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Genome Wide Association Studies for Identification of Markers Linked to Sucrose Traits in Sugarcane

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GENOME WIDE ASSOCIATION STUDIES FOR IDENTIFICATION OF MARKERS LINKED TO SUCROSE TRAITS IN SUGARCANE

A Dissertation
Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy in

The School of Plant, Environmental, & Soil Sciences

by
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B.A., B.A., Messiah College, 2008
M.S., University of Wisconsin – Madison, 2012
December 2018
To my wife Sarah
who took care of me,
and kept me mostly sane.
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<tr>
<td>AFLP</td>
<td>Amplified fragment length polymorphism</td>
</tr>
<tr>
<td>AMOVA</td>
<td>Analysis of molecular variance</td>
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<tr>
<td>ARS</td>
<td>Agricultural Research Service</td>
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<tr>
<td>cM</td>
<td>centiMorgan</td>
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<tr>
<td>CV</td>
<td>Coefficient of variation</td>
</tr>
<tr>
<td>CYC</td>
<td>Cane yield-component</td>
</tr>
<tr>
<td>D</td>
<td>Nei’s distance</td>
</tr>
<tr>
<td>DArT</td>
<td>Diversity arrays technology</td>
</tr>
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<td>DP</td>
<td>Diversity panel</td>
</tr>
<tr>
<td>ELSS</td>
<td><em>Erianthus</em>-like <em>Saccharum</em> spp.</td>
</tr>
<tr>
<td>EST</td>
<td>Expressed sequence tag</td>
</tr>
<tr>
<td>FDR</td>
<td>False discovery rate</td>
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<tr>
<td>GBS</td>
<td>Genotyping by sequencing</td>
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<tr>
<td>GLM</td>
<td>General linear model</td>
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<tr>
<td>GWAS</td>
<td>Genome wide association study</td>
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<tr>
<td>h</td>
<td>Gene diversity</td>
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<tr>
<td>$H^2$</td>
<td>Broad-sense heritability</td>
</tr>
<tr>
<td>I</td>
<td>Shannon’s information index</td>
</tr>
<tr>
<td>IBS</td>
<td>Identity by state</td>
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<td>InDel</td>
<td>Insertion-deletion</td>
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<tr>
<td>K</td>
<td>Kinship</td>
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<tr>
<td>LD</td>
<td>Linkage disequilibrium</td>
</tr>
<tr>
<td>Acronym</td>
<td>Description</td>
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<td>---------</td>
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<tr>
<td>MCMC</td>
<td>Markov chain Monte Carlo</td>
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<tr>
<td>MDS</td>
<td>Multidimensional scaling</td>
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<tr>
<td>MLM</td>
<td>Mixed linear model</td>
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<tr>
<td>MTA</td>
<td>Marker-trait association</td>
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<tr>
<td>NGS</td>
<td>Next generation sequencing</td>
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<tr>
<td>PCA</td>
<td>Principal component analysis</td>
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<tr>
<td>PCoA</td>
<td>Principal coordinate analysis</td>
</tr>
<tr>
<td>PCR</td>
<td>Polymerase chain reaction</td>
</tr>
<tr>
<td>PIC</td>
<td>Polymorphism information content</td>
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<tr>
<td>Q</td>
<td>Population structure</td>
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<tr>
<td>QTL</td>
<td>Quantitative trait locus</td>
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<tr>
<td>SDP1</td>
<td>Sugarcane diversity panel 1</td>
</tr>
<tr>
<td>SNP</td>
<td>Single nucleotide polymorphism</td>
</tr>
<tr>
<td>SSR</td>
<td>Simple sequence repeat</td>
</tr>
<tr>
<td>TRAP</td>
<td>Target region amplification polymorphism</td>
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<tr>
<td>TRS</td>
<td>Total recoverable sugar</td>
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<tr>
<td>USDA</td>
<td>United States Department of Agriculture</td>
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<tr>
<td>WCSRG</td>
<td>World Collection of Sugarcane and Related Grasses</td>
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ABSTRACT

Sugarcane, being a complex aneu-polyploid, poses unique challenges to fine mapping of quantitative trait loci (QTL) controlling agronomic traits of interest. Genome-wide association studies (GWAS) could be a better alternative to identify molecular markers associated with specific traits due to high linkage disequilibrium in sugarcane. In the first study, marker-trait associations (MTAs) were evaluated for three sucrose traits, Brix, total recoverable sugar (TRS), and percent sucrose on 48 elite and historic Louisiana breeding clones using 1,062 alleles. These sucrose traits were highly correlated (P-value < 0.0001) at >0.96. TASSEL 5.1 and JMP Genomics 8.0 were compared with eight models run in each program. Two identity by state (IBS) K-matrices were paired with four different Q-matrices: a Q-matrix from STRUCTURE 2.3.4, a principal component analysis each from TASSEL and JMP Genomics, and a maximum distance separable matrix from JMP Genomics. The Q-matrix contributed the majority of variation in the results, with minor differences between the software. Additionally, three markers were identified to be associated with sucrose traits. The second study was the first study to use genotyping by sequencing for MTA in sugarcane. It used JMP Genomics to evaluate MTAs on a Louisiana core collection for 10 cane yield-component (CYC) and sucrose traits: stalk count, stalk height, stalk diameter, stalk weight, TRS, Brix, percent sucrose, fiber, Pol, and purity using 6,299 single nucleotide polymorphisms (SNPs) and 235 insertions-deletions (InDels). There were some significant (P-value < 0.05) and highly significant (P-value < 0.0001) correlations among CYC traits, and between fiber and CYC traits. All sucrose traits except fiber were highly correlated. A total of 154 and 209 MTAs were identified for CYC and sucrose traits,
respectively. These associations were from 238 distinct markers with 56 markers associated with more than one trait. The third study assessed the genetic diversity among 1,236 clones from the World Collection of Sugarcane and Related Grasses (WCSRG) and 249 clones from the Louisiana breeding programs using 423 alleles. A 309-clone sugarcane diversity panel (SDP1) was developed for GWAS to identify markers associated with agronomic trait(s) of interest for their use in marker-assisted breeding in Louisiana and elsewhere.
CHAPTER 1. INTRODUCTION

Cultivated sugarcane (*Saccharum* spp. hybrids) is a C4 crop belonging to the subtribe Saccharinae under the tribe Andropogoneae of the family Poaceae. The Poaceae family is one of the larger plant families with over 11,000 species within ~700 genera (Moore et al. 2013; WCSP 2018). Of these, 85 genera and 960 species are under Andropogoneae that includes important C4 grasses such as the grain crops sorghum and maize, and the bioenergy crop *Miscanthus*.

Sugarcane is an important food and energy crop in the tropics and subtropics. Globally, it is the fifth most important crop based on a crop value of $61 billion after rice at $190 billion, wheat at $86 billion, soybean at $69 billion, and maize at $67 billion (FAOSTAT 2016). It accounts for 80 and 45% of global and US sucrose production, respectively (Group Sucre et Denrées 2015; USDA-ERS 2017). A total of 1,900 Mt of sugarcane are produced annually worldwide yielding ~144 Mt of sucrose for consumption and bioethanol (FAOSTAT 2018). In 2017, the US and Louisiana harvested 27.8 and 11.8 Mt of sugarcane on 344,000 and 168,000 ha, respectively (USDA/NASS 2018a). The harvested wet biomass in 2016 was 70.6, 82.4, and 73.5 t/ha globally, in the US, and in Louisiana, respectively (FAOSTAT 2018; USDA/NASS 2018a).

Sugarcane is arguably the number one row crop in Louisiana. Economically it has the highest annual crop value at $841 million contributing ~$2.5 billion to the direct economy of the state (American Sugar Cane League 2017; LSU AgCenter 2017). In 2017, sucrose was the third most produced commodity (1.72 Mt) in Louisiana following corn (2.29 Mt) and soybean (1.84 Mt), and followed by rice (1.20 Mt) (USDA/NASS 2018a).
Additionally, sugarcane produces ~3 Mt bagasse per year in Louisiana, which is often used as a fuel to produce steam or electricity for running the mills, processing the sugarcane, and for the sale of excess electricity (Webber III et al. 2016).

Sugarcane is one of the high biomass crops producing ~39 t/ha dry matter compared to other C4 crops such as Miscanthus (24.6 t/ha), maize (17.6 t/ha), and switchgrass (10.4 t/ha) (Heaton et al. 2008; Waclawovsky et al. 2010). With second generation biofuel, the lignocellulosic biomass could be used for bioethanol. It is estimated the residual bagasse following sucrose extraction could produce 3,000 L/ha of bioethanol, while bagasse and sucrose combined could produce 9,950 L/ha of bioethanol (Somerville et al. 2010). Sugarcane is considered as the most potential second-generation bioenergy crop (energy cane). Energy cane breeding is being carried out to develop clones with higher lignocellulosic biomass (van der Weijde et al. 2013; Hale et al. 2016).

Saccharum traditionally consists of six species of agricultural importance: two wild species, S. spontaneum (L.) (2n = 40-128), and S. robustum (Brandes & Jesw. Ex Gressl) (2n = 60, 80); and four domesticated species, S. officinarum (L.) (2n = 80), S. sinense (Roxburgh) (2n = 81-124), S. barberi (Jeswiet) (2n = 111-120), and S. edule (Hassk) (2n = 60-80) (Moore et al. 2013; Hoang et al. 2015). Genetic evidence suggests S. officinarum (for sucrose) and S. edule (for vegetable) are from two separate domestication events of S. robustum (Grivet et al. 2004, 2006). Further, modern sugarcane hybrids along with S. sinense and S. barberi are interspecific hybrids between S. officinarum and S. spontaneum. The genomes of S. sinense and S. barberi are 61-68% from S. officinarum and 32-39% from S. spontaneum (Piperidis et al. 2010).
Modern sugarcane had more backcrossing to *S. officinarum* resulting in 80% of the chromosomes coming from *S. officinarum* and 10-20% from *S. spontaneum*, with 5-17% being recombinant chromosomes between both species (D'Hont et al. 1996; Hoang et al. 2015).

Modern cultivars are interspecific hybrids derived from crosses between a female *S. officinarum* and a male *S. spontaneum* with 2n + n inheritance due to the female restitution phenomenon (Bremer 1961; Hoang et al. 2015). Three to six generations of intercrossing following hybridization stabilize the genome and improve sucrose traits before use as a cultivar (Bremer 1961; Piperidis et al. 2010). Fewer than 20 *S. officinarum* clones are involved in the genealogy of modern sugarcane cultivars with only a few being used extensively (Raboin et al. 2008). Thus, the cultivars have limited genetic variation. Basic crosses with *S. spontaneum*, other *S. spp.*, and *Miscanthus* spp. are being used to incorporate traits for abiotic and biotic stress tolerance and to broaden the genetic base (Ming et al. 2006; Moore et al. 2013; Todd et al. 2014; Hale et al. 2016).

