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## ORIGINAL RESEARCH ARTICLE

## Crop Breeding &amp; Genetics

# Genetic (co)variation and accuracy of selection for resistance to viral mosaic disease and production traits in an inter-ecotypic switchgrass breeding population

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Associate Editor: Michael D. Casler

## Funding information

US Department of Energy, Grant/Award Number: DE-SC0016108

## Abstract

Obtaining good accuracy and reliability of estimated breeding values is essential to increase the efficiency of a plant breeding program. Genetic variation was assessed for categorical (Vir<sub>c</sub>) and binary (Vir<sub>b</sub>) mosaic (caused by *Panicum mosaic virus*), dry matter (DMY) and predicted ethanol (Eto<sub>h</sub>) yields, and lignin content (Klason or KL, and acid-detergent or ADL) in a Summer–Kanlow switchgrass (*Panicum virgatum* L.) population. Breeding values were predicted with the restricted maximum likelihood–best linear unbiased prediction (REML–BLUP) approaches using a multivariate phenotypic (PBLUP) and animal (ABLUP) models, integrating a three-generation pedigree (1,622 half-sibs) in ABLUP and not in PBLUP. Models were compared in their precision (accuracy and reliability) in assessing genetic parameters and estimating breeding values. The models were similar in most aspects, allocating the highest heritability ( $h^2$ ) values to DMY ( $.38 \pm .035$  vs.  $.41 \pm .035$ ), Eto<sub>h</sub> ( $.46 \pm .031$  vs.  $.42 \pm .033$ ), and Vir<sub>c</sub> ( $.43 \pm .046$  vs.  $.37 \pm .047$ ) and the lowest ( $.17 \pm .032$  to  $.30 \pm .044$ ) to KL, ADL, and Vir<sub>b</sub>. Genetic correlations were always larger than residual and phenotypic correlations. Intermediate or strong additive genetic control suggest that selecting for high-biomass genotypes will slightly increase lignin content and simultaneously impart mosaic tolerance. Mitigating an increase in lignin content will require including Eto<sub>h</sub> in a selection index based on its much stronger negative correlation ( $r_G = -.63$ ) with lignin. In this population, accuracy values ranged from .06 to .94 (PBLUP) and from .26 to .92 (ABLUP) and corresponding reliability ranged from .004 to .89 and from .07 to .87. However, ABLUP improved average reliability of DMY and Eto<sub>h</sub> by 11% and of other traits by 4–5% over the PBLUP model. The ABLUP was a better model over PBLUP, which is a valid analysis in the absence of a pedigree.

**Abbreviations:** ABLUP, animal model best linear unbiased prediction; ADL, acid detergent lignin; BLUP, best linear unbiased prediction; DMY, dry matter yield; EBV, estimated breeding value; Eto<sub>h</sub>, predicted ethanol yield; KL, Klason lignin; PBLUP, phenotypic best linear unbiased prediction; REML, restricted maximum likelihood; Vir<sub>b</sub>, binary (0,1) mosaic rating; Vir<sub>c</sub>, categorical (1–5) mosaic rating

## 1 | INTRODUCTION

Extensive research on switchgrass (*Panicum virgatum* L.) continues to provide fundamental knowledge on breeding and management that particularly enhance its sustainability as a dual-purpose crop: bioenergy and forage (Anderson et al., 2016; Bouton, 2007; Edmé, Mitchell, & Sarath, 2017; Mitchell, Vogel, & Sarath, 2008; Sarath et al., 2008). Possibilities for improvement of digestibility, biomass, lignin content, and pest tolerance, among the different objective traits considered, exist across populations of switchgrass, be they lowland or upland ecotypes (Casler, 2012; Edmé et al., 2017; Jahufer & Casler, 2015). However, ecological differences in production exist among the two ecotypes, with two gradients in adaptation detected across the North American continent, from the south (lowland origin) to the north (upland origin) driven by temperatures, and from the east to the west driven mostly by availability of water (Casler, Stendal, Kapich, & Vogel, 2007; Casler, Vogel, Taliferro, & Wynia, 2004). These adaptive patterns, as carved by environmental forces, also bring genetic differences in growth and susceptibility or resistance to diseases and pests, whereby the lowland ecotypes, adapted to warmer climates and having been exposed to intense selection pressures from pathogens, tend to produce more biomass and to express greater tolerance to diseases and insects than the upland ecotypes (Gustafson, Boe, & Jin, 2003; Koch et al., 2019; Palmer et al., 2019; van Wallendael et al., 2020; Vogel, Schmer, & Mitchell, 2005). The upland ecotypes, with a more northern origin, have superior overwintering capability to the lowland.

Although diseases have been recognized to pose serious threat to switchgrass production, breeding for disease resistance has not been consistently integrated into switchgrass selection programs. Understanding the genetic basis of resistance to the most destructive diseases is key to manage or reduce the incidence levels in these populations without compromising yield and quality. For instance, rust disease, caused by a complex of fungal species including *Puccinia emaculata* Schwein, occurs throughout switchgrass growing areas in the United States and can affect yield and quality traits in switchgrass bred for forage and bioenergy (Sykes et al., 2016). Gustafson et al. (2003) indicated that both additive and nonadditive genetic variation could be exploited for improving rust resistance by selecting among and within families in switchgrass breeding populations. Leaf spot disease, caused by *Bipolaris* spp., affects switchgrass in the eastern and southern regions of the United States (Fajolu, 2012; Songsomboon et al., 2019). For all other diseases of switchgrass, however, the potential for improvement of resistance has not been explored. In Nebraska, viral mosaic (caused by *Panicum mosaic virus* in a complex with its satellite) is conspicuous in switchgrass field tests and drastically reduces growth of certain switchgrass populations (Chowda-Reddy et al., 2019;

### Core Ideas

- Across-generation BLUP analysis provides greater accuracy than one-generation analysis.
- An across-generation animal model is a better model than a phenotypic analysis.
- Decreasing lignin content by breeding in switchgrass will help increase ethanol yield.
- Genotypes with higher lignin content tend to have greater disease tolerance and resistance.

Muhle, 2019; Stewart et al., 2015); no classical genetics information exists yet to appraise the mode of inheritance of resistance against this disease. However, findings from genetic and genomic studies on disease resistance and growth traits are consistent with additive gene action being the predominant mode of inheritance.

