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Variability of nuclear DNA content and agromorphological characteristics of switchgrass (*Panicum virgatum* L.) germplasm in Lithuania

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Abstract

While searching for novel energy plants, researchers have become interested in switchgrass (*Panicum virgatum* L.), which is a C4 perennial grass. The objective of this study was to assess switchgrass populations by estimating the variability of nuclear DNA content and agromorphological characteristics.

Plant ploidy level was determined using a flow cytometry technique. The switchgrass collection comprised 31 populations differing in ploidy level. Seventeen populations were tetraploid with an average genomic DNA content of 2.5 picograms (pg). The individuals of 4 populations were found to have an average DNA content of 5.4 pg, which is specific to octoploids. The remaining 10 populations were estimated to be of a mixed ploidy level with DNA content ranging from 2.1 to 7.0 pg. The plants of tetraploid and mixed ploidy populations were characterised by significantly taller culms and more abundant fresh biomass production compared with octoploid populations. An analysis of dry matter revealed a similar trend. Earlier heading date was observed for tetraploid populations. All switchgrass populations tested exhibited a similar overwinter survival rate (93.7–96.7%). The most stable characteristics were found to be plant height, bunch diameter, leaf width and length (coefficient of variation 4.0–9.7%). Among all plant characteristics, the greatest variability was established for dry biomass yield (coefficient of variation 5.0–35.8%).

Key words: agromorphological characteristics, ploidy level, switchgrass, wild populations.

Introduction

Search for and research on energy plants used for biofuel production is currently one of the most rapidly developing alternative energy realms. In Lithuania, intensive efforts have been focused in recent years to identify perennial grasses suitable for conversion into biofuel. Attention has been drawn to switchgrass (*Panicum virgatum* L.), a C4 perennial grass, which is used worldwide, especially in the USA, for combustion and as a feedstock for the second generation bioethanol and biogas production (Black, 1971; Beale, Long, 1995; Fay et al., 2003).

The world switchgrass collection includes commercial varieties, breeding lines and two distinct groups of wild ecotypes – the upland and the lowland, which differ not only in agrobiological and phenotypic characteristics but also in ploidy level (Alexopoulou et al., 2008; Casler, 2010). There is information about agrobiological characteristics of switchgrass varieties, chromosome number in them and their suitability for combustion.

Switchgrass is a perennial grass which can be grown across a wide geographic range. Only ornamental

forms of switchgrass are currently grown in Lithuania. Switchgrass is cross-pollinating, highly heterozygous species with multiple ploidy levels ranging from $2n=2x=18$ to $2n=12x=108$ (Parrish, Fike, 2005; Narasimhamoorthy et al., 2008). Tetraploid ($2n=4x=36$) and octoploid ($2n=8x=72$) ecotypes are the most common. These two groups of ecotypes differ in both agrobiological and phenological characteristics (Casler, 2012). Some researchers maintain that such division into two separate groups is inaccurate (Missaoui et al., 2006; Zhang et al., 2011 a), because of the existence of the intermediate (hybrid) group of ecotypes for which stable level of ploidy is not inherent (Vogel, Mitchell, 2008; Zhang et al., 2011 b). It is believed that an increase in chromosome number in polyploid plant populations enhances the level of heterozygosity and creates prerequisites for better adaptation of the species, i.e. increases its adaptability across a broad geographic range (Parisod et al., 2010; Delaney, Baack, 2012). For breeding, seed production and maintenance of collections it is essential that the populations of switchgrass of different ploidy level are isolated from one another in order to prevent inter-population crossing (Delaney, Baack, 2012).