Sugarcane breeding efforts are currently focused on enhancing sucrose yield, disease and insect resistance, ratooning ability, biomass and fiber yield for bioenergy, and cold tolerance (Hale et al. 2009; Khan et al. 2013; Gouy et al. 2015). From seedling stage to commercial variety release, sugarcane variety development takes an estimated 12-15 years (Kimbeng and Cox 2003; Gouy et al. 2015); with an average of one commercial variety being released for every 250,000 seedlings (Cheavegatti-Gianotto et al. 2011). High numbers at early stages reduce selection efficiency due to space and time constraints such as lack of replications, seedling competition effects, and the high
cost of individual clone selection (Kimbeng and Cox 2003). Early stage selection efficiency may be enhanced by the use of molecular markers, which may also increase the selection response of traits that are difficult to select phenotypically (Gouy et al. 2015).

The high amount of linkage disequilibrium (LD) in sugarcane may give genome wide association studies (GWAS) an advantage over traditional biparental mapping for the identification of molecular markers. The high LD can be attributed to the relatively few generations between modern cultivars and the limited number of clones used in the initial hybridization (Debibakas et al. 2014). Except transgressive segregants, biparental populations have a limited number of recombination events potentially increasing the size of linkage blocks (Gouy et al. 2015). A quantitative trait locus (QTL) on a large linkage block would be difficult, if possible, to detect without a very large trait effect (Zhu et al. 2008). An association panel (diversity panel, DP), on the other hand, has more genetic variation and smaller linkage blocks.

*Saccharum* spp. and related genera have been collected into the World Collection of Sugarcane and Related Grasses (WCSRG) at the National Germplasm Repository of the USDA-ARS Subtropical Horticulture Research Station, Miami, FL. Various studies have described the genetic and phenotypic diversity in the WCSRG (Tai and Miller 2001, 2002; Nayak et al. 2014; Todd et al. 2014). A total of 342 *S. spontaneum* clones were used to develop a 75-clone core collection by Tai and Miller (2001). They used stratified random sampling over geographical origins, and principal component cluster groups to select the core collection. Tai and Miller (2002) also evaluated diversity through principal component analysis of sugar composition on 32 *S.*
officinarum, 30 S. barberi, 28 S. sinense, and 27 S. robustum. A DP consisting of 300 clones was developed based on simple sequence repeat (SSR)-based genetic diversity within the WCSRG (Nayak et al. 2014), which was phenotypically characterized for a number of agronomic traits (Todd et al. 2014). However, the DP did not include clones from outside of the world collection either in the basic breeding program at the USDA-ARS Sugarcane Research Unit in Houma, Louisiana or the elite cultivars / breeding lines used in Louisiana breeding programs.

Marker-trait association (MTA) studies on sugarcane have been conducted. Wei et al. (2006) used 1,068 AFLPs and 141 SSR markers to identify markers associated with resistance to four diseases using 154 cultivars, parents, and ancestors. They produced a population STRUCTURE (Q) matrix in STRUCTURE (Pritchard et al. 2000) for use in their models. They found 11 markers explained 59% of variance for resistance to smut, four markers explained 32% of variance for resistance to both pachymetra root rot and leaf scald, and five markers explained 26% of variance for resistance to Fiji leaf gall (Fiji disease virus). Debibakas et al. (2014) used a Q-K (kinship) model to evaluate 189 cultivars from 26 breeding programs with 3,949 AFLP and DArT markers for resistance to sugarcane yellow leaf virus. They found six independent markers accounting for 9-14% of the disease variance among the cultivars. Gouy et al. (2015) used Q and K combinations to assess both general linear models (GLM) and mixed linear models (MLM) for association of 13 different traits related to agro-morphology, sugar yield, bagasse content, and disease resistance with 3,327 AFLP, DArT, and SSR markers in 183 cultivars from 29 breeding programs. Eleven markers associated with three out of 13 traits were found using a Q-K model and false
discovery rate (FDR) corrections, and six out of 11 markers were linked to *Bru1*. Using Q-K analysis, Banerjee et al. (2015) identified 15 markers explaining 19-57% of the variance for various sucrose and yield attributes from a population consisting of 108 sugarcane genotypes from sub-tropical India genotyped with 989 SSR markers. Four SSR markers associated with red rot resistance were identified using Q-K analysis with 119 clones genotyped with 944 SSR alleles (Singh et al. 2016). Using DArT and TRAP markers in a multi-QTL model, 43 and 38 significant MTAs were identified for cane yield and sugar content, respectively in plant cane (Racedo et al. 2016). Siraree et al. (2017) identified 60 MTAs for 23 morphological and nine yield traits of sugarcane using a MLM with 1,546 SSR-generated dominant markers on a panel consisting of 92 sugarcane varieties from subtropical India. Twenty-one MTAs were found to be stable over three years explaining 16-37% of the phenotypic variance for nine yield traits. Very recently, Ukoskit et al. (2018) used Q-K analysis on a diversity panel consisting of 200 accessions and identified two genic SSRs associated with polarization (Pol) and sugar yield.

So far MTA studies have used with makers such as SSRs, ESTs, ALFPs, TRAPs, and DArTs, which generated up to 4,000 alleles (Debibakas et al. 2014; Gouy et al. 2015). Decreasing costs of next generation sequencing (NGS) technology makes genotyping by sequencing (GBS) ideal for improving marker density and coverage by generating millions of single nucleotide polymorphisms (SNPs) and insertions/deletions (InDels). The use of GBS to identify these structural variants offers the potential for much better coverage. Balsalobre et al. (2017) found 3,000 to 15,000 SNPs with around half being single dose markers, and Yang et al. (2017) used GBS to find 17,500 SNPs
among different *Saccharum* species. In the absence of a sugarcane draft genome, the genome of the related *Sorghum bicolor*, because of its microsynteny with sugarcane (Wang et al., 2010), has successfully been used as a reference to identify SNPs and InDels from GBS reads for use in linkage and QTL mapping (Balsalobre et al. 2017; Yang et al. 2017; Gutierrez et al. 2018).

To date, there is no report of a GWAS from sugarcane breeding programs in the United States. Therefore, the present study represents the first use of a GWAS to identify markers associated with cane yield-component (CYC) and sucrose traits for use in marker-assisted breeding toward the development of improved sugarcane cultivars in Louisiana, and to develop a sugarcane diversity panel for more robust future GWAS. In Chapter 2, genome-wide association mapping was conducted using different models with Q-K matrices in software TASSEL 5.1 and JMP Genomics 8.0. The objective was to compare TASSEL and JMP in conducting Q-K models using Q matrices from TASSEL, JMP, and STRUCTURE 2.3.4 (Pritchard et al. 2000), and K matrices from TASSEL and JMP for their use in GWAS to identify potential QTLs for Brix, TRS, and percent sucrose in a representative population comprising of 48 elite and historic sugarcane clones of Louisiana. Chapter 3 reports on the GWAS for identification of candidate markers associated with 10 CYC and sucrose related traits using of GBS-derived SNP and InDel markers. The study presented in Chapter 4 was conducted with an objective to develop an all-inclusive sugarcane diversity panel (SDP1) for use in GWAS for different agronomic traits.
1.1 REFERENCES


CHAPTER 2. A COMPARATIVE EVALUATION OF SOFTWARE AND METHODS FOR MARKER-TRAIT ANALYSIS IN SUGARCANE

2.1 INTRODUCTION

Sugarcane (*Saccharum* spp. hybrids) is an important food crop in the tropics and subtropics, which accounts for 80% of global sucrose production and 45% of sucrose production in United States, (Gouy et al. 2015; USDA-ERS 2017; Group Sucres et Denrées 2018). Additionally, it is estimated that the residual bagasse following sucrose extraction could produce 3,000 L/ha of bioethanol, while bagasse and sucrose combined could produce 9,950 L/ha of bioethanol (Somerville et al. 2010). In 2017, the U.S. produced 27.8 Mt on 344,000 ha in Louisiana, Florida, and Texas (USDA/NASS 2018). Of this, Louisiana produced 11.8 Mt on 168,000 ha, i.e., 42% of the total US crop. Sugarcane also has the highest annual crop value in Louisiana at $841 million in 2016 contributing ~$2.5 billion to the direct economy of the state (American Sugar Cane League 2017; LSU AgCenter 2017).

Modern sugarcane (2n=100-120) is a complex aneuployploid resulting from interspecific hybridization between *S. officinarum* (2n=8x=80; x=10) and *S. spontaneum* (2n=5x-16x=40-128; x=8) (D’Hont et al. 1998). Hybridization between a female *S. officinarum* and a male *S. spontaneum* allowed breeders to integrate vigor and disease resistance from *S. spontaneum* into the cultivated *S. officinarum* with minimal backcrossing due to female chromosomal restitution resulting in 2n+n=100-144 chromosomes (Bremer 1961; Lu et al. 1994; Gouy et al. 2013; Hoang et al. 2015). Cultivars are then derived after three to six generations of intercrossing following hybridization in order to stabilize the genome and improve sucrose traits (Bremer 1961; Piperidis et al. 2010). In modern cultivars, genome in situ hybridization results suggest
S. officinarum contributes 70 to 80% of the genome, S. spontaneum contributes 10 to 20%, and around 10% is recombinant chromosomes (D’Hont et al. 1996; Piperidis et al. 2010).

Sugarcane breeding efforts are directed at improving ratooning, sucrose yield, disease and insect resistance, biomass and fiber yield when used for bioenergy, and cold tolerance in subtropical regions such as Louisiana (Hale et al. 2009; Khan et al. 2013; Gouy et al. 2015). Sugarcane variety development takes around 12-15 years of selection and increase from the seedling stage to commercial variety release (Kimbeng and Cox 2003; Gouy et al. 2015). On an average, one commercial variety is released for every 250,000 seedlings (Cheavegatti-Gianotto et al. 2011). High numbers of progeny at early stages reduce selection efficiency due to space and time constraints such as lack of replications, seedling competition effects, and the high cost of individual clone selection (Kimbeng and Cox 2003). Molecular markers have the potential to increase the effectiveness of selection at these early stages, and to improve the selection response for traits that are difficult to evaluate phenotypically (Gouy et al. 2015; Gutierrez et al. 2018).