The switchgrass population being evaluated in this study was derived by crossing two tetraploid cultivars, namely ‘Kanlow’ (lowland, higher yield, and more resistant) and ‘Summer’ (upland, lower yield, and more susceptible) and is now in the fourth cycle of selection for high biomass yield and low lignin concentration (Edmé et al., 2017; Vogel, Mitchell, Casler, & Sarath, 2014). The retrospective construction of a pedigree for this population made the application of the animal model (Henderson, 1975, 1984) possible to the previous three-generation dataset. The animal model or individual plant model (as respectively coined by animal or plant breeders) integrates the pedigree in the joint estimation of genetic parameters for targeted traits, taking advantage of the multigenerational recombination history to more accurately estimate breeding values for parents and selection candidates (Piepho, Möhring, Melchinger, & Büchse, 2008). The benefits of using the best linear unbiased prediction (BLUP) animal model have been emphasized in animal breeding (Henderson, 1984; Gianola & Rosa, 2015) and are now being exploited in plant breeding, particularly in the context of genomics (Atkin, Dieters, & Stringer, 2009; Durel, Laurens, Fouillet, & Lespinasse, 1998; Oakey, Verbyla, Pitchford, Cullis, & Kuchel, 2006; Piepho et al., 2008).

Better breeding management decisions that maximize short- and long-term genetic gains can be made by accounting for the recombinational history (i.e., selection) of the population via the pedigree (i.e., the relationship matrix) in the analysis. The BLUP technique that underlies this analysis provides unbiased and more precise estimates of the parameters, thereby yielding more accurate and reliable prediction of the breeding values, which represent the genetic merits of parents and progeny at improving the population (White & Hodge, 1989). Piepho et al. (2008) indicated

that the BLUP analysis is also valid without involving the relationship matrix. Accordingly, this study used the BLUP analysis to model the three-generation dataset without the relationship matrix and compared it with the animal model. As commonly done, the comparison was resolved based on the accuracy and reliability associated with the prediction of breeding values. Accuracy is linearly related to the extent genetic gains are possible in a breeding program (i.e., higher accuracy implies higher selection response), and reliability indicates the level of confidence (or uncertainty) that can be placed on the predictions. These two criteria have been used extensively in animal breeding and less in plant breeding (Gianola & Rosa, 2015).

This study also explores the need for inclusion of disease resistance traits in the breeding program to avoid the unintended side effects of exclusive selection being applied on high biomass yield and low lignin content (Edmé et al., 2017). Reduction in lignin content, which by itself provides strength to plants and protection from environmental stresses, may undermine, over time, the ability of the working genetic populations to fight diseases and insect vectors (Sykes et al., 2016). These goals require a joint assessment of the genetic parameters to reveal the level of genetic (co)variation between disease, production, and quality traits and the status of their genetic correlations. Selection in this breeding program was previously based exclusively on phenotypic selection and a shift towards estimating genetic parameters via a multivariate (i.e., joint analysis of all traits) BLUP approach has been instigated in recent years (Edmé et al., 2017). The suitability of additionally integrating the pedigree into the multivariate model is being appraised by comparing the two approaches in their reliability to estimate genetic parameters and in their accuracy to predict breeding values of selection candidates.

To summarize, the specific objectives of this study were (a) to jointly estimate the genetic parameters for yield, quality, and disease (mosaic) based on a multivariate phenotypic (PBLUP) and animal (ABLUP) models, (b) to predict the breeding values associated with mosaic and production traits for parents and progeny, (c) to approximate the genetic relationships that exist among yield and disease traits in an upland  $\times$  lowland switchgrass population under improvement for bioenergy, and (d) to compare the ABLUP with the PBLUP approaches based on accuracy and reliability of predicting the breeding values (EBV) that are to be used ultimately for prediction of genetic gains.

## 2 | MATERIALS AND METHODS

### 2.1 | Description of breeding generations and data collection

The breeding population of interest started with crossing 11 plants each of Kanlow and Summer in pairs to create full-

sib families, with Kanlow as the pollen parent (Vogel et al., 2014). The full-sib progeny (Cycle 1) were planted in 2004 and mass selected in 2005 for high biomass yield and low lignin content, resulting in 35 plants designated as progenitors of the second generation. Open-pollinated seed were collected in 2006 from the 35 parents and planted in 2007 in five-replicate single family-row plots, with 10 plants each, in a randomized complete block design. A between-family selection identified six out of the 35 half-sib families in 2008, from which 111 individual plants were selected in 2009 according to a selection index applied in both years on high biomass (dry matter) yield (DMY) and reduced Klason lignin (KL) content. A crossing block was established in 2010 with two ramets (randomly distributed) of each of the 111 parents, from which open-pollinated seed were harvested to constitute 111 half-sib families of the third generation. In 2011, these families were planted in a randomized complete block design with three replicates of single-family row plots with five plants each. This progeny test was harvested on a family-plot basis in 2012 and 2013, and families were selected for high DMY and low KL using an index that weighed both traits equally (Edmé et al., 2017; Vogel et al., 2014). Selected families were harvested in 2015 and 2016 on an individual plant basis for the same traits to select parents of the fourth generation based on an index composed with breeding values.

Plants were subjectively scored for symptom severity of natural viral mosaic infection in the field in 2013, 2014, and 2015 on a five-point scale (Virc) that assigned 1 to very resistant (no symptoms) and 5 to very susceptible (>50% foliar infection with stunting) plants. The mosaic ratings were also converted into an all-or-none (binary, or Virb) trait by giving a 0-value to ratings of 1 and 2 and a value of 1 to ratings >2. All field experiments were carried out at one location, designated as the Agronomy Farm of the University of Nebraska-Lincoln, Eastern Nebraska Research and Extension Center (ENREC), near Mead, NE (41.09° N, 96.26° W), and managed according to established protocols (Vogel et al., 2014). Samplings and machine harvests of biomass were always performed after the first killing frost, with subsamples taken, dried in a forced-air oven, and ground before laboratory analyses to predict cell-wall components (KL, acid detergent lignin [ADL], and predicted ethanol yield [Etoh]) traits by near-infrared reflectance spectroscopy (Vogel et al., 2011).