A numerous collection of germplasm of switchgrass varieties and wild ecotypes obtained from the Plant Genetic Resources Conservation Unit of the United States Department of Agriculture and Agricultural Research Service has opened up possibilities for identification of the most promising material for cultivation under Lithuania's conditions. The wild switchgrass populations are expected to be an especially highly valuable material, since they are characterised by higher phenotypic and genotypic polymorphism than commercial varieties, which is a valid basis for deeper genetic research and for envisaging future directions in switchgrass breeding. Our study is the first attempt in Lithuania to estimate the genetic switchgrass collection with a focus on the variability of nuclear DNA content and agromorphological characteristics.

Material and methods

Experiments were conducted in the Central Lowland of Lithuania (55°23'49" N, 23°51'40" E), at Institute of Agriculture, Lithuanian Research Centre for Agriculture and Forestry during 2012–2013. The investigations were carried out at the Department of Grass Breeding and the Laboratory of Genetics and Physiology. Seeds for the germplasm collections of switchgrass were obtained from Plant Genetic Resources Conservation Unit (PGRCU) of the United States Department of Agriculture and Agricultural Research Service. The collection was composed of wild upland populations originated from North Dakota.

Plant ploidy level was estimated using a flow cytometer (Partec GmbH, Germany) (Lu et al., 1998). The analysis was performed in plant leaf tissue. Based on the manufacturer's instructions, the following regime was selected: gain = 700, L-L = 20, speed = 1. The data from the flow cytometric analysis were used to estimate plant genome size, i.e. nuclear DNA (deoxyribonucleic acid) content expressed in picograms (pg). The standard used for the comparison was wheat (*Triticum* spp.) with a known nuclear DNA content ($2n = 32$ pg) (Johnston et al., 1999), which in our study corresponded to the cytometer's peak position at reading 236. The formula used for converting fluorescence values to DNA content was: nuclear DNA content = (mean position of unknown peak)/(mean position of known peak) \times DNA content of known standard (Pecinka et al., 2006; Narasimhamoorthy et al., 2008). For ploidy level establishment, DNA content was analysed in 6–8 plants of each population.

The genetic collection of switchgrass under study was set up using the seedlings grown in a greenhouse. At the beginning of June, 28 seedlings per accession (2 replications, 14×2) were planted in the field at 50×50 cm distances. Average fresh biomass yield per plant (g) for the first and second cuts was determined having weighed all plants per plot of each replication. Dry biomass yield per plant was calculated from the data of fresh herbage mass, dry biomass content and plant number per plot. For dry biomass content, herbage samples of 0.5 kg were oven-dried at 105°C to a constant weight. The first cut was taken at the beginning of heading stage of each accession, the second cut after regrowth of aftermath. The following agromorphological characteristics were determined: overwinter survival rate, %, earliness (heading date), plant height, cm (at booting

stage), number of culms (at heading stage), bunch diameter (after the second cut), leaf width and length (at seed ripening stage).

The statistical analysis of the experimental data was done using software *ANOVA*, *STAT* from the package *SELEKCIJA* and *IRRISTAT* (Tarakanovas, Raudonius, 2003).

Results and discussion

Previous studies have reported that the lowland populations are exclusively tetraploid, whereas the upland type can vary in ploidy (tetraploid, hexaploid and octoploid), both within and among populations (Narasimhamoorthy et al., 2008; Costich et al., 2010; Zalapa et al., 2011; Zhang et al., 2011 b; Lu et al., 2013). Our results also showed that switchgrass collection varied in ploidy between populations.

In the plants of many populations (17, i.e. 54.8%), nuclear DNA content averaged 2.5 pg (ranged from 2.1 to 3.3 pg). We clustered these populations into the group of tetraploid ($2n = 4x = 36$) populations. In the switchgrass individuals of four populations (12.9%), we established the nuclear DNA content on average 5.4 pg (5.0–5.7 pg), which is specific to octoploid ($2n = 8x = 72$) plants (Table 1).