A genome wide association study (GWAS) has an advantage in sugarcane over traditional biparental techniques for finding molecular markers associated with trait(s) of interest due to the high amount of linkage disequilibrium (LD). The high LD is attributed to the relatively few generations between modern cultivars and the initial interspecific hybridization consisting of a limited number of clones (Debibakas et al. 2014). A biparental population with a limited number of recombination events could result in a quantitative trait locus (QTL) on a linkage block covering many centiMorgans (cM)
Detection of such QTL is possible for a trait that has a very large phenotypic effect (Zhu et al. 2008). A diversity panel used for GWAS, on the other hand, has comparative advantage with generally more genetic variation and smaller linkage blocks.

Marker-trait association (MTA) studies have been reported in sugarcane. Wei et al. (2006) used 1,068 AFLP and 141 SSR markers to identify markers associated with resistance to four diseases using 154 cultivars and their ancestral parents. Taking into account the population structure with Bayesian models (Q-models) for subsequent regression analysis, they found that 11 markers explained 59% of variance for resistance to smut, four markers explained 32% of variance for resistance to both pachymetra root rot and leaf scald, and five markers explained 26% of variance for resistance to Fiji leaf gall. Debibakas et al. (2014) evaluated 189 cultivars from 26 breeding programs with 3,949 AFLP and DArT markers for resistance to sugarcane yellow leaf virus. By using mixed linear models accounting for both population structure fixed effects and kinship random effects (Q-K model), they found six markers accounting for 9-14% of the disease variance among the cultivars. From a study involving 13 different traits, such as agro-morphology, sugar yield, bagasse content and disease resistance of 183 cultivars from 29 breeding programs and 3,327 AFLP, DArT, and SSR markers, Gouy et al. (2015) found 11 markers associated with three traits, and six out of 11 markers were linked to the brown rust major resistance gene Bru1. Using linkage disequilibrium (LD)-based MTA with a Q-K model, Banerjee et al. (2015) identified 15 markers explaining between 19 and 57% of the variance for various sucrose and yield attributes from a population consisting of 108 sugarcane genotypes from sub-tropical
India genotyped with 989 SSR markers. Four SSR markers associated with red rot resistance were identified from Q-K model with 119 clones genotyped with 944 SSR alleles (Singh et al. 2016). Using DArT and TRAP markers in a multi-QTL model, 43 and 38 significant MTA were identified for cane yield and sugar content, respectively in the plant cane crop of sugarcane (Racedo et al. 2016).

Yu et al. (2006) first proposed the use of the Q-K mixed-model in GWAS, which was subsequently incorporated into TASSEL (Bradbury et al. 2007) and JMP (SAS Institute, Cary NC). In the present study, genome-wide association mapping was conducted using different models with Q-K matrices in both TASSEL and JMP Genomics. The objective was to compare TASSEL and JMP in conducting Q-K models with a Q-matrix from TASSEL, JMP, and STRUCTURE (Pritchard et al. 2000), and K matrix from TASSEL and JMP for their use in GWAS to identify potential QTLs for Brix, TRS, and percent sucrose in a small population comprising of 48 elite and historic sugarcane clones of Louisiana.

2.2 MATERIALS AND METHODS

2.2.1 Plant material and phenotypic data

The present study consisted of 48 sugarcane clones (Table A.1) that included 43 elite breeding lines and released varieties bred at the Louisiana State University Agricultural Center (LSU AgCenter) Sugarcane Research Station, St. Gabriel, Louisiana (“L” or “LCP”), the USDA-Agricultural Research Station (ARS), Houma, Louisiana (“Ho” or “HoCP”), or the USDA-ARS, Canal Point, Florida (“CP”). Combined prefixes indicated collaboration with the second (i.e., “LCP” indicates collaboration with USDA-ARS, Canal
Point, Florida). The remaining five clones included the experimental clones US01-040 and US79-010, and the foreign commercial cultivars N27, NCo310, and TucCP77-42 that have been historically used in sugarcane breeding in Louisiana. These clones were a subset of those used by Avellaneda et al. (2018).

The 48 sugarcane clones were planted in 2010 and 2012 in 1.8 m plots in a randomized complete block design with two replications at the Louisiana State University Agricultural Center Sugar Research Station, St. Gabriel, LA. Six stalks from each plot were harvested in 2011 and 2013, respectively. Sucrose data on total soluble solids (Brix), percent sucrose, and theoretical recoverable sugar (TRS) were collected using a Spectracane Near Infrared System (Bruker Corporation, Billerica, MA).

### 2.2.3 Phenotypic data analysis

Phenotypic data were analyzed using a mixed linear model (MLM) as follows:

\[
p_{ijk} = \mu + g_i + s_j + r_{k(j)} + \varepsilon_{ijk},
\]

where \(p_{ijk}\) is the phenotypic trait, \(\mu\) is the overall mean, \(g_i\) is the \(i^{th}\) genotypic effect, \(s_j\) is the \(j^{th}\) site-year effect, \(r_{k(j)}\) is the \(k^{th}\) replication in the \(j^{th}\) site-year effect, and \(\varepsilon_{ijk}\) was the residual error for \(p_{ijk}\). For mean estimates, \(g\) was considered to be a fixed effect, while \(s\) and \(r\) were considered as random effects. The analysis was conducted using JMP Pro version 13.0.0 (SAS Institute, Cary, NC). Broad-sense heritability (\(H^2\)), as the degree of genetic determination, was estimated using the following equation where the coefficient of genotypic variation \(g\), \(s\), and \(r\) were all considered as random effects as genotypes are considered to be a random representation of Louisiana breeding clones, and mean estimates of the genotypes are not of interest for \(H^2\):
\[ H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_e^2}{n_{jk}}}, \]

where \( \sigma_g^2 \) is the genetic variance, \( \sigma_e^2 \) is the residual error variance, \( n_{jk} \) is the number of site-years by the number replicates (Benke et al. 2015; Racedo et al. 2016). JMP Genomics version 6.0 (SAS Institute, Cary NC) was also used to evaluate the correlation between TRS, Brix, and percent sucrose with Pearson’s product moment metrics.

2.2.2 DNA purification and genotyping

Leaf tissues were harvested from the 48 clones, placed directly on ice, and stored in -80 °C until DNA extraction. Genomic DNA was isolated from ~100 mg leaf tissues using the CTAB miniprep method as described previously (Parco et al. 2017). The DNA was checked for quality and quantity using a ND-100 spectrophotometer (Nanodrop Technologies Inc, Wilmington, DE).

In this study, 1,062 alleles were generated using 47 SSR and EST-SSR primer pairs, and 5 AFLP primer pairs (Table 2.1). Thirty-six SSR primer pairs came from the sugarcane microsatellite consortium (Cordeiro et al. 2000), and 11 EST-SSR primer pairs were designed from the sequences of genes differentially expressed in sugarcane under cold stress (Khan et al. 2013). The polymerase chain reaction (PCR) was performed in a 10 µL reaction mixture containing 1X reaction buffer, 2.5 mM MgCl\(_2\), 0.4 unit GoTaq Flexi DNA Polymerase, 200 µM dNTP mix (all PCR reagents from Promega, Madison, WI), 0.5µM each of forward and reverse primer, and 50 ng of genomic DNA. The thermal cycler program used was: (i) an initial denaturation at 95°C for 5 min; (ii)
Table 2.1. Number of alleles and polymorphic information content (PIC) obtained with 41 genomic and 11 EST-SSR markers for 48 sugarcane hybrids

<table>
<thead>
<tr>
<th>Marker Name</th>
<th>no. of alleles</th>
<th>PIC&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Marker Name</th>
<th>no. of alleles</th>
<th>PIC&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Genomic SSRs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 SMC1808LA</td>
<td>143 (4)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.139</td>
<td>37 ESSR_So1</td>
<td>66 (1)</td>
<td>0.178</td>
</tr>
<tr>
<td>2 SMC222CG</td>
<td>15</td>
<td>0.273</td>
<td>38 ESSR_So2</td>
<td>19</td>
<td>0.270</td>
</tr>
<tr>
<td>3 SMC361BS</td>
<td>17 (1)</td>
<td>0.204</td>
<td>39 ESSR_So3</td>
<td>4 (2)</td>
<td>0.133</td>
</tr>
<tr>
<td>4 SMC664CS</td>
<td>15 (1)</td>
<td>0.225</td>
<td>40 ESSR_So4</td>
<td>2 (1)</td>
<td>0.059</td>
</tr>
<tr>
<td>5 SMC851MS</td>
<td>29 (1)</td>
<td>0.298</td>
<td>41 ESSR_So5</td>
<td>7 (1)</td>
<td>0.196</td>
</tr>
<tr>
<td>6 SMC872CG</td>
<td>122 (4)</td>
<td>0.144</td>
<td>42 ESSR_So6</td>
<td>13 (2)</td>
<td>0.186</td>
</tr>
<tr>
<td>7 SMC257MS</td>
<td>46</td>
<td>0.126</td>
<td>43 ESSR_So7</td>
<td>6</td>
<td>0.127</td>
</tr>
<tr>
<td>8 SMC477CG</td>
<td>10 (2)</td>
<td>0.210</td>
<td>44 ESSR_So9</td>
<td>6 (4)</td>
<td>0.162</td>
</tr>
<tr>
<td>9 SMC749BS</td>
<td>29</td>
<td>0.212</td>
<td>45 ESSR_So10</td>
<td>7 (1)</td>
<td>0.262</td>
</tr>
<tr>
<td>10 SMC1604SA</td>
<td>82 (1)</td>
<td>0.218</td>
<td>46 ESSR_So11</td>
<td>7 (1)</td>
<td>0.180</td>
</tr>
<tr>
<td>11 SMC238MS</td>
<td>24</td>
<td>0.235</td>
<td>47 ESSR_So12</td>
<td>2 (1)</td>
<td>0.020</td>
</tr>
<tr>
<td>12 SMC787BS</td>
<td>7 (4)</td>
<td>0.149</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13 SMC1237FL</td>
<td>25</td>
<td>0.317</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14 SMC2024FL</td>
<td>17</td>
<td>0.211</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15 SMC432MS</td>
<td>19</td>
<td>0.187</td>
<td>A mSSCIR38</td>
<td>132</td>
<td>0.173</td>
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<tr>
<td>16 SMC2083FL</td>
<td>24 (3)</td>
<td>0.271</td>
<td>B mSSCIR65</td>
<td>11 (2)</td>
<td>0.222</td>
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<tr>
<td>17 SMC213MS</td>
<td>27 (1)</td>
<td>0.242</td>
<td>C mSSCIR72</td>
<td>11 (1)</td>
<td>0.181</td>
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<tr>
<td>18 SMC264CG</td>
<td>3 (1)</td>
<td>0.164</td>
<td>D mSSCIR60</td>
<td>2</td>
<td>0.170</td>
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<tr>
<td>19 SMC67CS</td>
<td>7</td>
<td>0.279</td>
<td>E mSSCIR13</td>
<td>8 (2)</td>
<td>0.201</td>
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<tr>
<td>20 SMC1527CL</td>
<td>8 (1)</td>
<td>0.356</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21 SMC1623CL</td>
<td>10 (1)</td>
<td>0.262</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22 SMC17AUQ</td>
<td>16 (2)</td>
<td>0.232</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>23 SMC1218LA</td>
<td>15</td>
<td>0.297</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24 SMC1732CL</td>
<td>4</td>
<td>0.361</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25 SMC07CUQ</td>
<td>7 (3)</td>
<td>0.156</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>26 SMC1814LA</td>
<td>8</td>
<td>0.273</td>
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<tr>
<td>27 SMC2042FL</td>
<td>2</td>
<td>0.079</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>28 SMC720BS</td>
<td>11 (2)</td>
<td>0.158</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 SMC1488CL</td>
<td>6</td>
<td>0.355</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 SMC662CS</td>
<td>5</td>
<td>0.341</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>31 SMC1232</td>
<td>15 (1)</td>
<td>0.277</td>
<td></td>
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<tr>
<td>32 SMC179S</td>
<td>9</td>
<td>0.286</td>
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<tr>
<td>33 SMC17CC</td>
<td>22</td>
<td>0.302</td>
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<td></td>
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<tr>
<td>34 SMC22DU</td>
<td>6 (1)</td>
<td>0.227</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35 SMC39BU</td>
<td>8 (2)</td>
<td>0.236</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>36 SMC805E</td>
<td>4 (3)</td>
<td>0.010</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Numbers in parentheses represent monomorphic alleles

