



Variance components and heritability of biomass yield in switchgrass (*Panicum virgatum* L.) grown in the Southern Great Plains



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ABSTRACT

Switchgrass (*Panicum virgatum* L.) is an important feedstock for biofuel production and also used for rangeland restoration and as a forage crop. Wide variability has been observed in switchgrass at both ecotypic and population levels. Variance component analysis can identify the relative contribution of different factors which can be used as guidance in selection of genotypes in breeding programs. The objectives of this study were to estimate and partition the sources of variance components and to estimate heritability of biomass yield in switchgrass. A total of 36 accessions including 31 plant introduction accessions collected from the Germplasm Resources Information Network (GRIN) and five improved populations developed at the Samuel Roberts Noble Foundation were used for estimating the variance components. Fourteen of these were lowland and 22 upland accessions. The accessions and populations were evaluated in Ardmore, Oklahoma from 2007 to 2011. Average biomass yield of lowland accessions was 2.41 ± 0.05 kg plant⁻¹ and that of upland accessions was 0.57 ± 0.01 kg plant⁻¹. Biomass yield increased up to 526% from 2008 to 2010; however, it decreased up to 88% from 2010 to 2011 growing seasons due to severe drought. Variance component analysis revealed that accessions accounted for 48.5 and 37.2% of the total variation in the lowland and upland ecotypes, respectively. Biomass yield was moderately heritable for switchgrass (0.5) and for lowland (0.6) and upland (0.44) ecotypes, indicating that biomass yield could be improved through selection. In general, lowland ecotypes are more productive; however, a few upland accessions (e.g., PI 476294, PI 657660, PI 642193) were found productive even during dry years, albeit less biomass was produced than lowland ecotype.

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1. Introduction

Switchgrass (*Panicum virgatum* L.) is a perennial, warm season native grass used for hay production, grazing, and soil conservation (Casler et al., 2007, 2011). Switchgrass has been considered as a cellulosic biofuel feedstock because of its higher biomass yield potential and ease of adaptation to marginal environments. Genetic improvement of switchgrass is constrained because of its complex genetics related to self-incompatibility, multiple ploidy levels, and its relatively large genome size (Costich et al., 2010; Lu et al.,

2013; Martínez-Reyna and Vogel, 2002). Significant improvement of this important biofuel and forage crop is possible by exploiting genetic and genomic factors. Biomass yield improvement is one of the major targets of switchgrass breeding programs. Understanding the nature and magnitude of genetic variation is crucial in selecting genotypes with desirable traits, which can be utilized in breeding programs to improve switchgrass for both biofuel production and forage-based grazing systems (Dudly and Moll, 1969). Variation in switchgrass tends to be high regardless of ecotypes, populations and accessions and offers opportunity for its improvement through breeding (Gunter et al., 1996; Hultquist et al., 1996; Narasimhamoorthy et al., 2008).

Partitioning variance components of economically important traits, such as biomass yield, helps identify the major sources of variation influencing biomass (Lynch and Walsh, 1997). The selection response is closely related to the magnitude of additive genetic variance. However, selection efficiency decreases as environmental variance obscures the relationship between genotypes and phenotypes (Lynch and Walsh, 1997). While diverse genetic background

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provides opportunities for genotype selection, various environmental conditions need to be considered for evaluation of these genotypes.

Variance components in maize (*Zea mays* L.) have been analyzed to identify the relative contribution of factors, together with heritability, for guidance in selection of genotypes in breeding programs (Grieder et al., 2012; Strigens et al., 2012). When the phenotypic variation is predominantly under genetic control, resulting in high levels of heritability, selection for the particular trait would be highly effective. On the other hand, if genotype $\times$ environment ($G \times E$) interactions were strong, then the results of selection for the trait would depend on the type of environment in which the selection nurseries are planted (Grieder et al., 2012). For example, there are two common ecotypes in switchgrass (i.e., lowland and upland) that differ in geographic adaptation, thus their phenotypic traits are strongly influenced by environments. In addition to spatial environments, switchgrass performance also depends on temporal variation, and no two years are identical regarding the value and distribution of temperature and precipitation during the growing season. In switchgrass, a paucity of work has focused on variance components analysis in biomass yield, except for one study in which three half-sib families were evaluated (Das et al., 2004).

Understanding components of variance and heritability of economically important traits is crucial for developing a successful breeding program. The objectives of this study were to: (i) estimate and partition the sources of variation in biomass yield of switchgrass at population, ecotype and accession levels, and (ii) estimate heritability of biomass yield. For this study, we used general linear mixed models and restricted maximum likelihood to partition the sources of variation for yield in switchgrass into genetic, environmental, and residual components as well as a genotype by environment interaction; these components were used to calculate broad-sense heritability, which can be used for making selection decisions. We also take a hierarchical approach to data analysis whereby we restrict inferences to switchgrass as a crop, and then partition the data into ecotypes (i.e., lowland and upland) and finally by accession. These data will allow us to understand the factors contributing to variation of yield at each level of classification with implications on biomass production and selection potential in the presence of variable environmental conditions (e.g., severe drought).