The remaining 10 tested populations (32.3%) were of mixed ploidy. These populations were composed of different ploidy plants. Analysis of 74 plants showed that 21 individuals were tetraploid, 5 – hexaploid (average DNA content 4.2 pg, from 4.1 to 4.5 pg), 8 – octoploid, 17 – decaploid (average DNA content 6.5 pg, from 5.6 to 7.0 pg). Various nuclear DNA content was determined in 23 remaining plants. DNA content ranged from 2.1 to 7.0 pg. In these samples cytometer showed two peaks corresponding to different ploidy levels.

Lu et al. (1998) and Narasimhamoorthy et al. (2008) have suggested that $2n$ nuclear DNA content in tetraploid switchgrass plants averages 3.1 pg and in octaploid plants 6.1 pg. Previous studies have reported that DNR content in nucleus of tetraploid plants was 3.1 pg and octoploid – 5.2 pg (Costich et al., 2010; Casler, 2012). Hopkins et al. (1996) indicated that the nuclear DNA content for tetraploid switchgrass plants varied in the range of 2.7 to 3.2 pg (on average 3.1 pg) and that of octoploids ranged from 4.8 to 5.8 pg (on average 5.2 pg).

Our results agree with the findings of other studies. Narasimhamoorthy et al. (2008) are consistent that a large proportion of switchgrass ecotypes growing in Central America territories have mixed ploidy levels. Aneuploidy is observed in the populations with a higher ploidy level, which results in fertility reduction in their progeny and even higher genomic instability (Zhang et al., 2011 b). The diploid set of chromosomes ($2n = 2x = 18$) in switchgrass populations is very rare (Zhang et al., 2011 b). Successful breeding is only possible when populations of the same ploidy level are hybridised (Hopkins et al., 1996), while crosses between the populations of different ploidy levels typically result in inhibited seed set or production of abnormal seed. Nonetheless, the populations of mixed ploidy are interesting in the studies on the genetic species diversity and evolution.

Table 1. The nuclear DNA content and ploidy level of investigated switchgrass populations

Lithuanian catalogue number	PGRUCU catalogue number	Ploidy level	Number of plants per accession	Average DNA content in pg
Tetraploid populations				
24	PI 642310 01 SD	4x	8	2.4
25	PI 642311 01 SD	4x	8	2.8
26	PI 642312 01 SD	4x	8	2.3
30	PI 642292 01 SD	4x	7	2.1
31	PI 642293 01 SD	4x	8	2.5
33	PI 642291 01 SD	4x	7	2.6
42	PI 642286 01 SD	4x	8	2.3
47	PI 642296 01 SD	4x	8	2.2
50	PI 642299 01 SD	4x	8	2.6
57	PI 642306 01 SD	4x	7	3.2
104	PI 642232 01 SD	4x	8	2.5
105	PI 642233 01 SD	4x	8	2.6
106	PI 642234 01 SD	4x	8	2.1
107	PI 642235 01 SD	4x	8	2.5
127	PI 642259 01 SD	4x	8	3.1
130	PI 642262 01 SD	4x	8	3.3
134	PI 642266 01 SD	4x	8	2.1
Octoploid populations				
113	PI 642242 01 SD	8x	8	5.6
114	PI 642243 01 SD	8x	7	5.3
119	PI 649249 01 SD	8x	7	5.7
129	PI 642261 01 SD	8x	8	5.0
Mixed ploidy levels populations				
116	PI 642245 01 SD	4x / 10x / 8x + 4x*	2 / 3 / 2	3.2 / 7.0 / 4.5 + 2.7**
118	PI 642247 01 SD	6x / 8x + 4x	4 / 2	4.5 / 5.1 + 2.1
115	PI 642244 01 SD	4x 10x / 10x + 4x	1 / 6 / 1	2.5 / 7.0 / 5.6 + 2.6
53	PI 642302 01 SD	4x / 10x / 10x + 6x	4 / 1 / 3	3.2 / 6.9 / 6.7 + 3.8
125	PI 642257 01 SD	4x / 10x	7 / 1	3.3 / 6.6
112	PI 642240 01 SD	8x / 10x + 4x	4 / 2	5.7 / 5.8 + 2.7
117	PI 642246 01 SD	10x / 10x + 4x	6 / 1	6.7 / 5.6 + 2.6
124	PI 642256 01 SD	4x / 8x + 4x	2 / 6	3.2 / 4.9 + 2.7
126	PI 642258 01 SD	4x / 6x + 4x	5 / 3	3.2 / 4.5 + 2.6
32	PI 642294 01 SD	6x / 10x + 6x	5 / 3	3.9 / 7.0 + 4.1