<sup>b</sup> Average PIC
amplification for 36 cycles at 95°C for 45 s, 58°C for 45 s, 72°C for 1 min; and (iii) a final extension at 72°C for 5 min. Amplification products were electrophoresed in a 6% polyacrylamide gel using a high efficiency gel electrophoresis system (HEGS, Nihon Eido, Tokyo, Japan) according to the manufacturer’s instructions. The gel was stained with ethidium bromide, and then visualized and documented in a Kodak Gel Logic 200 documentation system (Kodak Inc, New Brokhaven, CT).

AFLP marker analysis followed Vos et al. (1995) with modification as described by Suman et al. (2011). Five-hundred ng of DNA were digested with EcoRI and Msel enzymes and the digested products were ligated with enzyme-specific adapters. The ligated products were preamplified with EcoRI+ A and Msel+ C primers. Two µl of 50x diluted preamplified products were amplified with primers having selective nucleotides at the 3’ end. Four microliters of the AFLP products were heat-denatured and resolved in a 6% denaturing polyacrylamide sequencing gel run with 0.5 TBE electrophoresis buffer in a Li-Cor 4300 DNA analyzer (Li-Cor, Lincoln, NE) as described earlier by Suman et al. (2011).

Amplified fragments (alleles) were manually scored as “1” (present, dominant) and “0” (absent). Alleles with a minor allele frequency less than 5% were discarded prior to downstream statistical analysis to reduce false similarity between clones due to shared absence of alleles while still capturing rare alleles.

2.2.4 Population structure

Population structure was determined using DARwin software 6.0.12 (Perrier and Jacquemoud-Collet 2006), STRUCTURE 2.3.4 (Pritchard et al. 2000), and JMP Genomics. In DARwin, a present / absent dissimilarity matrix was calculated using Dice
dissimilarity scores (Perrier et al. 2003). Weighted neighbor-joining algorithms were used to construct a phylogenetic tree, which was evaluated for robustness with 1,000 bootstrap repetitions. Polymorphism information content (PIC) value for each SSR marker was calculated by averaging the PIC of each allele. The allele PIC was calculated using the formula:

$$PIC = 1 - \sum f_i^2,$$

where $f_i^2$ is the frequency of the $i$th allele presence or absence (Weir 1990).

In STRUCTURE 2.3.4, models were run for the number of populations $K = 2$ through 10, and $K = 3$ was selected as per documentation. The Markov chain Monte Carlo (MCMC) methods were run for 100,000 iterations of burn-in and 100,000 subsequent iterations were used for model parameter estimation. Five model runs were used to check for non-symmetric modes. An average of the five runs was used as the final result.

Principal coordinate analysis (PCoA) was performed using a PCA analysis module in JMP Pro. The calculations used single-value decomposition, i.e., JMP Pro’s wide estimation method.

2.2.5 Association mapping

The association between markers and traits was evaluated using a Q-K analysis of the model (Yu et al. 2005). The MLM from the phenotypic analysis using JMP Pro was used to calculate estimates of the phenotypic trait for use as the dependent variable. Both JMP Genomics and TASSEL 5.1 (http://www.maizegenetics.net) platforms were used to conduct the Q-K analyses. An identity by state (IBS) distance
matrix (K) from each program was paired with four population STRUCTURE (Q) matrices including one from STRUCTURE, TASSEL using principal component analysis (PCA) of covariances (default), JMP using PCA of correlations (default), and JMP using multidimensional scaling (MDS). The \(-\log(P)\) from JMP Genomics and the p-value from TASSEL were both converted to \(-\log_{10}(P)\). \(R^2\) from each software was obtained, and the rank was based on \(R^2\) where the marker with the largest \(R^2\) was given a rank of 1 for each model. Markers were sorted by their rank in the overall average of all 16 models.

2.3 RESULTS

2.3.1 Phenotypic data analysis

The phenotypic data (Table A.1) were analyzed using an MLM to obtain estimates for association mapping. Data summary is presented in Table 2.2. TRS, Brix, and percent sucrose were found to be normally distributed and highly correlated, as expected. TRS and Brix were 0.93 correlated, while correlations between Brix and percent sucrose, and between TRS and percent sucrose were 0.96 and 1.00,

<table>
<thead>
<tr>
<th>Trait</th>
<th>Range</th>
<th>Mean ± standard error</th>
<th>(\sigma_g^2)</th>
<th>(H^2)</th>
<th>(CV_g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TRS Kg/t</td>
<td>min</td>
<td>max</td>
<td>mean</td>
<td>error</td>
<td></td>
</tr>
<tr>
<td>Brix %</td>
<td>15.16</td>
<td>22.01</td>
<td>19.57 ± 0.11</td>
<td>1.04**</td>
<td>0.87</td>
</tr>
<tr>
<td>Sucrose %</td>
<td>10.95</td>
<td>19.30</td>
<td>16.44 ± 0.12</td>
<td>1.52**</td>
<td>0.87</td>
</tr>
</tbody>
</table>

** Significant at P-value < 0.0001

\(\sigma_g^2\): Genotypic variance
\(H^2\): The degree of genetic determination
\(CV_g\): % coefficient of genetic variation
TRS, Total recoverable sugar
respectively. TRS ranged from 70.41 to 141.00 Kg/t with a mean of 115.71 Kg/t. Brix ranged from 15.16 to 22.01 % with a mean of 19.57 %. Percent sucrose ranged from 10.95 to 19.30 % with a mean of 16.44 %. For each trait, the genotype effect was significant (p-value < 0.0001). Broad-sense heritability was high ranging from 0.83 to 0.85 for TRS and Brix, respectively. Comparing genotypic variance Brix had the least at 5.2 % followed by percent sucrose at 7.5%, and TRS had the most at 8.7%.

2.3.2 Population structure

Clustering of the 48 clones was evident in the neighbor-joining tree from the dice dissimilarity matrix (Figure 2.1). The majority of the clones selected in Canal Point, FL grouped together, which was close to the subcluster with those selected in Houma, LA. The most robust subcluster consisted of the historic and experimental clones grouped together in 96 percent of the bootstraps. They were, however, fairly distinct from each other as well as from the rest of the clones. Clones from the LSU AgCenter did not show a single subcluster; rather formed mini-subclusters with one or two clones from either Houma or Canal Point, FL. Expectedly, a few LSU AgCenter clones were close to the subcluster with historic clones.

A clear population structure was observed with sub-populations based on the breeding program where a clone was selected (Figure 2.2). The STRUCTURE analysis and PCA (Figure 2.3) both produced the same results. In both, there was a tight clustering of clones from Canal Point, FL and Houma, LA together with the clones L01-281, L01-283, L01-299, L03-371, and L05-466. In the PCA, there were sub-clusters of the Canal Point, FL clones, the Houma, LA clones, and the five LSU AgCenter clones.
**Figure 2.1.** Phylogenetic tree of the sugarcane clones from three United States breeding programs, experimental, and historic clones. Neighbor-joining tree of a Dice dissimilarity matrix from 48 clones using 1,062 SSR and AFLP alleles.

There was also an independent mini-subgroup of the rest of the Louisiana clones, and historic/experimental clones.
Figure 2.2. Population structure of 48 sugarcane clones using 1,062 SSR and AFLP alleles for three United States breeding programs, experimental, and historic clones. Values in the vertical axis represent the likelihood in percent of an individual belonging to one of the three colored subpopulations.

