock with a high Cel:HCel content is needed to provide a high yield, as glucose is readily fermentable into ethanol and there are technical and economical impediments to the development of commercially viable processes utilizing hemicellulosic derived sugars (Chandel et al., 2011). Calculation based on the data presented in Figure 1 demonstrates an increase of this ratio with advancing plant maturity from 1.29 to 1.48 in NDF of biomass in the first harvest year and from 1.55 to 1.85 in that in the second harvest year. Therefore, according to this trait switchgrass biomass at SFS2 could be the most promising candidate to lignocellulosic ethanol production, despite relatively high lignin content. Regarding high calorific lignin concentration in the residue of the lignocellulosic ethanol production Öhman et al. (2006) discussed the possibility to use it as a material for combustion.



HS1 – at heading stage, 1st harvest year, HS2 – at heading stage, 2nd harvest year; SFS1 – at seeds filling stage, 1st harvest year, SFS2 – at seed filling stage, 2nd harvest year; Cel – cellulose, HCel – hemicellulose, ADL – acid detergent lignin, WSC – water soluble carbohudrates

Figure 1. Distribution of cell wall components in lignocellulose (A) and of carbohydrates fractions in ΣCH_2O (B) subject to switchgrass (SWG) maturity and year of herbage use

The high values of standard deviation (SD) and a large range of components' concentration variation (Tables 2 and 3) showed that there were differences in carbohydrates and ADL content between switchgrass accessions. The DMY of energy plants is the most important trait and often could be a weighted factor for output of essential energy compounds in feedstock. Seeking to identify and select the most promising accessions, 5 switchgrass accessions in the first harvest year and 7 switchgrass accessions in the second harvest year were assessed for the yields of DM, structural, nonstructural and sum of carbohydrates, and lignin (Table 4). The variation of DMY per plant was high – from 58.1 to 122 g of switchgrass in the first harvest year when cut at heading stage, from 172 to 355 g when cut at seed filling stage, from 281 to 382 g of switchgrass in the second harvest year when cut at heading stage, from 423 to 639 g when cut at seed filling stage. The accessions that stood out in terms of this trait and showed higher DMY than average for switchgrass at both stages in the groups of the first and second harvest years were Nos 67, 69 and 46, 60, respectively. The average DMY of switchgrass exhibited the DMY of reed canary grass variety 'Chiefton' at the respective development stage and harvest year, except for DMY, when plants in the first harvest year were cut at seed filling stage. According to literature, switchgrass yielding capability does not perform well in the first harvest year: as a small-seeded species that initially allocates a large amount of energy to developing a strong root system, switchgrass will typically attain only 33–66% of its maximum production capacity during the initial and second years before reaching its full capacity during the third year after planting (McLaughlin, Kszos, 2005). That explains relative poor DMY of switchgrass in the first harvest year.

Table 4. Genotypic variation in the dry matter (DM), carbohydrates fractions (NSC, HoCel, ΣCH_2O) and lignin (ADL) yields (Y) of switchgrass in relation to plant maturity and age in comparison with that of reed canary grass (RCG) variety 'Chiefton'

Lithuanian catalogue No. of sample	Y at heading stage, g per plant					Y at seed filling stage, g per plant				
	DMY	NSCY	HoCelY	ΣCH_2OY	ADLY	DMY	NSCY	HoCelY	ΣCH_2OY	ADLY
	1st harvest year									
67	107	7.58	67.3	74.9	4.54	291	39.3	173	212	26.7
69	122	8.81	75.9	84.7	7.18	355	47.2	217	265	25.7
74	58.1	6.51	32.1	38.6	3.25	223	32.1	131	163	15.4
77	59.2	4.91	34.8	39.6	2.78	172	17.9	103	121	16.5
79	71.5	5.43	44.2	49.5	2.84	249	28.4	147	175	15.9
Average	**83.6**	**6.65**	**50.8**	**57.5**	**4.12**	**258**	**33.0**	**154**	**187**	**20.1**
RCG	62.6	8.57	34.8	43.3	3.05	387	108	218	326	22.1
	2nd harvest year									
46	382	30.9	238	269	23.3	639	59.0	414	473	72.8
47	312	26.5	207	233	18.3	572	65.2	358	423	65.8
51	281	20.5	181	201	19.0	565	67.8	360	428	67.8
57	303	25.1	201	226	18.7	445	65.9	275	341	44.5
60	349	31.4	228	260	20.8	638	76.6	426	503	60.4
62	361	31.0	230	261	20.1	558	58.0	356	414	56.9
64	294	33.2	187	220	14.6	423	60.1	265	325	36.7
Average	**326**	**28.4**	**210**	**239**	**19.3**	**549**	**59.0**	**414**	**473**	**72.8**
RCG	230	26.7	135	161	10.4	471	90.5	275	368	24.7