Note. PGRUCU – Plant Genetic Resources Conservation Unit; * and ** – corresponding ploidy levels and DNA content in plants, with various DNA content in leaf tissues.

Dhooghe et al. (2011) suggest that for the determination of ploidy it is expedient to use a considerably more effective technique – flow cytometry, while the conventional chromosome count method should be employed for the verification of ploidy results. We agree with Hopkins et al. (1996), who maintain that flow cytometry is a suitable technique to distinguish tetraploid individuals from octoploid ones, while in order to identify diploid, hexaploid and aneuploid individuals it is recommended to apply a direct chromosome count in cytological preparations.

Researchers have expressed rather divergent views regarding the relationship between ploidy level and agromorphological characteristics of switchgrass populations. Casler (2005) has pointed out that analysis of morphological characteristics is an effective tool for discriminating between tetraploid and octoploid populations, whereas Lowry et al. (2014) have stated that many researchers have not discerned the correlation between plant characteristics and ploidy level.

A number of researchers have reported the plants of tetraploid populations to be taller compared to those of

octoploid populations (Cortese et al., 2010; Zhang et al., 2011 a).

Our research evidence agrees with this proposition. The plants in our tetraploid and mixoploid populations had significantly ($P < 0.05$) taller culms. Plants in tetraploid populations formed significantly ($P < 0.05$) more stems, compared with octoploid and mixed ploidy plants (Table 2). According to bunch diameter and leaf width, all the three groups of populations were very similar, leaf length of tetraploid plants lagged behind the octoploids and mixed ploidy level plants (on average 3.6 cm shorter).

We established the within-population variation of plant characteristics. Plant height, leaf width and length, bunch diameter parameters varied little or moderately (CV 4.6–11.3%) in all populations. The stems number variation rate was medium (CV 13.1%) in mixed ploidy plants, while in populations of tetraploids and octoploids it was high (CV 20.7–29.9%).

Fresh and dry biomass yield is one of the major indicators of plant productivity (Table 3). The average data of the first cut and annual yield (1st + 2nd cuts)

Table 2. Diversity of agromorphological characteristics in the populations of switchgrass differing in ploidy level

Ploidy level	Plant height cm		Number of culms		Bunch diameter cm		Leaf width cm		Leaf length cm	
	Mean ± SE	CV	Mean ± SE	CV	Mean ± SE	CV	Mean ± SE	CV	Mean ± SE	CV
Tetraploid	115.8 ± 2.4 a*	8.6	72.3 ± 3.6 a	20.7	18.9 ± 0.5	11.3	9.8 ± 0.10	4.6	42.7 ± 1.0 a	9.7
Octoploid	97.3 ± 1.9 b	4.0	64.6 ± 9.7 b	29.9	17.9 ± 1.0	10.8	10.4 ± 0.3	6.4	46.1 ± 2.1 b	9.2
Mixed	107.3 ± 3.3 a	8.7	62.3 ± 2.9 b	13.1	18.9 ± 0.4	6.4	10.1 ± 0.3	7.7	46.5 ± 1.4 b	8.7

Note. SE – standard error, CV – coefficient of variation %; * – values with the same letter are not significantly different ($p < 0.05$).