2.3.3 Marker-trait association

Eight models each were run in TASSEL and JMP Genomics with comparisons being made between the two software, the two IBS-derived K-matrices from TASSEL and JMP Genomics, and the four Q-matrices from STRUCTURE, TASSEL-derived PCA (on covariance), JMP Genomics-derived PCA (on correlation), and JMP Genomics MDS. Models were averaged in each case. An average of the eight models run by the given software was used for the comparison between the software (Table 2.3). The results showed that there was very little difference between the two platforms, although there were minor differences in the rank particularly for the markers with higher order ranking. The \(-\log_{10}(P)\) were nearly the same, and more importantly, the top nine markers
Figure 2.3. Principal coordinate analysis of 48 sugarcane clones using 1,062 SSR alleles for three United States breeding programs, experimental, and historic clones.

associated with each trait after rounding were the same. However, using TASSEL, the $R^2$ value was 0.01-0.02 units less than when using JMP Genomics. The markers 1-66, 1-25, and 15-5 showed the most significant associations with the traits. These markers were the most consistent across models explaining on average 15-20% of the variance
Table 2.3. Comparison between averages of eight models for TASSEL and JMP Genomics. Markers are shown where at least one of the 16 model runs had a \(-\log_{10}(P) > 2\) resulting in the top nine markers by overall rank for Brix, percent sucrose, and total recoverable sugar (TRS) in sugarcane.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Markera</th>
<th>Marker effect (+ / -)</th>
<th>TASSEL Rank (avg.)</th>
<th>(-\log_{10}(P))</th>
<th>R²</th>
<th>JMP Rank (avg.)</th>
<th>(-\log_{10}(P))</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brix</td>
<td>15-5</td>
<td>-</td>
<td>1.75</td>
<td>2.31</td>
<td>0.18</td>
<td>1.75</td>
<td>2.31</td>
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<td>55.625</td>
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</tbody>
</table>

a The marker name refers to the marker number followed by the allele number in Table 2.1

for sucrose traits. Marker 1-66 explained the most variance with 19% for TASSEL models, and 20% for JMP Genomics models. All had a \(-\log_{10}(P)\) greater than two (P-value < 0.01).
The IBS K-matrices were very similar between TASSEL and JMP Genomics (Table 2.4). An average over the eight models with each K-matrix–four Q-matrices for each K-matrix in each software–was used for comparison. There was very little

Table 2.4. Comparison between averages of models run using the TASSEL K matrix and the JMP Genomics K matrix. Markers are shown where at least one of the 16 model runs had a $-\log_{10}(P) > 2$ resulting in the top nine markers by overall rank for BRIX, percent sucrose, and total recoverable sugar (TRS) in sugarcane.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Marker&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Marker effect (+ / -)</th>
<th>Rank (avg.)</th>
<th>$-\log_{10}(P)$</th>
<th>$R^2$</th>
<th>Rank (avg.)</th>
<th>$-\log_{10}(P)$</th>
<th>$R^2$</th>
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</tr>
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<td>0.09</td>
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</table>

<sup>a</sup>The marker name refers to the marker number followed by the allele number in Table 2.1
difference between the results obtained with the two matrices. Again, there were some minor differences in the rank of the markers that were particularly of the higher order in the ranking. The \(-\log_{10}(P)\) were nearly the same, but with slightly more variation than in the software comparison. Also, with this comparison the \(R^2\) values were very similar. The markers 1-66, 1-25, and 15-5 were again the highest ranked for marker-trait associations. Marker 1-48 tied third with 15-5 for TRS using the JMP Genomics K-matrix.

On the other hand, significant variation was observed between the four Q-matrices from STRUCTURE, TASSEL PCA (on covariance), JMP Genomics PCA (on correlation), and JMP Genomics MDS (Table 2.5). Models were averaged over both the K-matrices and the two software with four runs for each Q-matrix. At least two markers out of 1-66, 1-25, and 15-5 were in the top three by ranking for all models. All three of these markers were top-ranked for the JMP Genomics PCA and MDS Q-matrices with the exception of TRS using the MDS matrix where marker 15-5 was ranked 4\textsuperscript{th}. Except for two instances, the markers 1-66, 1-25, and 15-5 had \(-\log_{10}(P)\) values greater than two; marker 1-25 had a \(-\log_{10}(P)\) value of 1.95 using the STRUCTURE Q-matrix and marker 15-5 had a \(-\log_{10}(P)\) value of 1.90 using the TASSEL PCA Q-matrix. With the Q-matrices, markers 1-66, 1-25, and 15-5 had \(R^2\) values ranging from 0.13 in Brix for marker 1-25 to 0.27 also in Brix for marker 1-66. The remaining markers displayed high variation in their ranking and \(R^2\) values. For instance, marker 7-87 in percent sucrose had a \(-\log_{10}(P)\) value of 0.99 and an \(R^2\) value of 0.06 using the STRUCTURE Q-Matrix, while it had a \(-\log_{10}(P)\) value of 2.17 and an \(R^2\) value of 0.16 using the JMP MDS Q-matrix.
Table 2.5. Comparison between averages of models run using the STRUCTURE, TASSEL PCA, JMP PCA, and JMP Genomics MDS Q matrices. Markers are shown where at least one of the 16 model runs had a $-\log_{10}(P) > 2$ resulting in the top nine markers by overall rank for BRIX, percent sucrose, and total recoverable sugar (TRS) in sugarcane.

<table>
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<th>Trait</th>
<th>Markera</th>
<th>Marker effect (+ / -)</th>
<th>STRUCTURE Q</th>
<th>TASSEL PCA Q</th>
<th>JMP PCA Q</th>
<th>JMP MDS Q</th>
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<td>Rank (avg.)</td>
<td>$-\log_{10}(P)$</td>
<td>R²</td>
<td>Rank (avg.)</td>
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</tr>
<tr>
<td>Sucrose</td>
<td>14-35</td>
<td>+</td>
<td>5.5</td>
<td>1.88</td>
<td>0.13</td>
<td>131.5</td>
</tr>
<tr>
<td>TRS</td>
<td>1-66</td>
<td>-</td>
<td>1</td>
<td>2.29</td>
<td>0.16</td>
<td>3</td>
</tr>
<tr>
<td>TRS</td>
<td>1-25</td>
<td>-</td>
<td>4</td>
<td>2.04</td>
<td>0.14</td>
<td>2</td>
</tr>
<tr>
<td>TRS</td>
<td>15-5</td>
<td>-</td>
<td>3</td>
<td>2.04</td>
<td>0.14</td>
<td>5</td>
</tr>
<tr>
<td>TRS</td>
<td>1-48</td>
<td>-</td>
<td>8</td>
<td>1.75</td>
<td>0.12</td>
<td>1</td>
</tr>
<tr>
<td>TRS</td>
<td>7-87</td>
<td>-</td>
<td>102</td>
<td>1.10</td>
<td>0.06</td>
<td>40</td>
</tr>
<tr>
<td>TRS</td>
<td>1-28</td>
<td>-</td>
<td>73.5</td>
<td>1.26</td>
<td>0.08</td>
<td>9.5</td>
</tr>
<tr>
<td>TRS</td>
<td>1-C</td>
<td>+</td>
<td>5</td>
<td>1.91</td>
<td>0.13</td>
<td>41</td>
</tr>
<tr>
<td>TRS</td>
<td>7-38</td>
<td>-</td>
<td>52</td>
<td>1.41</td>
<td>0.09</td>
<td>4</td>
</tr>
<tr>
<td>TRS</td>
<td>14-35</td>
<td>+</td>
<td>2</td>
<td>2.04</td>
<td>0.14</td>
<td>90</td>
</tr>
</tbody>
</table>

a The marker name refers to the marker number followed by the allele number in Table 2.1
2.4 DISCUSSION

Model comparison analysis showed that TASSEL and JMP Genomics yielded very similar results. With care, results from one could be replicated in the other, as the software directed the user’s approach differently through default settings. A difference without user option occurs in the handling of the K-matrix. TASSEL uses a relationship matrix with 1’s on the diagonal, and JMP uses the square root matrix (0’s on the diagonal). In this study, the difference between K-matrix led to some rounding error, which can be attributed to some of the differences between running the JMP Genomics IBS K-matrix in TASSEL (squared square-root matrix) and running the TASSEL IBS K-matrix in JMP Genomics.

The main source of difference in the comparison between software was due to the handling of missing data. TASSEL requires the missing data to be imputed, and JMP allows the imputation of missing data, but will complete the analysis without it. In this study, the most significant difference was the handling of missing data in TASSEL, which had a denominator degree of freedom of 48 for the individual marker analysis, whereas in JMP Genomics the denominator degree of freedom was 43. This resulted in TASSEL having lower $R^2$ values than JMP Genomics. Missing data handling also partially contributed to the slight difference in the rank and -$\log_{10}(P)$ values between the software.

Another difference between TASSEL and JMP Genomics was in the calculation PCA. TASSEL gives a very clear check box allowing the user to choose to conduct the analysis using either covariance or correlation. JMP Genomics does not provide such option. JMP Genomics does not document what method it uses for PCA, although they
appear to be based on correlation. JMP Genomics does, however, allow the user to correct for population stratification using the EIGENSTRAT method (Price et al. 2006).

In conclusion, TASSEL and JMP Genomics were compared by running eight different models in each associating an IBS K-matrix from each and four Q matrices from STRUCTURE, TASSEL using PCA of covariances, JMP using PCA of correlations, and JMP using multidimensional scaling (MDS). The software differed mainly in rounding to JMP Genomics using a square root matrix for kinship, handling of missing data, and options for computing PCA. Validation of the marker-trait associations obtained from the present study in a larger population with high density marker coverage with minimal missing data will provide a clear picture of the comparative advantage of one model over the other.

2.5 REFERENCES


CHAPTER 3. GENOME-WIDE ASSOCIATION STUDY TO IDENTIFY MARKERS ASSOCIATED WITH CANE YIELD-COMPONENT AND SUCROSE TRAITS IN LOUISIANA SUGARCANE

3.1 INTRODUCTION

Sugarcane (*Saccharum* spp. hybrids) accounts for 45% of sucrose production in United States, and 80% of sucrose production globally (Gouy et al. 2015; USDA-ERS 2017; Group Sucres et Denrées 2018). In addition to sucrose production, the biproduct bagasse is often used as a fuel to produce steam or electricity for running the mills, processing the sugarcane, and for the sale of excess electricity (Webber III et al. 2016). Sugarcane is an economically significant crop in Louisiana with an annual value of $841 million, higher than any other crop contributing ~$2.5 billion to the direct economy of the state (American Sugar Cane League 2017; LSU AgCenter 2017). In 2017, Louisiana produced 11.8 Mt of cane on 168,000 ha, i.e., 42% of the total 27.8 Mt on 344,000 ha produced in the U.S., with Florida and Texas together contributing the other 58% (USDA/NASS 2018). The bagasse produced is estimated at 3 Mt per year in Louisiana (Webber III et al. 2016).