Like quality composition and DMY, biomass quality components' yields from plants of switchgrass accessions were influenced by all three factors – accession, plant maturity stage and harvest year (Table 4). Switchgrass biomass was characterised by higher amount of structural carbohydrates, lignin but by lower NSC yield than RCG. The similar differences of biomass chemical composition between C3 type plant reed canary grass and C4 type plant switchgrass were published in literature (Dien et al., 2006). Switchgrass seems more suitable for its use as a bioethanol and solid biofuel feedstock. Among switchgrass accessions, the moderately yielding octoploid No. 64 at heading stage produced quite high NSC yield (33.2 g $plant^{-1}$), and low output of ADL (14.6 g $plant^{-1}$). That fact showed that switchgrass germplasm could contain some promising biogas producers, equal to reed canary grass variety 'Chiefton'. Furthermore unlike cell wall polysaccharides, these non-cell wall carbohydrates are directly fermentable to bioethanol without harsh pre-treatment (Dien et al., 2006).

In the study of Monti et al. (2008) it was clearly shown that the quality of biomass may drastically change with crop and biomass partition. Our (unpublished yet) findings and some data in literature (Monti et al., 2008; Shahandeh et al., 2011) revealed that leaves always showed the highest ash and minerals content than stems and reproductive organs. For direct combustion, switchgrass plant tissues with lower mineral concentrations (stems) are preferable, as high ash concentrations in leaves could be involved in reactions leading to ash fouling and slagging in biomass combustors (Monti et al., 2008). Therefore quality not only of whole plant biomass but also partitioning of quality attributes in the biomass should be considered. The significance of the effect of accession and plant part on carbohydrate fractions and lignin concentrations are shown in Table 5. Switchgrass plant part significantly ($P < 0.01$) affected concentration of all biomass quality attributes tested, but did not affect concentration of one of structural carbohydrates – HCel. Accession main effect was significant at the $P < 0.01$ level for WSC, NSC and ADL concentrations and at the $P < 0.05$ level for NDF, i.e. lignocellulose concentration. Statistically, there was no significant difference for structural carbohydrates – Cel, HCel and their sum HoCel as well as for starch and sum of structural carbohydrates and NSC, i.e. ΣCH_2O contents among the seven populations of switchgrass. An accession × plant part interaction was statistically insignificant for most variables, only for starch and ADL concentrations it was significant at the $P < 0.05$ level (Table 5).

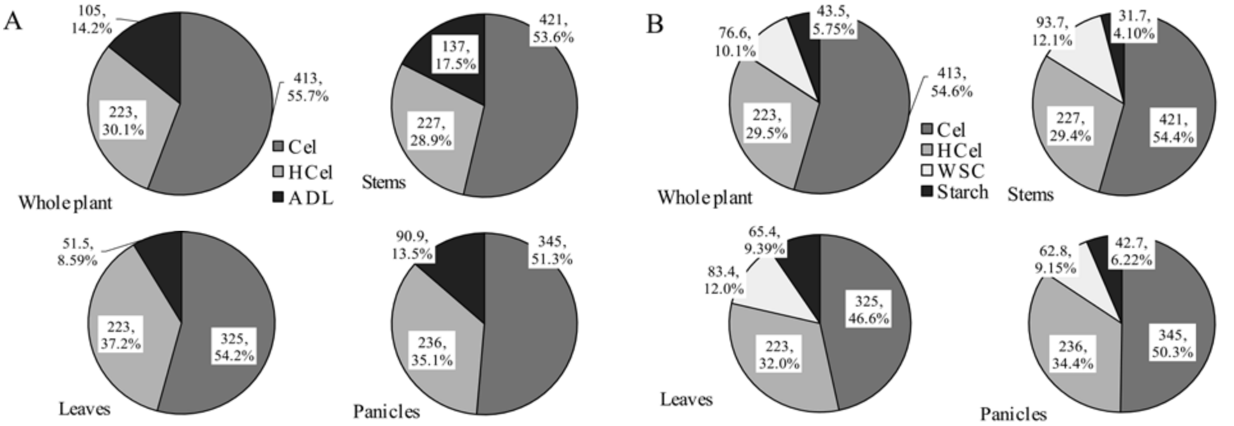
Table 5. Statistical significance of the source of variation for the concentrations of carbohydrates and lignin in switchgrass at seed filling stage in response to plant parts (whole aboveground plant part, stems, leaves, panicles; factor A) and seven switchgrass accessions (factor B)