2. Materials and methods

2.1. Plant materials

Switchgrass Plant Introductions (PI; $N=168$) are listed in the USDA-Germplasm Resources Information Network (GRIN). A representative subset of 31 PI accessions, collected from 18 different U.S. states and three international countries (Argentina, Belgium, and Turkey), were acquired from GRIN. Five populations developed at the Samuel Roberts Noble Foundation (SRNF) also were included (Table 1). Each of the 36 germplasm accessions (i.e., 31 PIs and five breeding populations) was represented by 10 genotypes, resulting in a final experimental size of 360 genotypes. Five ramets of each of the 10 genotypes per accession were grown in the SRNF greenhouse, four for use in field evaluation, and the fifth copy was maintained in the greenhouse.

2.2. Field evaluation and planting design

The experimental plots were located at the SRNF-Research Park ($34^{\circ}11'N$, $97^{\circ}05'W$). Soil of the experimental site was Normangee clay loam (fine, smectitic, thermic Udertic Haplustalfs) with mean

pH=5.7. Ramets were transplanted on 1 August 2007 following an R-360 honeycomb design (1.5×1.5 m spacing; Fasoulas and Fasoula, 1995). Accessions and genotypes within an accession were randomized for the first replication, which was carried over to the other three replications. There were 12 rows in each replication and 30 genotypes were planted in each row. Supplemental irrigation was provided for one month after planting (once/week) and then grown in rainfed conditions. Nitrogen (46:0:0) fertilizer was applied at the rate of 112 kg ha^{-1} (based on soil test results) during field preparation in 2007. Additional N fertilizer was applied every year at the beginning of crop re-growth in early spring (based on soil test results). Weeds were controlled by cultivating the plots between rows during early spring in 2008 and 2009. Dual II Magnum (Metolachlor) at 3.41 L ha^{-1} and Prowl H₂O (Perdamethalin) at 3.98 L ha^{-1} were applied as pre-emergence, and 2,4-D at 2.84 L ha^{-1} with surfactant at 1.42 L ha^{-1} was applied as post-emergence herbicides.

Biomass was harvested from each individual plant after the killing frost each year. Samples of chopped biomass (~ 150 g) were taken from each plant, weighed immediately after harvest, oven dried (50°C for 72 h), obtained moisture content and computed the dry matter yield of individual plants. Harvesting was not possible in 2009 because of continuous rainfall during harvest, which saturated the soil and rendered harvest impossible.

2.3. Data analysis

We estimated variance components of biomass yield in switchgrass using fixed and random effects implemented in general linear mixed models (GLMM) with restricted maximum likelihood (REML) estimators in the computer program SAS[®] 9.3 (MIXED procedure; Littell et al., 2006). Variation in biomass yield was partitioned into genetic (accession and genotype $\times$ accession), environmental (year and rep $\times$ genotype $\times$ accession), genetic by environmental interaction (accession $\times$ year), and residual components. We followed a hierarchical approach to data analysis, first analyzing switchgrass at the crop level, then for each ecotype (i.e., lowland versus upland), and last for each accession. Throughout, we used a variance components covariance structure, modeled variance components as categorical random effects, and report covariance parameter estimates ($\pm$ SE) for each component; estimates were then expressed as a percentage (%) of the total phenotypic variance of yield.

For the switchgrass-crop model, ecotype was modeled as a fixed effect, which adjusts model parameters relative to the average yield of the population. In the switchgrass-crop model, we used the Kenward–Rogers denominator degrees of freedom adjustment (Kenward and Roger, 1997) for the fixed-effects component (i.e., ecotype) of the model to account for unbalanced data and multiple random effects (Littell et al., 2006). Ecotype was not modeled as a genetic component because ecotype is a classification grouping based on the geographic origin of the accessions.

In addition to the switchgrass-crop model, we also modeled ecotype-specific variance components of yield for lowland and upland ecotypes separately. These models will reveal changes in phenotypic variance of yield for each ecotype. We used a fully random effects model because ecotype was no longer included as a fixed effect. Similar to the switchgrass-crop model, all variance components (accession, genotype $\times$ accession, year, rep $\times$ genotype $\times$ accession, and accession $\times$ year), including residual variation, were modeled as categorical random effects. The last level of analysis was to partition sources of variance for each accession ($n=36$). This analysis partitioned the sources of variance to help in making selection decisions, whereby the percentage of genetic contribution to yield can be used as an indication to the potential for phenotypic selection. In this analysis, we modeled

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