Table 3. Variation of fresh and dry biomass yield of switchgrass populations differing in ploidy level

Ploidy level	1 st cut		2 nd cut		1 st + 2 nd cuts	
	mean ± SE	CV	mean ± SE	CV	mean ± SE	CV
Fresh biomass yield, g plant ⁻¹						
Tetraploid	334.2 ± 16.8 a*	20.9	400.0 ± 17.3 a	17.8	734.3 ± 29.4 a	16.5
Octoploid	187.8 ± 8.7 b	9.2	413.0 ± 17.5 a	8.5	600.8 ± 15.1 b	5.0
Mixed	268.8 ± 15.8 b	16.3	460.2 ± 24.9 b	15.4	729.0 ± 30.0 a	11.8
Dry biomass yield, g plant ⁻¹						
Tetraploid	79.3 ± 4.4 a	22.8	134.9 ± 5.4	16.6	214.2 ± 8.4	16.3
Octoploid	44.3 ± 2.3 b	10.4	160.9 ± 28.3	35.8	205.2 ± 28.2	27.5
Mixed	60.6 ± 3.3 b	15.3	154.1 ± 9.3	17.1	214.7 ± 9.1	12.0

Note. SE – standard error, CV – coefficient of variation %; * – values with the same letter are not significantly different ($p < 0.05$).

showed that tetraploid and mixed ploidy populations accumulated significantly ($P < 0.05$) more fresh biomass compared with octoploid populations. Analysis of the dry biomass yield of the first cut revealed that tetraploid switchgrass populations maintained their superiority over octaploid and mixed ploidy populations, i.e. significantly ($P < 0.05$) outyielded them. Plants of mixed ploidy populations produced the highest ($P < 0.05$) second cut fresh biomass yield. However, the dry biomass yield of the second cut of tetraploid populations fell behind that of octoploid and mixed ploidy populations. According to the annual dry biomass yield (1st + 2nd cuts), tetraploid and mixed ploidy populations were very similar; however, they inappreciably surpassed octaploid plants. The analysis of the first cut of dry biomass yields showed that tetraploid population significantly ($P < 0.05$) surpassed the octoploid and mixed ploidy populations. Slightly higher dry biomass yield was determined in the

octoploid and mixed ploidy populations after second cut. There was no significant difference between annual (1st + 2nd cuts) dry biomass yield in tetraploid and mixed ploidy populations and was only slightly higher than in octoploid population. Population catalogue Nos. 106, 57 and 130 were distinguished for the high fresh mass yield. The fresh/dry biomass yield for these populations averaged 824.4/248.0 – 917.2/260.0 (g plant⁻¹).

The coefficient of variation of fresh biomass yield ranged from 11.8% to 20.9% in tetraploid and mixed ploidy populations; while in octoploid plants it shifted slightly – from 5.0% to 9.2%. The lowest stable indication was dry biomass levels. Coefficient of variation of dry biomass yield varied from 10.4% to 35.8% in tetraploid and octoploid populations, while in mixed ploidy populations it varied just from 12.0% to 17.1%. The data provided in Table 4 show that all switchgrass populations were similar in overwinter survival rate.

Table 4. Overwinter survival and heading date of switchgrass

Ploidy level	Average overwinter survival rate %	Earliness			
		heading date	plant %	heading date	plant %
Tetraploid	96.0	30 06–01 07	75.0 a*	08 07	25.0 a
Octoploid	93.7	30 06–01 07	33.3 b	08 07	66.7 b
Mixed	96.7	30 06–01 07	20.0 b	08 07	80.0 b

Note. * – values with the same letter are not significantly different ($p < 0.05$).

According to the weather data from the Dotnuva Agrometeorological Station, the winter of 2012–2013 was adverse for overwinter survival of switchgrass collections. The winter was cold, with a long-lasting snow cover and frozen soil. Notwithstanding this fact, wild switchgrass populations exhibited a good overwinter survival rate averaging 93.7–96.7%. An insignificantly worse overwinter survival rate was recorded for the

four tetraploid populations (Nos. 134, 42, 30 and 24) – 89.3%, two octoploid populations (Nos. 114 and 119) – 85.7–89.3% and one mixed ploidy population (No. 118) – 85.7%.