Source of variation	df	NDF	Cel	HCel	HoCel	WSC	Starch	NSC	ΣCH_2O	ADL
Treatments	27	**	**	NS	**	**	**	**	**	**
Factor A	3	**	**	NS	**	**	**	**	**	**
Factor B	6	*	NS	NS	NS	**	NS	**	NS	**
A × B	18	NS	NS	NS	NS	NS	*	NS	NS	*

df – degrees of freedom, NDF – lignocellulose, Cel – cellulose, HCel – hemicellulose, HoCel – holocellulose, WSC – water soluble carbohydrates, NSC – nonstructural carbohydrates, ΣCH_2O – sum of carbohydrates, ADL – acid detergent lignin; NS – not significant, * – significant at the 0.05 level, ** – significant at the 0.01 level

Lignocellulose, referred to as the sum of Cel, HCel and ADL, content was higher (at $P < 0.01$) in the stems (785 g kg^{-1} DM) and whole plant (741 g kg^{-1} DM) than in leaves (599.5 g kg^{-1} DM) and panicles (672.7 g kg^{-1} DM) (Fig. 2A). The main source for that variation in NDF concentrations was differences in allocation of Cel and ADL concentrations in plant aboveground components. Cel and ADL concentrations were significantly higher (at $P < 0.01$) in leaves and panicles, than in stems and in whole aboveground part of plants. HCel concentration subject to plant part differed only slightly, with exception for panicle biomass. This plant part contained higher HCel concentration than biomass of stems (at $P < 0.05$) and all aboveground plant biomass (at $P < 0.01$).

Murray et al. (2008) noted the similar regularity of fluctuation in concentrations of NDF structural components in leaves and stems of sorghum plants. Such Cel and HCel distribution influenced higher ratio of Cel:HCel in stems and in whole aboveground part of plants (1.85), than that in leaves and panicles (1.46), and this could be more beneficial for higher ethanol output (McKendry, 2002). Lignin which is very valuable component of material intended for direct combustion was abundant in switchgrass all plant parts and especially in stem biomass. Data of Mann et al. (2009) publications confirm our results, that leaves are less lignified than stems. Stems contained statistically ($P < 0.01$) higher WSC amount (mean 93.7 g kg^{-1} DM) compared to leaves (83.4 g kg^{-1} DM) and panicles (62.8 g kg^{-1} DM), but statistically ($P < 0.01$) lower amount of starch compared to leaves and panicles (31.7, 65.4 and 42.7 g kg^{-1} DM, respectively) (Fig. 2B). Our results are in accordance with Longland and Byrd (2006), who stated that starch production and storage occurs in the chloroplasts of the leaf or with Hastert et al. (1983), who observed numerous starch granules in bundle sheath cells for leaf blades using light and transmission electron microscopy. Only a few grasses use starch as a primary reserve in the stems and stem storage parenchyma cells, that encircle the vascular bundle, are considered an in-route storage compartment, which theoretically could be a competing sink along the path to terminal sinks such as the roots and seeds (Slewinski, 2012). It is known, that mature seeds contain about 40% of starch in DM, but switchgrass seeds are very small and their share in panicle is negligible. It can be a reason why starch concentration in panicles amounted only to 42.7 g kg^{-1} DM. As WSC, starch and Cel after hydrolysis are a source of hexoses, that are readily fermentable to ethanol, we considered that ratio Cel:HCel could be extended to the ratio [WSC + starch



Cel – cellulose, HCel – hemicellulose, ADL – acid detergent lignin, WSC – water soluble carbohydrates

Figure 2. Distribution of cell wall components in lignocellulose (A) and of carbohydrates fractions in ΣCH_2O (B) subject to switchgrass aboveground part at seed filling stage

+ Cel]:HCel. Despite higher concentration of starch in leaves and panicles, the new-calculated ratio showed that biomass of switchgrass stems and whole aboveground part (2.39 and 2.40, respectively *vs.* 2.13 and 1.91 in leaves and panicles) could be highly valuable feedstock not only for solid but also for liquid biofuel production. According to chemical composition, leaves of switchgrass plants at late maturity are suitable for biogas and forage production or composting.