Modern sugarcane (2n=100-120) is a complex aneuployploid resulting from interspecific hybridization between *S. officinarum* (2n=8x=80; x=10) and *S. spontaneum* (2n=5x-16x=40-128; x=8) (D’Hont et al. 1998; Moore et al. 2013; Aitken et al. 2014). Breeders made hybridization between a female *S. officinarum* and a male *S. spontaneum* to integrate plant vigor and disease resistance from *S. spontaneum* into the cultivated *S. officinarum* (Bremer 1961; Lu et al. 1994; Gouy et al. 2013; Hoang et al. 2015). This hybridization requires minimal backcrossing due to female chromosomal restitution resulting in 2n+n=100-144 chromosomes. Three to six generations of
intercrossing following hybridization are needed to stabilize the genome and reestablish sucrose traits (Bremer 1961; Piperidis et al. 2010). Genome in situ hybridization suggested that *S. officinarum* contributes 70 to 80%, *S. spontaneum* contributes 10 to 20% to the genome in modern cultivars, and around 10% are recombinant chromosomes (D’Hont et al. 1996; Piperidis et al. 2010; Moore et al. 2013).

Sugarcane breeding efforts are currently focused on enhancing sucrose yield, disease and insect resistance, ratooning ability, biomass and fiber yield for bioenergy, and cold tolerance (Hale et al. 2009; Khan et al. 2013; Gouy et al. 2015). From seedling stage to commercial variety release, sugarcane variety development takes an estimated 12-15 years of selection (Kimbeng and Cox 2003; Gouy et al. 2015); with an average of one commercial variety being released for every 250,000 seedlings (Cheavegatti-Gianotto et al. 2011). High numbers at early stages reduce selection efficiency due to space and time constraints such as lack of replications, seedling competition effects, and the high cost of individual clone selection (Kimbeng and Cox 2003). Early stage selection efficiency may be enhanced by the use of molecular markers, which may also increase the selection response of traits that are difficult to select phenotypically (Gouy et al. 2015).

The high amount of linkage disequilibrium (LD) in sugarcane may give genome wide association studies (GWAS) an advantage in sugarcane over traditional biparental techniques for the identification of molecular markers governing traits of economic importance. The high LD can be attributed to the limited number of progenitor clones used during the nobilization process and to the relatively few generations between modern cultivars (Debibakas et al. 2014). A limited number of recombination events are
present in a biparental population potentially increasing the size of linkage blocks (Gouy et al. 2015). A quantitative trait locus (QTL) on a large linkage block would be difficult, if possible, to detect without a very large trait effect (Zhu et al. 2008). An association-panel generally has more genetic variation and smaller linkage blocks.

A few marker-trait associations (MTA) from GWAS have been reported in sugarcane. Wei et al. (2006) used a model corrected for population structure (Q) to identify potential markers for resistance to smut, Pachymetra root rot, leaf scald, and Fiji leaf gall. Debibakas et al. (2014) used a Q-K (population structure-kinship) mixed linear model (MLM) to identify six independent markers for sugarcane yellow leaf virus. Gouy et al. (2015) used Q and K combinations to assess both general linear models (GLM) and MLMs for MTA in 13 traits related to agro-morphology, sugar yield, bagasse content, and disease resistance. Using Q-K analysis, Banerjee et al. (2015) evaluated MTA in various sucrose and yield traits. In another study, four SSR markers associated with red rot resistance were identified using Q-K analysis (Singh et al. 2016). Using a Q corrected model, 43 and 38 significant MTA were identified for cane yield and sugar content, respectively by Racedo et al. (2016). Recently, Ukoskit et al. (2018) used MLM on a diversity panel consisting of 200 accessions and identified two genic SSRs associated with polarization (Pol) and sugar yield.

The sugarcane genome size (10 Gb) and complexity have made coverage and saturation with markers such as SSRs, EST-derived AFLPs, and DArTs difficult (Wang et al. 2010; Gutierrez et al. 2018). Decreasing costs of next generation sequencing (NGS) technology makes genotyping by sequencing (GBS) ideal for improving marker density and coverage by generating millions of single nucleotide polymorphisms (SNPs).
and insertions/deletions (InDels). In the absence of a sugarcane draft genome, the
genome of the related Sorghum bicolor, because of its microsynteny with sugarcane
(Wang et al., 2010), has successfully been used as a reference to identify SNPs and
InDels from GBS reads for use in linkage and QTL mapping (Balsalobre et al. 2017;
Yang et al. 2017; Gutierrez et al. 2018). The present study is the first study to use GBS-
derived SNP and InDel markers for MTA. It reports the identification of candidate
markers associated with 10 cane yield-component (CYC) and sucrose related traits.

3.2 MATERIALS AND METHODS

3.2.1 Plant materials and phenotypic data

This study consisted of 97 elite and historic sugarcane clones from the Louisiana
sugarcane breeding program (Table A.2). Ninety-two were Louisiana sugarcane clones
which included elite breeding lines and released varieties. These were produced at the
Louisiana State University Agricultural Center (“L” or “LCP”) and at the USDA-
Agricultural Research Station (ARS) in Houma, Louisiana (“Ho” or “HoCP”).
Designations with “CP” indicate the crosses were made at the USDA-ARS in Canal
Point, Florida. The hybrids US 01-040 and US 79-010 are experimental clones, and N
27, NCo 310, and POJ 234 are foreign commercial cultivars used in sugarcane
breeding in Louisiana. These clones were previously used by Avellaneda et al. (2018).

The 97 sugarcane clones were planted in 2015 and 2016 in both heavy soil and
light soil. Heavy soil consisted of both Commerce silty clay loam and Sharkey clay. Light
soil was Commerce silt loam. The clones were planted in 3 m long plots with 1.8 m row
spacing. The plantings had at least 5 plots each of HoCP98-540 and L01-299 as checks
to account for in-field variation.

Data was collected in 2016 from two locations of plant cane, and in 2017 from two locations of plant cane and two locations of first ratoon crops. Stalk counts, stalk heights, and stalk diameters were measured in field prior to harvesting. Samples were later harvested from each plot to obtain stalk weights, and sucrose data. The sucrose data were collected using a Spectracane near infrared spectroscopic system (Bruker Corporation, Billerica, MA, USA) for theoretical recoverable sugars (TRS), total soluble solids (Brix), percent sucrose, fiber, Pol, and juice purity metrics.

3.2.2 Phenotypic data analysis

In-field variation was modeled by a simple linear regression on the data of the HoCP98-540 and L01-299 checks along the rows. The regression line was used to adjust observed values proportionate to their location along the rows when the checks were significant in the model. Both modeling by nearest-neighbor and modeling variation between rows were not used due to the size of random error in proportion to the in-field variation, and to the study dimensions (two to three rows with 30 to 50 plots in each).

Phenotypic data were modeled using a mixed linear model (MLM) as follows:

\[ t_{ijkl} = \mu + g_i + p_{j(i)} + s_k + y_l + \epsilon_{ijkl}, \]

where \( t_{ijkl} \) is the phenotypic trait, \( \mu \) is the overall mean, \( g_i \) is the \( i^{th} \) genotypic effect, \( p_j \) is the \( j^{th} \) cane-crop (plant cane or first ratoon crop) of the \( i^{th} \) genotypic effect, \( s_k \) is the \( k^{th} \) soil type, \( y_l \) is the \( l^{th} \) year, and \( \epsilon_{ijkl} \) was the residual error for \( t_{ijkl} \). For estimating means, \( g \) and \( p \) were considered to be fixed effects, while \( s \) and \( y \) were considered to be random effects. The analysis was conducted using JMP Pro version 14.0.0 (SAS Institute, Cary
NC). This model was also evaluated for levels of cane-crop independently (i.e. for plant cane and first ratoon crop estimates), and for soil type in plant cane independently (i.e. heavy soil and light soil estimates). Soil type models were within plant cane only to avoid weighting estimates by a single year of ratoon crops and for ease of interpretation.

Broad-sense heritability ($H^2$) and the coefficient of genotypic ($CV_g$) variation were measured in plant cane with g, s, and y all being considered as random effects as genotypes are considered to be a random representation of Louisiana breeding clones, and mean estimates of the clones are not of interest for $H^2$. Broad-sense heritability was estimated with the equation:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2/n_{kl}},$$

where $\sigma_g^2$ is the genetic variance, $\sigma_e^2$ is the residual error variance, and $n_{kl}$ is the number of soil types by the number of years (Benke et al. 2015; Racedo et al. 2016).

### 3.2.3 DNA purification and genotyping

Genomic DNA was isolated from ~100 mg leaf tissues of the sugarcane clones using the CTAB miniprep method as described previously (Parco et al. 2014). The DNA was checked for quality and quantity using a ND-100 spectrophotometer (Nanodrop Technologies Inc, Wilmington, DE). Then, 500 ng of DNA from each clone was used for GBS library preparation as per Elshire et al. (2011). Briefly, the DNA was restricted by a rare cutting endonuclease *PstI* enzyme and ligated with adapters for barcoding. This barcoded DNA was then pooled and 96-plex 100 bp single-end sequenced in a single flow cell on an Illumina HiSeq2500 platform.
The sequence reads were cleaned by removing the adapter and restriction enzyme remnants and then filtered to those with a Phred quality score ≥ 20. Two reference-based SNP callers, GBS TASSEL (Glaubitz et al. 2014), and Samtools (Li et al. 2009) were used as described earlier (Gutierrez et al. 2018). The *Sorghum bicolor* genome (v.3.0) was used as the reference. Uniquely mapped reads were used for variant calling. Samtools pipeline was used as per the default parameters. SNPs and InDels common to both software tools were filtered further by removing those not occurring in at least 50% of the clones. In total 6,299 SNPs and 235 InDels were used in subsequent analyses.

### 3.2.4 Population structure

Population structure was evaluated using STRUCTURE 2.3.4 (Pritchard et al. 2000), and JMP Genomics 9.0. In STRUCTURE, the number of populations, $K$, was expected to be at least 2. Models were run for $K = 2$ through 10, and $K = 3$ was selected as per documentation. The Markov chain Monte Carlo were run for 25,000 iterations of burn-in (the model converged around 10,000 iterations) and 25,000 subsequent iterations were used for model parameter estimation. Ten model runs were used to check for non-symmetric modes, and none were found. An average of the ten runs was used for the final result. JMP Genomics was used to build an identity by state (IBS) matrix and dendrogram, and for principal coordinate analysis (PCoA). PCoA calculations used single-value decomposition, i.e., the wide estimation method in JMP.
3.2.5 Association mapping

The association between markers and traits was evaluated using a Q-K analysis as described in Yu et al. (2005). JMP Genomics was used to impute missing SNPs and conduct the Q-K analyses. The IBS distance matrix from JMP Genomics was used as the K-matrix, and the matrix from STRUCTURE was used as the Q-matrix. The MLM from the phenotypic analysis using JMP Pro was used to calculate estimates of the phenotypic traits for use as the dependent variables. Analysis was run on five models of the phenotypic traits, the full model, plant cane, first ratoon, plant cane in heavy soil, and plant cane in light soil. The P-value cut-off was set at 0.05, i.e., \(-\log(P)\) of 3.