### 2.2 | Pedigree

Starting with Generation 0, the complete pedigree includes 1,622 individuals (phenotyped) and spans three generations. Parental populations were included as references in all progeny tests and as representatives of every generation when applicable. The first generation consisted of full-sib families developed from biparental crosses and subsequent generations

were recombined as half-sib families by open-pollination. As of now, the breeding population is managed with discrete generations by moving selection candidates (in the progeny tests) forward from each one to the next. Mosaic ratings were not available for the first two generations, but plots of the parental populations from the original and second generations were available and therefore scored.

## 2.3 | Statistical and genetic analyses

A multivariate (six-trait) analysis was carried out with biomass yield (DMY), KL content, ADL, Etoh, and mosaic ratings (analyzed as Virc on a five-point categorical and as Virb on a two-point binary scale). Yield, quality data (all generations), and mosaic ratings (parents and third generation in 2012–2015) were included in the joint analysis since the years of measurements overlap in the third generation. The two forms of lignin content (ADL and KL) were included together here for evaluation purposes, since either is used in breeding for forage and bioenergy. In matrix form, the following linear mixed (PBLUP and ABLUP) model was applied:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\alpha} + \mathbf{e}$$

where  $\mathbf{y}$  represents the vector of observations of yield, quality, and disease data,  $\boldsymbol{\beta}$  is the vector of fixed effects (overall mean, years, and replications),  $\boldsymbol{\alpha}$  is the vector of random additive genetic effects, and  $\mathbf{e}$  is the vector of random residuals.  $\mathbf{X}$  and  $\mathbf{Z}$  are incidence matrices that relate fixed and random effects to the vector of observations in  $\mathbf{y}$ . The additive genetic and residual effects were assumed to be independent, and the expectations for fixed and random [ $\boldsymbol{\alpha} \sim \text{MVN}(0, \mathbf{A}\otimes\mathbf{G}$ );  $\mathbf{e} \sim \text{MVN}(0, \mathbf{I}\otimes\mathbf{R})$ ] effects were solved with the mixed model equations (Henderson, 1975):

$$\begin{bmatrix} \mathbf{X}\mathbf{X}' \rightarrow \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} \rightarrow \mathbf{Z}'\mathbf{Z} + \mathbf{A}^{-1}\lambda \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix}$$

in which  $\mathbf{A}^{-1}$  represents the inverse of the pedigree-derived relationship matrix in the ABLUP model and is replaced by  $\mathbf{I}$  in the PBLUP model,  $\mathbf{I}$  being the identity matrix of the 1,622 individuals in the pedigree,  $\mathbf{G}$  and  $\mathbf{R}$  are the respective additive genetic and residual variance–covariance matrices,  $\otimes$  is the Kronecker product,  $\hat{\mathbf{b}}$  and  $\hat{\mathbf{u}}$  are the respective estimates and predictors of the fixed and random effects, and the off-diagonals correspond to the genetic or residual covariances among the six traits. The shrinkage factor  $\lambda$  is equal to the ratio  $\sigma_e^2/\sigma_a^2$  (i.e., error variance to the additive genetic variance), and ' indicates the transpose form of the matrix.

Linear mixed models were used also for the two mosaic ratings, which were considered as Gaussian variables in this analysis. The frequency distributions of these traits in the pop-

ulation were satisfactorily normal to justify this approach. A threshold (categorical or binary) model needs to be tested and could be more appropriate for these types of traits, which tend to violate the assumption of normal distribution for ANOVA (Gianola, 1982). However, inconsistent or similar results were obtained in several studies that compared linear and threshold models (Heringstad, Rekaya, Gianola, Klemetsdal, & Welgel, 2003; Ødegård, Kettunen, & Sommer, 2010; Ødegård, Olesen, Gjerde, & Klemetsdal, 2007), as the accuracy of the latter is rather dependent on the frequency of the disease in the breeding population. Nonetheless, the threshold model is being contemplated in this breeding program and will be examined in a subsequent publication.

(Co)variance components were estimated from the mixed models using ASReml version 4.1 (Gilmour, Gogel, Cullis, Welham, & Thompson, 2015), which implements, in a restricted maximum likelihood (REML) procedure, the average information algorithm and sparse matrix methods to handle a large and complex data structure. The components were used to estimate heritability values for and correlations between DMY, KL, ADL, Etoh, Virc, and Virb. Narrow-sense ( $h_i^2$ ) or individual (i) heritability estimates were derived as

$$h_i^2 = \sigma_\alpha^2 / (\sigma_\alpha^2 + \sigma_e^2)$$

The genotype  $\times$  year interaction effects were added to the denominator whenever present for a trait. Genetic correlations ( $r_G$ ) between the traits were calculated as

$$r_G = \sigma_{\alpha 12} / (\sigma_{\alpha 1}^2 \sigma_{\alpha 2}^2)^{0.5}$$

where  $\sigma_{\alpha 12}$  is the genetic covariance between two traits, and the denominator is the product of their respective genetic variances. Phenotypic ( $r_P$ ) correlation and environmental ( $r_E$ ) were also obtained as

$$r_P = \sigma_{p 12} / (\sigma_{p 1}^2 \sigma_{p 2}^2)^{0.5}$$

$$r_E = \sigma_{e 12} / (\sigma_{e 1}^2 \sigma_{e 2}^2)^{0.5}$$

with the different elements being the respective phenotypic or environmental (co)variances associated with two traits. Standard errors of all parameter estimates were approximated using the Delta method (Holland, Nyquist, & Cervantes-Martinez, 2003) via the Taylor series approximation as implemented in ASReml (Gilmour et al., 2015). In the ABLUP model, convergence was obtained with the “corgh” genetic correlation structure along with a “US” covariance structure in the residuals (Isik, Holland, & Maltecca, 2017). For the PBLUP model, the best model and parameters (i.e., none out



of bound) were obtained with a combination of a “diagonal” genetic and “US” residual (co)variance structures (Gilmour et al., 2015).

Breeding values (EBV) were computed for parents and progeny as BLUP predictions by REML. The accuracy of prediction ( $r_{\hat{g}g}$ ), expressed as a correlation between predicted ( $\hat{\alpha}$ ) and true ( $\alpha$ ) breeding values, was obtained from the formula:

$$r_{\hat{g}i, \hat{g}i} = \sqrt{1 - (\text{PEV}_{\alpha i} / \sigma_{\alpha}^2)}$$

with PEV being the prediction error variance obtained as the squared values of the standard errors of individual (i) predictions (i.e., EBV), and  $\sigma_{\alpha}^2$  being the additive genetic variance for the targeted traits; the reliability of the predictions ( $r_{\hat{g}g}^2$ ) was obtained ultimately.