Variation in chemical composition among varieties was lower than that among plant parts (Tables 5 and 6). This notwithstanding, there were significant differences in concentration of some components of chemical composition among the 7 switchgrass accessions within all aerial plant parts. The most frequently statistically significant differences from mean were established for ADL in biomass of whole aerial part and stems, WSC of whole aerial part and panicles, ΣCH_2O of leaves (Table 6). Variation among germplasm in the HoCel concentration did not show reliable differences from average within any plant aboveground part. There were also no appreciable differences in cellulose within stem, leaf and panicle portions separately (range was from 408 g kg^{-1} to 447 g kg^{-1} in stems, from 304 to 342 g kg^{-1} in leaves and from 324 to 366 g kg^{-1} in panicles). The statistically significant differences among ecotypes/

Table 6. Chemical composition of the biomass of aboveground plant parts of switchgrass germplasm of the second year of growth and cut at seed filling stage

Name of biomass quality attribute	Lithuanian catalogue No. of sample							$LSD_{05/01}$
	46	47	51	57	60	62	64	
	Content in biomass of whole plant aerial part, g kg^{-1} DM							
1	2	3	4	5	6	7	8	9
Lignocellulose (NDF)	762	740	758	718	763	741	712	33.0/50.0
Cellulose (Cel)	432*	415	408	410	419	412	397	17.8/26.9
Hemicellulose (HCel)	216	210	230	208	249*	226	229	24.5/37.2
Holocellulose (HoCel)	648	625	638	618	668	638	626	33.7/51.1
Water soluble carbohydrates (WSC)	54.4*	67.7	79.4	99.1**	73.6	67.4	94.5*	13.9/21.1
Starch	38.0	46.2	40.9	49.3	46.4	36.1	47.5	11.3/17.1
Nonstructural carbohydrates (NSC)	92.4*	114	120	148*	120	104	142	22.4/34.1
Sum of carbohydrates (ΣCH_2O)	741	735	755	766	788	742	767	35.1/53.2
Acid detergent lignin (ADL)	114**	115**	120*	100	94.6*	102	86.8*	5.08/7.70
	Content in biomass of stems, g kg^{-1} DM							
Lignocellulose (NDF)	801	792	797	745*	794	790	743*	26.4/40.0
Cellulose (Cel)	417	407	430	421	447	416	408	30.6/46.4
Hemicellulose (HCel)	239	211*	228	210	244*	236	223	16.2/24.5
Holocellulose (HoCel)	656	618	658	631	691	652	631	25.4/38.4
Water soluble carbohydrates (WSC)	76.4	84.0	87.1	114	86.6	89.6	118	28.8/43.7
Starch	17.5	29.4	36.3	34.5	30.4	33.1	40.5	18.1/27.4
Nonstructural carbohydrates (NSC)	93.9	113	123	149	117	123	159	41.9/63.4
Sum of carbohydrates (ΣCH_2O)	748	740	778	771	778	775	784	30.3/45.9
Acid detergent lignin (ADL)	145*	169**	126	125*	132	138	112*	9.51/14.4

Table 6 continued

1	2	3	4	5	6	7	8	9
Content in biomass of leaves, g kg^{-1} DM								
Lignocellulose (NDF)	592	588	600	582	592	627	614	39.7/60.1
Cellulose (Cel)	332	304	321	322	312	341	342	28.9/43.8
Hemicellulose (HCel)	205	227	226	208	231	233	231	32.5/49.3
Holocellulose (HoCel)	537	531	547	530	543	574	573	33.9/51.4
Water soluble carbohydrates (WSC)	74.2	84.2	84.2	97.3	71.3	82.3	90.6	18.0/27.3
Starch	50.9	75.0	56.5	96.7**	52.7	50.1	76.2	19.9/30.1
Nonstructural carbohydrates (NSC)	125	159	141	194**	124	132	167	27.9/42.3
Sum of carbohydrates (ΣCH_2O)	661*	690	687	725*	667*	706	740**	25.7/38.9
Acid detergent lignin (ADL)	55.5	57.5	52.9	51.1	49.4	53.6	40.7*	7.94/12.0
Content in biomass of panicles, g kg^{-1} DM								
Lignocellulose (NDF)	694	677	690	690	663	680	614	70.8/ 107
Cellulose (Cel)	356	349	347	366	339	334	324	34.0/51.5
Hemicellulose (HCel)	239	215	254	238	228	263	213	38.5/58.3
Holocellulose (HoCel)	595	564	601	604	567	597	537	68.2/103
Water soluble carbohydrates (WSC)	55.2*	57.3	49.5*	64.3	64.4	66.7	81.9**	6.69/10.1
Starch	52.0	57.3	46.8	23.0	56.8	30.4	32.4	2.54/38.6
Nonstructural carbohydrates (NSC)	107	115	96.3	87.3	121	97.1	114	23.9/36.2
Sum of carbohydrates (ΣCH_2O)	703	678	697	692	688	696	655	54.0/81.8
Acid detergent lignin (ADL)	97.9	114**	89.3	85.0	96.1	83.0	76.5*	11.5/17.4