3.3 RESULTS

3.3.1 Phenotypic data analysis

The phenotypic data (Table A.2) were evaluated using an MLM to obtain estimates for association mapping. Data are summarized in Table 3.1. All traits were found to be normally distributed. Sucrose yield averaged 8.84 t/ha, but ranged from 1.96 to 19.00, with a significant genetic variance (P < 0.001) with a coefficient of genetic variation (CVg) of 21.7%, and an H² of 0.72.

The average values for stalk count, height, diameter and weight were 6.75 stalks/m², 266 cm, 24.20 mm and 1.08 kg, respectively. The genetic variance was significant (P< 0.001) for all CYC traits. Broad-sense heritability for these traits ranged from 0.52 for stalk height to 0.82 for stalk weight. There was a broad range of genetic variation with CVg ranging from 4.3% for stalk height to 17.9% for stalk count.
Table 3.1. Descriptive statistics and broad-sense heritability (plant cane) for the phenotypic traits in sugarcane.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Range</th>
<th>Mean ± standard error</th>
<th>$\sigma_g^2$</th>
<th>$H^2$</th>
<th>$CV_g$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sucrose yield</td>
<td>t/ha</td>
<td>1.96 - 19.00</td>
<td>8.84 ± 1.39</td>
<td>3.67**</td>
<td>0.72</td>
</tr>
<tr>
<td>Stalk count</td>
<td>stalk/m²</td>
<td>1.21 - 16.03</td>
<td>6.75 ± 1.13</td>
<td>1.39**</td>
<td>0.67</td>
</tr>
<tr>
<td>Stalk height</td>
<td>cm</td>
<td>158 - 345</td>
<td>265.93 ± 24.31</td>
<td>132.97**</td>
<td>0.52</td>
</tr>
<tr>
<td>Stalk diameter</td>
<td>mm</td>
<td>18 - 33</td>
<td>24.20 ± 1.18</td>
<td>2.62**</td>
<td>0.77</td>
</tr>
<tr>
<td>Stalk weight</td>
<td>Kg</td>
<td>0.43 - 1.92</td>
<td>1.08 ± 0.097</td>
<td>0.033**</td>
<td>0.82</td>
</tr>
<tr>
<td>TRS</td>
<td>Kg/t</td>
<td>73.06 - 149.15</td>
<td>124.62 ± 9.08</td>
<td>55.47**</td>
<td>0.79</td>
</tr>
<tr>
<td>Brix</td>
<td>%</td>
<td>14.97 - 22.75</td>
<td>20.02 ± 1.04</td>
<td>0.52**</td>
<td>0.78</td>
</tr>
<tr>
<td>Percent sucrose</td>
<td>%</td>
<td>11.14 - 20.48</td>
<td>17.41 ± 1.14</td>
<td>0.80**</td>
<td>0.80</td>
</tr>
<tr>
<td>Fiber</td>
<td>%</td>
<td>9.00 - 15.92</td>
<td>12.35 ± 0.47</td>
<td>0.82**</td>
<td>0.88</td>
</tr>
<tr>
<td>Pol</td>
<td>%</td>
<td>46.94 - 89.63</td>
<td>75.20 ± 5.30</td>
<td>16.85**</td>
<td>0.77</td>
</tr>
<tr>
<td>Purity</td>
<td>%</td>
<td>71.62 - 92.85</td>
<td>85.30 ± 1.34</td>
<td>2.67**</td>
<td>0.73</td>
</tr>
</tbody>
</table>

** Significant at P-value < 0.001

$\sigma_g^2$, Genotypic variance

$H^2$, The degree of genetic determination

$CV_g$, % coefficient of genetic variation

TRS, Total recoverable sugar

The average values for TRS, Brix, percent sucrose, fiber, Pol, and purity were 124.62 Kg/t, and 20.02, 17.41, 12.35, 75.20, and 85.30%, respectively. The genetic variance for the sucrose traits was significant for all traits with all P-values < 0.001. Broad-sense heritability for these ranged from 0.73 for purity to 0.88 for fiber. There was less genetic variation than for the CYC traits with the $CV_g$ ranging from 1.9% for purity to 7.3% for fiber.

CYC traits had some correlation between traits, and sucrose traits had strong correlation between all traits except fiber (Table 3.2). For CYC traits, stalk count and height, height and weight, and diameter and weight were strongly correlated (P-value < 0.0001) with correlation values of 0.388, 0.439, and 0.802, respectively. Stalk count and
Table 3.2. Pearson’s product moment correlations between cane yield-component and sucrose traits in sugarcane.

<table>
<thead>
<tr>
<th></th>
<th>Count</th>
<th>Height</th>
<th>Diameter</th>
<th>Weight</th>
<th>TRS</th>
<th>Brix</th>
<th>Sucrose</th>
<th>Fiber</th>
<th>Pol</th>
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<tr>
<td>Count</td>
<td>1.000</td>
<td></td>
<td></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>0.388**</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>[0.20 – 0.55]a</td>
<td></td>
<td>[-0.49 – -0.14]</td>
<td>[-0.15 – 024]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diameter</td>
<td>-0.328*</td>
<td>0.047</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>[-0.49 – -0.14]</td>
<td>[-0.15 – 024]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight</td>
<td>-0.161</td>
<td>0.439**</td>
<td>0.802**</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>[-0.35 – 0.04]</td>
<td>[0.26 – 0.59]</td>
<td>[0.72 – 0.86]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TRS</td>
<td>0.018</td>
<td>-0.031</td>
<td>0.007</td>
<td>0.0004</td>
<td>1.000</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>[-0.18 – -0.22]</td>
<td>[-0.23 – -0.17]</td>
<td>[-0.19 – -0.21]</td>
<td>[-0.20 – -0.20]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brix</td>
<td>-0.019</td>
<td>-0.068</td>
<td>0.013</td>
<td>0.015</td>
<td>0.950**</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>[-0.22 – -0.18]</td>
<td>[-0.26 – -0.13]</td>
<td>[-0.19 – -0.21]</td>
<td>[-0.19 – -0.21]</td>
<td>[0.93 – 0.97]</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sucrose</td>
<td>0.009</td>
<td>-0.040</td>
<td>0.009</td>
<td>0.004</td>
<td>0.997**</td>
<td>0.971**</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>[-0.19 – -0.21]</td>
<td>[-0.24 – -0.16]</td>
<td>[-0.19 – -0.21]</td>
<td>[-0.20 – -0.20]</td>
<td>[0.996 – 0.998]</td>
<td>[0.96 – 0.98]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fiber</td>
<td>0.317**</td>
<td>0.373*</td>
<td>-0.273*</td>
<td>-0.015</td>
<td>-0.047</td>
<td>-0.016</td>
<td>-0.040</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td></td>
<td>[0.13 – 0.49]</td>
<td>[0.19 – 0.53]</td>
<td>[-0.45 – -0.08]</td>
<td>[-0.21 – -0.19]</td>
<td>[-0.24 – -0.15]</td>
<td>[-0.21 – -0.18]</td>
<td>[-0.23 – -0.16]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pol</td>
<td>0.008</td>
<td>-0.043</td>
<td>0.010</td>
<td>0.005</td>
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<td>0.975**</td>
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* P-value < 0.05
** P-value < 0.0001
a 95% confidence interval

diameter were negatively correlated (P-Value < 0.05) with a correlation value of -0.328. All sucrose traits, except fiber, were strongly correlated ranging from 0.732 to 0.9998. Fiber was correlated with count, and height, and negatively with diameter with values of 0.317, 0.373, and -0.273, respectively.
3.3.2 Population structure

The population consisting of 97 sugarcane clones had structure, but it was not translatable. The heat map and dendrogram from the IBS K-matrix showed strong differentiation between ten clones and the rest of the population (Figure 3.1). These ten

![Figure 3.1. Heat map and dendrogram generated with the kinship matrix (K). The K-matrix is an identity by state matrix of the 97 clones using 6,534 SNP and InDel markers in sugarcane.](image-url)
clones were CP72-370, CP85-830, Ho09-825, HoCP00-950, HoCP02-610, L94-432, L01-299, L09-112, L09-114, and L12-201. The remainder of the population was divided into two main groups.

The STRUCTURE analysis and PCoA both had similar results to the IBS K-matrix (Figure 3.2, 3.3). In both, the same ten clones separated from the majority of the population. In the PCoA, this separation corresponded with the variation explained by coordinate 1. However, the separation between the two main groups was not discrete with the STRUCTURE analysis, and the groups were composed of different clones than in the K-matrix. In the PCoA, there was no clear differentiation of the remaining clones into subgroups. Coordinate 2 separated out three clones accounting for 2.23% of the variation, which did not have any corollaries in the other two analyses.

3.3.3 Marker-trait association

For each of the phenotypic traits, five models were run in JMP, a full model and four sub-models: plant cane, first ratoon, plant cane in heavy soil, and plant cane in light soil. These models combined identified 570, 460, 697, and 656 makers significantly ($P<0.05$) associated with stalk count, stalk height, stalk diameter, and stalk weight, respectively (Figure 3.4). These numbers were reduced to only those makers found in all models resulting in 39, 26, 57, and 32 markers for stalk count, stalk height, stalk diameter, and stalk weight, respectively.

For sucrose traits using the same five models, 541, 520, 528, 562, 517, and 687 MTAs were identified for TRS, Brix, percent sucrose, fiber, Pol, and purity, respectively (Figure 3.5). The number of makers common across all models was 39, 42, 39, 45, 37, and 9 for TRS, Brix, percent sucrose, fiber, Pol, and purity, respectively.
Figure 3.2. The population structure (Q) matrix from STRUCTURE. The Q-matrix was derived from the analysis of 97 clones using 6,534 SNP and InDel markers in sugarcane. The values in the vertical axis represent the likelihood in percent of an individual belonging to one of the three colored subpopulations.

Markers with $R^2 > 0.05$ as well as a $-\log(P) > 3$ were considered significant (Table 3.3, 3.4). Only two markers, one each for Brix and percent sucrose, had an $R^2 < 0.05$. The top markers with significant ($-\log(P) > 3$) association with stalk count, stalk height, stalk diameter, and stalk weight were SNP5806, SNP5501, SNP0938, and SNP2578 with $R^2$ values of 0.143,
Figure 3.3. Principal coordinate analysis (PCoA) of 97 sugarcane clones using 6,534 SNP and InDel markers.