### 3 | RESULTS

#### 3.1 | Genetic parameters

The genetic parameters estimated under the two genetic models (PBLUP and ABLUP) were relatively similar, if not for a few cases (Table 1). The differences primarily arose whenever the ABLUP model recovered a significant genotype  $\times$  year interaction, as observed for KL and Virb (the binary mosaic rating). In estimating the variances for KL, the ABLUP model distributed 19 and 41% of the phenotypic variance to the additive genetic and residual variances, respectively. The PBLUP model assigned 22 and 78% to the respective additive genetic and residual variances, resulting in these three variances being higher than those under the ABLUP model. For Virb, the additive genetic variance was 2% higher (29% vs. 27%) and the residual variance 22% lower (51% vs. 73%) with the ABLUP model than with the PBLUP model. Even though there was no interaction present for estimating ADL, the additive genetic variance was 5% higher (29% vs. 24%) and the residual variance was 5% lower (71% vs. 76%) under the ABLUP model compared with the PBLUP model. The multivariate PBLUP model did not detect any significant genotype–year interaction for any trait, and this interaction was then omitted.

The narrow-sense heritability values ranged from .22 (KL) to .46 (Etoh) as estimated by the PBLUP model and from .19 (KL) to .46 (Etoh) when estimated by the ABLUP model. As a consequence of the profiles of the estimated variances, the narrow-sense heritability values were higher for three (DMY, ADL, and Virb) of the six traits and lower for two (KL and Virc) based on the ABLUP model. A similar  $h_1^2$  value was recorded for Etoh under both genetic models. Looking at the standard errors, the heritability values for ADL and Virb were measured with greater precision by the ABLUP model and for

Etoh and Virc by the PBLUP model, but with a much narrower difference according to the latter model.

#### 3.2 | Phenotypic, genetic, and environmental correlations

Using either the PBLUP or the ABLUP model, the genetic correlations among the traits were all higher than the phenotypic correlations and were assigned the same signs (positive or negative, Tables 2 and 3). The phenotypic and residual correlations were in general small or not significantly different from zero, except for the correlations of Etoh with either ADL or KL, of KL with ADL, and of Virc with Virb. The same four genetic correlations were not significant (i.e.,  $r_G < 2\text{SE}$ ) under either genetic model, and that involves the relationships between the two measurements of mosaic with Etoh and with KL. Only considering the significant genetic correlations revealed that three (involving ADL–DMY, Etoh–KL, and Virc–Virb) were higher under the ABLUP than under the PBLUP model, which itself produced six  $r_G$  values higher than those predicted by the ABLUP model. The standard errors were of comparative magnitude or precision, with smaller or higher (absolute) values for the same number of cases attributed to either of the two models. The environmental correlations were also small, except for the correlations of Etoh with either ADL or KL, of KL with ADL, and of Virc with Virb, which ranged from .39 to .54 under the PBLUP and from .30 to .37 under the ABLUP model (Table 4).

#### 3.3 | Accuracy and reliability

The accuracy ( $r_{\hat{g}g}$ ) of estimated breeding values (EBV) for each individual genotype included as a selection candidate (parents and progeny) was obtained from the two models. These  $r_{\hat{g}g}$  values represent the correlation estimates between predicted and true (but unknown) values of the EBV. As such, they can be and have been compared for the efficiency of each model at reliably selecting the candidates. In this Summer  $\times$  Kanlow population, the  $r_{\hat{g}g}$  values ranged from .06 to .94 when assessed with the PBLUP model and from .26 to .92 using the ABLUP model (Table 5). These corresponded to reliability values ( $r_{\hat{g}g}^2$ ) ranging from .004 to .89 (PBLUP) and from .07 to .87 (ABLUP). The ranges of these values were wider with the PBLUP model and narrower with the ABLUP model, showing that the latter model largely improved the lower tails of the prediction distributions. However, looking at each trait individually, the ABLUP model, which exploited the pedigree information to predict breeding values, improved the average accuracy and reliability of DMY and Etoh by 11% and those of the remaining traits by 4–5%

**TABLE 1** Variance components and narrow-sense ( $h^2_i$ ) heritability estimated for six traits across three generations of a Summer × Kanlow switchgrass population for two BLUP (best linear unbiased prediction) models: a phenotypic PBLUP without pedigree, and an animal ABLUP factoring the numerator relationship matrix

Trait <sup>a</sup>	PBLUP model			ABLUP model			
	Variance	Estimate	SE <sup>b</sup>	% <sup>b</sup>	Estimates	SE	%
DMY	Additive	0.023	0.003	38	0.025	0.003	41
	Residual	0.038	0.002	62	0.036	0.002	59
	Phenotypic	0.061	0.002		0.061	0.002	
KL	$h^2_i$	.38	.04		.41	.035	
	Additive	92.41	14.98	22	75.67	14.64	19
	Residual	324.21	16.36	78	161.94	19.10	41
ADL	Genotype × year	ns	ns		157.13	18.91	40
	Phenotypic	416.62	15.15		394.74	15.00	
	$h^2_i$	.22	.04		.27	.04	
ADL	Additive	7.09	1.21	24	8.42	1.17	29
	Residual	21.89	1.22	76	20.25	1.04	71
	Phenotypic	28.97	1.06		28.68	1.00	
Etoh	$h^2_i$	.25	.04		.17	.03	
	Additive	16.48	1.48	46	16.65	1.62	46
	Residual	19.28	1.08	54	19.49	1.08	54
Virb	Phenotypic	35.76	1.38		36.13	1.40	
	$h^2_i$	.46	.03		.42	.04	
	Additive	0.43	0.05	43	0.42	0.06	41
Virb	Residual	0.57	0.05	57	0.60	0.05	59
	Phenotypic	1.00	0.04		1.02	0.04	
	$h^2_i$	.43	.05		.37	.05	
Virb	Additive	0.06	0.02	27	0.07	0.02	29
	Residual	0.18	0.02	73	0.12	0.02	51
	Genotype × year	ns	ns		0.05	0.02	20
Phenotypic	Phenotypic	0.24	0.01		0.24	0.01	
	$h^2_i$	.27	.06		.30	.04	

<sup>a</sup>DMY, dry matter yield; KL, Klason lignin; ADL, acid detergent lignin; Etoh, predicted ethanol yield; Virb, mosaic rated as 1–5; Virb, mosaic rated as 0, 1.