DM – dry matter; * – significant at the 0.05 level, ** – significant at the 0.01 level; LSD$_{05/01}$ – average from value of component in respective plant part

varieties were more distinct when comparing respective values of biomass quality attributes among accessions themselves than those of an individual accession with average value. Biomass of whole aerial plant part and stems of two samples Nos 57 and 64 exhibited lower concentrations of NDF, HoCel and lignin, higher of WSC and NSC than that of other accessions. These populations distinguished among others by greater WSC, starch, and naturally NSC, as well as ΣCH_2O concentrations also in leaves. Generally, the whole plant biomass of the higher-yielding switchgrass No. 46 had significantly higher concentration of lignin ($P < 0.01$), cellulose ($P < 0.05$), lower WSC and NSC ($P < 0.05$) and tended to higher NDF content than most of the other accessions. Similar tendencies in quality of biomass of switchgrass No. 46 were observed within separate plant parts (stems, leaves and panicles). There were evident correlations of switchgrass DM yield per plant with quality parameters of whole aerial plant part at seed filling stage. Among the components of chemical composition tested WSC and NSC showed the closest, however negative relationship with DMY ($r = -0.982, -0.959$; $P < 0.01$), DMY correlated positively with lignocellulose ($r = 0.781$, $P < 0.05$), cellulose ($r = 0.882$, $P < 0.01$) and lignin, though weakly ($r = 0.517$).

Summarising the results discussed in the current study it is noteworthy to mention that plant accessions, plant part and harvesting time affected the carbohydrates fractions composition and lignin concentration in biomass. It is feasible to improve the feedstock for purposive fuel production by choosing a suitable accession, plant part with appropriate composition, and development stage for harvesting.

Conclusions

1. The important factors, affecting chemical composition of switchgrass (SWG) biomass cell-wall are plant maturity at biomass harvesting and grass harvest year:

a) lignocellulose (NDF), cellulose (Cel), sum of structural carbohydrates (HoCel), sum of carbohydrates (ΣCH_2O) and lignin (ADL) content in biomass of both plant development stages in the second harvest year were reliably higher, whereas an average hemicellulose (HCel) concentration was lower than that respectively in the first harvest year;

b) the concentration of NDF, carbohydrate components (Cel, HoCel and ΣCH_2O) and especially ADL at seed filling stage were significantly higher comparing with the respective data at heading;

c) nonstructural carbohydrates (NSC) and their separate fractions (water soluble carbohydrates (WSC) and starch) concentrations were similar in switchgrass biomass of the first and second harvest years.

2. There are significant differences in biomass quality among the switchgrass accessions within aerial plant parts. The most frequently statistically significant differences from mean were established for ADL of whole aerial plant and stems, WSC of whole aerial plant and panicles and ΣCH_2O of whole aerial plant and leaves.

3. Switchgrass biomass of whole aboveground plant part and stems at seed filling stage could be suitable material for the production of the bioethanol of the second generation and direct combustion:

a) plants of this stage accumulated ΣCH_2O from 693 to 742 g kg^{-1} DM, ΣCH_2O concentration in stems was the highest (average 742% g kg^{-1} DM), in leaves and panicles it was considerably lower (631% and 644% g kg^{-1} DM, respectively);

b) high ratio of [WSC + starch + Cel]:HCel showed that biomass of switchgrass stems and whole aboveground part (2.39 and 2.40) could be highly valuable feedstock not only for solid but also for liquid biofuel production;

c) high lignin concentration in switchgrass biomass of whole aboveground plant part and stems at seed filling stage in second harvest year (an average

105 and 137 g kg^{-1} DM, respectively) showed its great suitability for solid biofuel production.