Tetraploid plants were characterized by earliness of maturity in our collection. Seventy five percent of tetraploid plant ears emergence started 7 days earlier than that of octoploid and mixed ploidy populations. Results of

other studies on this issue are controversial. Cortese et al. (2010) have reported tetraploid populations to be of a later maturity compared with octoploid. Lowry et al. (2014) suggest that the phenotypic characteristics (heading, full anthesis, seed maturity dates) of switchgrass populations are largely dependent on the latitude of their origin rather than on ploidy level. We agree with the opinion that that these characteristics are determined by the interaction of various factors (origin, environment).

Conclusions

1. Wild populations of the switchgrass collection differed in ploidy level: tetraploid (genomic DNA content of 2.5 pg), octoploid (genomic DNA content of 5.4 pg) and mixed (genomic DNA content from 2.1 to 7.0 pg).

2. The plants of tetraploid and mixed ploidy populations produced significantly ($P < 0.05$) taller culms. According to leaf length, tetraploid plants lagged behind octoploid and mixed ploidy plants; however, tetraploids tended to form more culms. All the three groups of populations were very similar in terms of bunch diameter and leaf width.

3. Tetraploid and mixed ploidy populations accumulated significantly ($P < 0.05$) more fresh biomass compared with octoploid populations. The same trend was observed for dry biomass yield.

4. The overwinter survival rate for all populations ranged from 93.7% to 96.7%. The plants of tetraploid populations exhibited earlier heading date. The highest variability was recorded for dry biomass yield (coefficient of variation 5.0–35.8%).

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Rykštėtosios soros (*Panicum virgatum* L.) populiacijų DNR kiekio ir agromorfologinių požymių įvairovė Lietuvoje

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Lietuvos agrarinių ir miškų mokslų centro Žemdirbystės institutas

Santrauka

Ieškant naujų energinių augalų, susidomėta daugiamečiu C4 fotosintezės tipo augalu – rykštėtąja sora (*Panicum virgatum* L.). Tyrimo tikslas – įvertinti rykštėtosios soros populiacijas, nustatyti DNR (deoksiribonukleorūgšties) kiekio ir agromorfologinių požymių įvairovę.

Augalų ploidiškumas buvo nustatytas taikant tėkmės citometrijos metodą. Rykštėtosios soros kolekciją sudarė 31 įvairaus ploidiškumo populiacija. Iš jų 17 buvo tetraploidinės – vidutiniais duomenimis, genomis DNR kiekis buvo 2,5 pikogramo (pg); 4 populiacijų individuose nustatytas oktoploidams būdingas DNR kiekis – 5,4 pg. Kitų 10 populiacijų ploidiškumas įvairavo – augalų ląstelių branduoliuose DNR kiekis kito nuo 2,1 iki 7,0 pg. Nustatyta, kad esmingai aukštesni stiebai ir didesnis kiekis žalios biomasės būdingesni tetraploidinių bei mišraus ploidiškumo populiacijų augalams nei oktoploidiniams. Panaši tendencija nustatyta analizuojant sausos biomasės kiekį. Tyrimo duomenimis, tetraploidinių populiacijų augalams būdinga ankstesnė plaukėjimo pradžia. Visų rykštėtosios soros populiacijų žiemojimas panašus – 93,7–96,7 %. Stabiliausi požymiai – augalų aukštis, kero skersmuo, lapų plotis ir ilgis (variacijos koeficientas 4,0–9,7 %). Didžiausia požymių įvairovė nustatyta analizuojant sausos biomasės kiekį (variacijos koeficientas 5,0–35,8 %).

Reikšminiai žodžiai: agromorfologiniai požymiai, laukinės populiacijos, ploidiškumas, rykštėtoji sora.