<sup>b</sup>SE, standard error; %, proportion of the phenotypic variation explained by the other sources of variation; ns, nonsignificant from 0 (i.e., values were negative).



**TABLE 2** Additive genetic correlations ( $r_G$ ) based on two best linear unbiased prediction (BLUP) models with (ABLUP above the diagonal) or without (PBLUP below the diagonal) the pedigree for six traits measured on a Summer  $\times$  Kanlow switchgrass population being improved for bioenergy (high biomass and ethanol yields and reduced lignin content and disease incidence)

$r_G$ values <sup>a</sup>						
PBLUP trait <sup>b</sup>	DMY	KL	ADL	Etoh	Virc	Virb
DMY	<b>1</b>	.25	.16	-.11	-.31	-.36
KL	.25	<b>1</b>	.80	-.63	-.15	-.18
ADL	.13	.80	<b>1</b>	-.54	-.22	-.27
Etoh	-.15	-.60	-.61	<b>1</b>	.04	.11
Virc	-.33	-.17	-.29	.08	<b>1</b>	.93
Virb	-.45	-.22	-.33	.12	.88	<b>1</b>

<sup>a</sup>Bold values are significantly different from 0 based on estimates being  $\geq 2$  SE.

<sup>b</sup>DMY, dry matter yield; KL, Klason lignin; ADL, acid detergent lignin; Etoh, predicted ethanol yield; Virc, mosaic rated as 1–5; Virb, mosaic rated as 0, 1.

**TABLE 3** Phenotypic correlations ( $r_p$ ) based on two best linear unbiased prediction (BLUP) models with (ABLUP above the diagonal) or without (PBLUP below the diagonal) the pedigree for six traits measured on a Summer  $\times$  Kanlow switchgrass population being improved for bioenergy (high biomass and ethanol yields and reduced lignin content and disease incidence)

$r_p$ values <sup>a</sup>						
ABLUP trait <sup>b</sup>	DMY	KL	ADL	Etoh	Virc	Virb
DMY	<b>1</b>	.08	.11	-.07	-.13	-.17
KL	.07	<b>1</b>	.62	-.50	-.10	-.08
ADL	.12	.47	<b>1</b>	-.44	-.09	-.06
Etoh	-.09	-.38	-.44	<b>1</b>	.01	.02
Virc	-.13	-.09	-.10	.02	<b>1</b>	.90
Virb	-.16	-.06	-.07	.03	.80	<b>1</b>

<sup>a</sup>Bold values are significantly different from 0 based on estimates being  $\geq 2$  SE.

<sup>b</sup>DMY, dry matter yield; KL, Klason lignin; ADL, acid detergent lignin; Etoh, predicted ethanol yield; Virc, mosaic rated as 1–5; Virb, mosaic rated as 0, 1.

**TABLE 4** Environmental correlations ( $r_E$ ) based on two best linear unbiased prediction (BLUP) models with (ABLUP above the diagonal) or without (PBLUP below the diagonal) the pedigree for six traits measured on a Summer × Kanlow switchgrass population being improved for bioenergy (high biomass and ethanol yields and reduced lignin content and disease incidence)

Trait <sup>b</sup>	$r_E$ values <sup>a</sup>					
	DMY	KL	ADL	Etoh	Virc	Virb
DMY	–	–.01	.08	–.03	–.01	–.04
KL	.00	–	<b>.54</b>	<b>–.43</b>	–.06	–.02
ADL	.12	<b>.36</b>	–	<b>–.39</b>	–.01	.04
Etoh	–.04	<b>–.30</b>	<b>–.37</b>	–	–.02	–.05
Virc	.01	–.05	–.01	–.02	–	<b>.87</b>
Virb	–.02	–.004	.02	–.02	<b>.77</b>	–

<sup>a</sup>Bold values are significantly different from 0 based on estimates being  $\geq 2$  SE.

<sup>b</sup>DMY, dry matter yield; KL, Klason lignin; ADL, acid detergent lignin; Etoh, predicted ethanol yield; Virc, mosaic rated as 1–5; Virb, mosaic rated as 0, 1.

**TABLE 5** Values of accuracy ( $r_{g,\hat{g}}$ ) and reliability ( $r_{g,\hat{g}}^2$ ) of prediction of estimated breeding values for six traits measured across three generations of a Summer × Kanlow switchgrass population being improved for bioenergy (high biomass and ethanol yields and reduced lignin content and disease incidence) based on two best linear unbiased prediction (BLUP) models without (PBLUP) or with the pedigree (ABLUP)

Model	Trait <sup>a</sup>						
	Parameter	DMY	KL	ADL	Etoh	Virc	Virb
PBLUP	$r_{g,\hat{g}}$	.50 <sup>b</sup> (.07–.93)	.50 (.12–.88)	.54 (.19–.89)	.50 (.06–.94)	.49 (.14–.85)	.48 (.16–.80)
	$r_{g,\hat{g}}^2$	.43 (.004–.86)	.39 (.014–.77)	.41 (.04–.79)	.45 (.004–.89)	.37 (.02–.72)	.33 (.03–.63)
ABLUP	$r_{g,\hat{g}}$	.61 (.31–.91)	.54 (.27–.81)	.58 (.29–.87)	.62 (.31–.92)	.55 (.27–.82)	.53 (.26–.80)
	$r_{g,\hat{g}}^2$	.46 (.09–.83)	.37 (.07–.66)	.42 (.08–.76)	.48 (.10–.85)	.38 (.07–.68)	.35 (.07–.64)

<sup>a</sup>DMY, dry matter yield; KL, Klason lignin; ADL, acid detergent lignin; Etoh, predicted ethanol yield; Virc, mosaic rated as 1–5; Virb, mosaic rated as 0, 1.

<sup>b</sup>Ranges of the values are given in parentheses.

over the PBLUP model. Accuracy and reliability parameters are important to the breeder in making sound advancement decisions on parental selection for the next generation, on predicting gains from selection, and/or on deployment of cultivars from a breeding program (White & Hodge, 1989).