4. Switchgrass biomass is less suitable for the biogas production compared to that of reed canary grass due to higher output of lignin and lower NSC yield; however, some switchgrass germplasm could be of interest for biogas producers: biomass of octoploid switchgrass ecotype No. 64 by chemical composition was similar to that of reed canary grass.

5. Variation of DM yield and quality in the switchgrass germplasm collection was revealed to be quite promising for selecting superior accessions for renewable energy purposes. The accessions that showed higher DM yield than average for switchgrass at both stages in the groups of the first and second harvest years were ecotypes Nos 67, 69 and 46, 60, respectively.

6. DMY showed a close, however negative relationship with WSC and NSC ($r = -0.982, -0.959$; $P < 0.01$), and positively correlated with lignocellulose ($r = 0.781$, $P < 0.05$), cellulose ($r = 0.882$, $P < 0.01$) and lignin ($r = 0.517$).

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Angliavandenių ir lignino pasiskirstymas energinio augalo rykštėtosios soros (*Panicum virgatum* L.) biomasėje

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Santrauka

Rykštėtąją sorą (*Panicum virgatum* L.) tyrinėjant kaip daugiafunkcinį energinį augalą, svarbu visapusiškai ištirti organinių medžiagų sudėtį ir pasiskirstymą biomasėje. Angliavandenių ir lignino koncentracijos kaitos pobūdis tirtas pirmųjų ir antrųjų derliaus metų rykštėtosios soros biomasėje, nupjautoje augalams esant plaukėjimo ir sėklų brandos tarpsnių, o šių kokybės komponentų pasiskirstymas augalų antžeminėje biomasėje įvertintas antrųjų derliaus metų sėklų brandos tarpsnio produktyviausių augalų stiebuose, lapuose ir žiedynuose. Antrųjų derliaus metų abiejų brandos tarpsnių augalų biomasėje lignoceliuliozės (NDF), celiuliozės (Cel), lignino, suminės struktūrinių angliavandenių arba holoceliuliozės (HoCel) ir visų angliavandenių (ΣCH_2O) koncentracijos buvo esmingai didesnės, o vidutinė hemiceliuliozės (HCel) koncentracija esmingai mažesnė nei atitinkamos komponentų koncentracijos pirmųjų derliaus metų augalų biomasėje. Nestruktūrinių angliavandenių ir jų atskirų frakcijų (vandenyje tirpių angliavandenių bei krakmolo) koncentracijos buvo panašios pirmųjų ir antrųjų derliaus metų augalų biomasėje. NDF, Cel, HoCel bei ΣCH_2O ir ypač lignino koncentracijos abiejų derliaus metų augaluose, nupjautuose sėklų brandos tarpsniu, buvo esmingai didesnės, lyginant su atitinkamais plaukėjimo tarpsnio duomenimis. Didelė lignino koncentracija (105 g kg^{-1}sausųjų medžiagų (SM)) sėklų brandos tarpsnio antrųjų derliaus metų augalų biomasėje rodo jos tinkamumą kietojo kuro gamybai. Angliavandenių (ΣCH_2O) gausa (693–742 g kg^{-1} SM) šio tarpsnio biomasėje rodo rykštėtosios soros tinkamumą antrosios kartos bioetanolio gamybai. Antraisiais derliaus metais plaukėjimo tarpsniu nupjauti augalai formavo gana didelį nestruktūrinių angliavandenių derlių (vidutiniškai 28,4 g $augalo^{-1}$) ir mažą lignino išeigą (vidutiniškai 19,3 g $augalo^{-1}$), t. y. turėjo pageidautinus žaliavos biodujoms gaminti požymius, o sėklų brandos tarpsniu pjauta biomasė tam buvo mažiau tinkama. Rykštėtosios soros augalų dalys (lapai, stiebai, žiedynai) turėjo esminės ($P < 0,01$) įtakos tirtų biomasės kokybės komponentų koncentracijai biomasėje, išskyrus HCel koncentraciją. Tirtų pavyzdžių sausųjų medžiagų derlius teigiamai koreliavo su NDF ($r = 0,781$, $P < 0,05$), Cel ($r = 0,882$, $P < 0,01$) bei lignino ($r = 0,517$) ir neigiamai – su vandenyje tirpių bei nestruktūrinių angliavandenių ($r = -0,982, -0,959$; $P < 0.01$) kiekiais biomasėje.

Reikšminiai žodžiai: angliavandeniai, augalo antžeminės dalys, biomasė, energiniai augalai, ligninas, *Panicum virgatum*.