## 4 | DISCUSSION

A recurrent selection protocol is followed by the USDA-ARS forage breeding program in Lincoln, NE, to advance selection candidates from one generation to the next in a discrete fashion using half-sib family structures. Since the inception of the program, selection was purely phenotypic and univariate, but backed by a selection index strategy (Vogel & Pedersen, 1993). In recent years, selection is geared towards a multivariate approach involving all generations and traits in one mixed linear model analysis for BLUP prediction of breeding values (Edmé et al., 2017). The rationales for this approach are justified on grounds that (a) these EBVs represent the best and unbiased estimates for selection of parents in the crossing blocks for cultivar release based on their own performance and on that of their progeny, and this will be used to shorten the time from crossing to cultivar deployment; (b) these EBVs are the best estimates to select individual progeny (not replicated) in the progeny tests, as their prediction also benefited from data coming from their parents (previous generation) and relatives; (c) making gains from selection and recommending durable cultivars require sound and reliable estimates of genetic parameters; (d) building a more efficient breeding strategy requires exploiting the architectures of all objective traits (old and new) in the breeding objective to optimize the selection index; and (e) an optimization of the “multiple-population-and-species” strategy, in effect in this breeding program, needs to be revisited in line with the lack of resources. The following discussion will refer to the results from the ABLUP model, as it is the adopted model based on the accuracy and reliability of the estimates.

Improving a population by recurrent selection is tackled by ensuring the population is of an appropriate size to increase selection intensity and harbors sufficient genetic diversity and variation, by using efficient mating and field designs that separate the type and amount of genetic variation from non-genetic effects, and by securing the steady supply of precise estimates of genetic parameters (heritability, [co]variances, correlations) from appropriate statistical and genetic models. Edmé et al. (2017) examined the use of a multivariate genetic analysis of the population in the last generation and indicated that the trait architecture was well aligned with the breeding objective of increasing biomass yield and reducing lignin content with enough genetic variation to support genetic gains in this Summer  $\times$  Kanlow switchgrass population. In that study, individual heritability estimates were  $.33 \pm .22$  for

DMY,  $.22 \pm .17$  for KL, and  $.36 \pm .22$  for Etoh. The present study integrated data from the two previous generations in the PBLUP model and additionally the across-generations pedigree in the ABLUP model. Individual heritability values were larger using either the PBLUP or ABLUP model and measured with much greater precision ( $SE \leq 0.05$ ) than those for the three traits included in Edmé et al. (2017). The addition of three other traits in the models did not compromise the precision with which the parameters were estimated. This indicates that a multivariate BLUP across-generations analysis, with or without the pedigree, is an improvement over the one-generation multivariate BLUP analysis.

A different picture also emerged with regards to the genetic correlations estimated with the one-generation analysis in Edmé et al. (2017) and with this three-generation study. The correlations of DMY with KL and Etoh are now much lower and of different signs than those obtained with the former analysis. The one-generation analysis indicated that genotypes with high biomass yield would have lower lignin content ( $r_G = -.33$ ) and higher ability to produce ethanol ( $r_G = .60$ ). The three-generation analysis contends that high biomass yield is positively associated with high KL ( $r_G = .24$ ) and negatively associated with Etoh ( $r_G = -.15$ ), even though the correlations were small (Table 2). Integrating the early founders in the ABLUP or PBLUP analysis might have pushed the correlations towards a more positive (but low) level between DMY and KL. Moreover, the Summer  $\times$  Kanlow population has a very recent breeding history (Vogel et al., 2014), and sufficient recombination and linkage disequilibrium have not been generated yet to shape its trajectory to a “stable” level. Case in point, it is composed of genotypes with different combinations of the three traits, giving the possibility to discriminate those with high biomass yield, high Etoh, and low KL from those with high biomass yield, high Etoh, and high KL. However, both studies support the evidence that increasing Etoh (ethanol production) will come from selecting genotypes with low lignin content (KL or ADL), as underscored by  $r_G$  values being between  $-.60$  and  $-.66$  (Table 2). In a quantitative trait loci mapping project, Milano, Lowry, and Juenger (2016) indicated that, in the context of switchgrass, the genetic architecture of traits is complex with limited pleiotropy or tight linkage to explain trait divergence. This can only be explained by the relatively short breeding history of these populations coupled with the underlying polyploid background.

A good understanding of the genetic architecture of traits is essential for managing breeding populations and developing selection indices (Falconer & MacKay, 1996; Lynch & Walsh, 1998). Unfavorable correlations, particularly between growth and quality traits, are common in plant breeding and present constraints to jointly improve these two types. The joint or independent action of the genetic and environmental sources of variation will determine the expressivity of traits and thereby shape their covariation (Cheverud, 1984).

This work also studied the interrelationships between the heritability of the traits with their correlations (phenotypic, genetic, and environmental) to better understand the underlying genetic control. Of great interest to this breeding program is the four-factors relationship: biomass yield, lignin content, ethanol yield, and disease resistance. Comparing the two measures of lignin content or of disease scoring was to indicate which of the two would be better suited to the selection process. All six traits are under either intermediate ( $h_1^2 = .17-.27$ ) or strong ( $h_1^2 = .30-.46$ ) genetic control, which was consistent with the PBLUP and ABLUP models. The DMY, Etoh, Virc, and Virb were evidenced by each model as having the highest heritability values, though the PBLUP model was superior for the latter two traits. Genetically, DMY was moderately and negatively correlated with these three traits, but the phenotypic and environmental correlations, although negative also, were small and nonsignificant. This indicates that the environment tended to influence these traits (growth pattern and direction) to the same extent as the genetics, even though the genes are different but linked. The small negative association between DMY and Etoh may have resulted from the positive, but small, correlation of DMY with KL or ADL, which are strongly and negatively correlated with Etoh. Selecting for DMY would not strongly undermine the identification of genotypes with high potential for ethanol production. Moreover, the DMY–KL relationship has a genetic basis ( $r_G = .24$ ), showing opposing signs for  $r_G$  and  $r_E$ , and thus indicating that a differential allocation of carbohydrates to biomass and to lignin might be the basis for their covariation. The same is true for the relationships between Etoh and the two mosaic traits, even though there is no causal or biological genetic basis ( $r_G = .04-.11$ ) per se, their covariation can be explained indirectly via their conflicting reliance on lignin content: high KL for physical resistance and low KL for ethanol production.

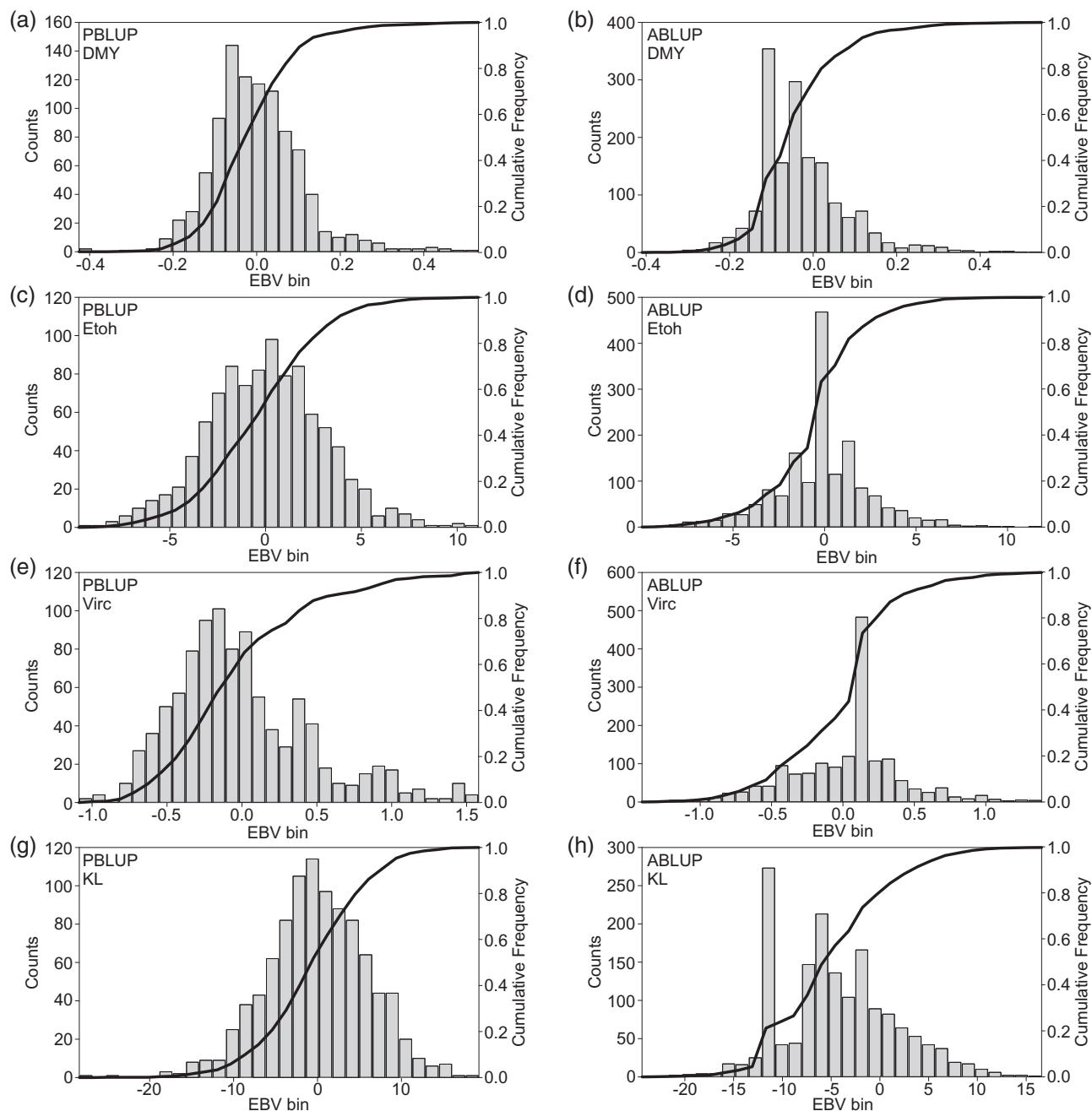
The two lignin measurements (ADL and KL) represent the same trait as were the two mosaic ratings (Virc and Virb). Either lignin form, with a moderate heritability, can be used as a selection and/or objective trait in a breeding program to identify genotypes for the lignocellulosic (fermentation) platform for which reduction of lignin is critical (Edmé et al., 2017). However, the Klason form has a stronger genetic correlation ( $-.63$ ) with Etoh than ADL ( $-.54$ ), indicating that reduction of KL, particularly, can be more effective at yielding genotypes with high potential for producing ethanol. The ADL/KL–Etoh relationship was particularly unique in the sense that all three components of the correlations were large and with similar signs, pointing to a stronger genetic basis operating along a somewhat less strong environmental influence.

Deconstructing the disease phenotype into its subphenotypic components (1–5 rating) will provide a better control

( $h_1^2 = .37-.43$ ) on incidence than using the binary rating ( $h_1^2 = .27-.30$ ). A binary scoring of mosaic, though having a lower  $h_1^2$ , would allow faster phenotyping compared with the more laborious, but more heritable, categorical scoring and be particularly useful in the context of a breeding program, such as this one, dealing with relatively large populations. The genetics and the environment acted in the same pattern and direction on these four traits (ADL, KL, Virc, and Virb), but leaving the phenotypic and environmental correlations small and nonsignificant. Wilson et al. (2006) indicated that accounting for the temporal coupling of genetics and environment gives a more informed knowledge of how the two shape the variance (heritability) and covariation of traits in a wild sheep population. A salient result of this research is that genotypes with high lignin content tended to have lower disease incidence ( $r_G = -.25$ ), suggesting that integrating the disease phenotyping data into the selection index will be more informative than not.

The goal of any breeding program is to make gains from the breeding and selection protocols put in place to identify elite genotypes with the specific combinations of genes or traits of interest. Estimation of breeding values of the selection candidates is central to this process, as EBVs determine the individual genetic merits or the potential of parents and progeny at transmitting and increasing the frequency of key genes throughout generations (Falconer & McKay, 1996). One way to make progress, as a change of trait mean (or index value) of the population, is to increase the accuracy of prediction, accuracy being directly proportional to increasing genetic gains (Lynch & Walsh, 1998): the breeder's equation  $\Delta G = ir_{\hat{g}g}\sigma_a$ , with  $i$  being the intensity of selection. The accuracy of prediction measures how close or far the EBV are to their true values as a correlation ( $r_{\hat{g}g}$ ), since estimates are usually calculated with some imprecision (the standard errors attached to the values). In this study, the ranges of  $r_{\hat{g}g}$  values were narrower with the ABLUP model (.26–.92) than with the PBLUP model (.06–.94). Both models benefited from the inclusion of more data to adjust the accuracy of prediction. However, the ABLUP model was more refined with the integration of the pedigree, or more precisely the additive relationship matrix, to improve the accuracy and reliability further over the PBLUP model for most members of the population (Table 4).

Furthermore, looking at each trait separately, the ABLUP model improved the average accuracy and reliability of DMY ( $h_1^2 = .41$ ) and Etoh ( $h_1^2 = .42$ ) by 11% and those of the remaining traits ( $h_1^2 = .17-.37$ ) by 4–5% over the PBLUP model. However, a greater shrinkage of the breeding values towards the mean occurred with the ABLUP than with the PBLUP model, as typical for animal modeling of genetic data (Figure 1). Some uncertainty or bias (true half-sibs or not) might have also come from using an incomplete pedigree in a half-sib progeny test with the male side of the pedigree



**FIGURE 1** Distribution of breeding values for three traits with high and three traits with low heritability as estimated by two best linear unbiased prediction (BLUP) models without (PBLUP) or with (ABLUP) a three-generation pedigree of a Summer  $\times$  Kanlow switchgrass population being improved for bioenergy (high biomass and ethanol yields and reduced lignin content). DMY, dry matter yield; EBV, estimated breeding value; Etoh, predicted ethanol yield; Virc, categorical (1–5) mosaic rating; KL, Klason lignin

being unknown (Piepho et al., 2008). Genotyping of the candidates is underway and will be used to ascertain the male parentage of the progeny. With high accuracy values ( $r_{\hat{g}g} \geq .8$ ) attached to an individual, the EBVs do not have much room for improvement and will not change considerably with the inclusion of more data (White & Hodge, 1989). The situation is different with lower values ( $r_{\hat{g}g} \leq .4$ ) of accuracy. Across traits, average accuracy values ranged from .48 to .54 for the PBLUP model and from .53 to .62 for the ABLUP model.

Considering that the maximum theoretical accuracy to be expected from a half-sib family structure is .50, a progeny test, like this one, is the only way to extend it further beyond this point (Falconer & McKay, 1996; Lynch & Walsh, 1998). Edmé et al. (2017) contemplated increasing the population size of the progeny tests to improve the precision of the genetic parameter estimates and breeding values. This study seems to indicate that a multivariate BLUP analysis, with or without a pedigree, is a good alternative to increasing family size and



will be efficient at minimizing the risks (accuracy and reliability) of selection and, thus, at improving selection response.

Several studies have investigated the amount of information (data and/or pedigree depth) necessary to obtain greater accuracy of breeding values in animal or plant breeding (Atkin et al., 2009; Durel et al., 1998; Furlani et al., 2005; Mehrabani-Yeganeh, Gibson, & Schaeffer, 1999; Purba, Flori, Baudouin, & Hamon, 2001). The more detailed study by Atkin et al. (2009) indicated that including 5–7 yr of data backed by three to five generations of pedigree are necessary to obtain accurate and reliable estimates of breeding values for the Australian sugarcane (*Saccharum* spp. hybrids) breeding program. More gains in accuracy were provided by having more years of data than by a deeper pedigree. The data seemed to have accounted for the noise or the environmental component and the pedigree for the flow of genes from parents to progeny and for their expression in immediate sib relatives within and across generations. In this switchgrass breeding program, research is already underway to genotype parents and progeny and to increase the quantity, quality, and type of data collected (without overtaxing available resources) that will further refine the BLUP analysis of these progeny tests. No such extensive study or values are available in the switchgrass or perennial grass literature for comparisons.

## 5 | CONCLUSION

To make progress in a breeding program, selecting on EBVs is more appropriate than selecting on raw phenotypic information. A motivating finding of this study is that integrating the pedigree with the across-generations dataset in the evaluation of parents and progeny will bring greater precision (accuracy) in the estimation of breeding values and ultimately increase reliability in the prediction of genetic gains. In the absence of a pedigree, a multivariate BLUP analysis of the complete dataset is also a better model than a one-generation evaluation. The objective with this breeding population is to develop switchgrass cultivars for the lignocellulosic (fermentation) platform, whereby increasing biomass and ethanol yields and decreasing lignin content and disease incidence are important. All six traits were found to have adequate genetic variation (under intermediate or strong genetic control), such that selecting for high-biomass genotypes will slightly increase lignin content and simultaneously impart mosaic tolerance. One way to mitigate the increase in lignin content with the increase in biomass will be to include Etoh in a selection index, based on its much stronger negative correlation ( $r_G = -.63$ ) with lignin content. Either of the two forms of lignin or of the two scorings of mosaic can be used to make progress in a breeding program. Evaluating the relative importance of these six traits in a selection index and in their

response to selection will be a worthwhile endeavor for this breeding program.

## AUTHOR CONTRIBUTIONS

Serge J. Edmé: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Writing-original draft; Writing-review & editing. Gautam Sarath: Funding acquisition; Investigation; Project administration; Writing-review & editing. Nathan Palmer: Funding acquisition; Investigation; Project administration; Visualization; Writing-review & editing. Gary Y. Yuen: Funding acquisition; Investigation; Writing-review & editing. Anthony A. Muhle: Investigation; Methodology; Writing-review & editing. Rob Mitchell: Project administration; Writing-review & editing. Satyanarayana Tatineni: Funding acquisition; Writing-review & editing. Christian Tobias: Resources; Writing-review & editing.

## ACKNOWLEDGMENTS

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

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**How to cite this article:** Edmé SJ, Sarath G, Palmer N, et al. Genetic (co)variation and accuracy of selection for resistance to viral mosaic disease and production traits in an inter-ecotypic switchgrass breeding population. *Crop Science*. 2021;*61*:1652–1665. <https://doi.org/10.1002/csc2.20392>