0.122, 1.39, and 0.139, respectively. The markers SNP1190, SNP3258, SNP4204, SNP1571, SNP1190, and SNP5851 showed highest association with TRS, Brix, percent
Figure 3.4. Markers identified to be associated with cane yield-component traits in sugarcane. Venn diagrams from population structure (Q)-kinship (K) analysis of 97 clones using 6,534 SNP and InDel markers. The models included a full model of all 6 site-years, plant cane, first ratoon, plant cane in heavy soil (Commerce silty clay loam and Sharkey clay), and plant cane in light soil (Commerce silt loam).

Sucrose, fiber, Pol, and purity explaining 15.0, 13.7, 14.9, 12.4, 14.7, and 14.2 % of the phenotypic variance, respectively.
Figure 3.5. Markers identified to be associated with sucrose traits in sugarcane. Venn diagrams from Q-K analysis of 97 clones using 6,534 SNP and InDel markers. The models included a full model of all 6 site-years, plant cane, first ratoon, plant cane in heavy soil (Commerce silty clay loam and Sharkey clay), and plant cane in light soil (Commerce silt loam).
Table 3.3. Markers associated with sugarcane yield-component traits with \(-\log(P) > 3\) and an $R^2 > 0.05$.

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* Markers significant for more than one trait
a % non-missing data of the marker across the 97 clones
b Sorghum reference chromosome number

Altogether, there were 154 MTAs for CYC traits and 209 MTAs for sucrose traits (Table 3.3, 3.4). These associations had 142 distinct markers for CYC traits, and 101 distinct markers for sucrose traits, with a total of 238 distinct makers. Fifty-six of these markers were associated with more than one trait, with 12, 39, and five markers associating with only CYC traits, only sucrose traits, or traits from either, respectively (Table 3.5).
Table 3.4. Markers associated with sugarcane sucrose traits with $-\log(P) > 3$ and an $R^2 > 0.05$.

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* Markers significant for more than one trait

a % non-missing data of the marker across the 97 clones

b Sorghum reference chromosome number

TRS, Total recoverable sugar
Table 3.5. Markers significant for two or more traits in sugarcane with \(-\log(P) > 3\) and an \(R^2 > 0.05\).

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<td>SNP0274</td>
<td>TRS, Sucrose</td>
<td>SNP4720</td>
<td>TRS, Brix, Sucrose, Pol</td>
</tr>
<tr>
<td>SNP0321</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>SNP5103</td>
<td>TRS, Brix, Sucrose, Pol</td>
</tr>
<tr>
<td>SNP0323</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>SNP5167</td>
<td>TRS, Brix, Sucrose, Pol</td>
</tr>
<tr>
<td>SNP0582</td>
<td>TRS, Sucrose, Pol</td>
<td>SNP5168</td>
<td>TRS, Brix, Sucrose, Pol</td>
</tr>
<tr>
<td>SNP0866</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>SNP5851</td>
<td>TRS, Sucrose, Pol, Purity</td>
</tr>
<tr>
<td>SNP1028</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>SNP6047</td>
<td>TRS, Sucrose, Pol, Purity</td>
</tr>
<tr>
<td>SNP1072</td>
<td>Brix, Pol</td>
<td>SNP6275</td>
<td>TRS, Brix, Sucrose, Pol</td>
</tr>
<tr>
<td>SNP1190</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>SNP6275</td>
<td>TRS, Brix, Sucrose, Pol</td>
</tr>
<tr>
<td>SNP1265</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>Cane yield-component and sucrose traits</td>
<td></td>
</tr>
<tr>
<td>SNP1435</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>SNP1604</td>
<td>Diameter, Fiber</td>
</tr>
<tr>
<td>SNP1662</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>SNP2751</td>
<td>Diameter, Fiber</td>
</tr>
<tr>
<td>SNP1823</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>SNP2752</td>
<td>Diameter, Fiber</td>
</tr>
<tr>
<td>SNP1841</td>
<td>TRS, Sucrose, Pol</td>
<td>SNP3170</td>
<td>Weight, Brix</td>
</tr>
<tr>
<td>SNP2110</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td>SNP4451</td>
<td>Height, TRS, Brix, Sucrose, Pol</td>
</tr>
<tr>
<td>SNP2140</td>
<td>TRS, Brix, Sucrose, Pol</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### 3.4 DISCUSSION

The present study provides the first application of GBS derived SNP and InDel markers to MTA in sugarcane. Previous MTA studies in sugarcane have used markers...
such as SSRs, ESTs, ALFPs, TRAPs, and DArT, which do not generate enough markers to cover the genome (Wang et al. 2010; Gutierrez et al. 2018). The use of GBS to identify SNP markers offers the potential for much better genome coverage. GBS marker data are being increasingly used in sugarcane. It has already been used in biparental studies to build high-density linkage maps, and to map QTLs (Balsalobre et al. 2017; Yang et al. 2017; Gutierrez et al. 2018). The present study identified 363 MTA between 238 candidate markers and 10 CYC and sucrose traits using 6,534 GBS-derived markers and a panel of locally adapted diverse clones (Table 3.3, 3.4).

A total of 6,299 SNPs and 235 InDels with no more than 50% missing data were used for the MTA analysis in this study. Previous research suggests a larger quantity of cleaner markers should be possible (Balsalobre et al. 2017; Yang et al. 2017; Gutierrez et al. 2018). Balsalobre et al. (2017) restricted missing data to 25% and found 15,906 markers. Gutierrez et al. (2018) found over 27,000 SNPs, which reduced to 5,835 SNPs after requiring presence in biparental parents, and restricting missing data at no more than 10%. The restriction was increased to 50% in this study.

The phenotypic data used in this study was comparable to the data used in other studies. In particular, our metrics were similar to those found by Gouy et al. (2015). Their means for stalk count, stalk height, stalk diameter, and Brix of 9.13 stalks/m², 265 cm, 26.12 mm, and 18.82% were close to what was found in this study of 6.75 stalks/m², 266 cm, 24.20 mm, and 20.02%, respectively. Their sucrose yield (17.12 t/ha) in Reunion Island (Indian Ocean) was twice of what was found in the present study (8.84 t/ha). However, the yield in the present study is similar to that found by Racedo et al. (2016) in Tucumán, Argentina, where the mean yield in plant cane was 9.22 t/ha.
Broad-sense heritability was also close. We found broad-sense heritability to range from 0.52 in stalk height to 0.88 for fiber. Gouy et al. (2015) had a range from 0.6 for sucrose yield to 0.83 for stalk diameter. Racedo et al. (2016) had a range in crop yield from 0.513 to 0.835.

The population structure, as analyzed by a STRUCTURE matrix, an IBS K-Matrix, and PCoA analysis did not show as intuitive a delineation in the populations as observed in the previous study (Chapter 2), where there was a clear clustering of foreign and experimental clones and USDA developed clones. Previously, clones from the LSU AgCenter mainly clustered in their own group, but some also clustered with USDA clones. In this study, there was consensus between analyses, but the pattern was not recognizable. Gouy et al. (2015) had similar results with no clear population structure. It was suggested to be due in part to there being relatively few generations between the original hybridization of sugarcane and current clones, and due in part to common clones between breeding programs and overlapping generations of parents. This creates a scenario where the population has grown rapidly from a few founders, leading to chaotic relatedness (Voight and Pritchard 2005; Gouy et al. 2015). The population in the present study is presumed to be subjected in part to chaotic relatedness and that some of the differences from the previous study may be due to a larger population size representing more gradual diversity from one clone to another.

MTA identified 238 distinct markers associated with CYC and sucrose traits with 56 of these being associated with two or more traits. As expected, common markers were found to be associated with highly correlated CYC and sucrose traits. For this analysis, an unadjusted P-value cut off of 0.05 was used to determine significance. Type
I error, a common problem in GWAS, was corrected for by two ways. First, the population structure and kinship were considered in the models. Wei et al. (2010) found that accounting for population structure and pedigree relationship reduced the false positives. Second, the MTA was required to be consistent across the subpopulations in the model as well as in the full model itself. In addition, the increase in marker density in the present investigation, compared to previous studies, could also minimize the Type I error component.

The markers showing significantly high associations with CYC and sucrose traits, especially those found across different crop types and crop edapho-climatic environments will be of immediate interest. These markers need to be validated in the future with biparental mapping populations and more diverse clones. The validated markers will be of great significance to the sugarcane breeding program in marker-assisted selection of desirable clones – this will ultimately pay dividend to the sugarcane industry(ies).

3.5 REFERENCES


4.1 INTRODUCTION

Cultivated sugarcane (Saccharum hybrids) is a C4 crop belonging to the subtribe Saccharinae under the tribe Andropogoneae of the family Poaceae. The Poaceae family is one of the larger plant families with over 11,000 species under 600 to 700 genera (Moore et al. 2013; WCSP 2018). Of these, 85 genera and 960 species are of the tribe Andropogoneae that includes important C4 grasses such as the grain crops sorghum and maize, and the bioenergy crop Miscanthus.

Sugarcane (Saccharum spp L.) is a high biomass yielding crop, important for food and bioenergy in the tropics and subtropics. Sugarcane produces around 39 t/ha (dry matter) compared to other high-biomass producing crops such as Miscanthus (24.6 t/ha), maize (17.6 t/ha), and switchgrass (10.4 t/ha) (Heaton et al. 2008; Waclawovsky et al. 2010). Globally, it has the fifth highest crop value at $61 billion per year following rice, wheat, soybean, and maize (FAOSTAT 2016). It also accounts for 80% of global sucrose production and 45% of sucrose production in the United States (Group Sucre et Denrées 2015; USDA-ERS 2017).

Historically, six species were considered important in the Saccharum genus: two wild species, S. spontaneum (L.) (2n = 40-128), and S. robustum (Brandes & Jesw. Ex Gressl) (2n = 60, 80); and four domesticated S. officinarum (L.) (2n = 80), S. sinense (Roxburgh) (2n = 81-124), S. barberi (Jeswiet) (2n = 111-120), and S. edule (Hassk) (2n = 60-80) (Moore et al. 2013; Hoang et al. 2015). Genetic evidence suggests S.
*robustum* is the progenitor of both *S. officinarum* and *S. edule* (Grivet et al. 2004, 2006), and that most modern cultivars, along with *S. sinense* and *S. barberi* are interspecific hybrids between *S. officinarum* and *S. spontaneum*. Around 32-39% of the *S. sinense* and *S. barberi* genomes come from *S. spontaneum*, while for modern cultivars the percentage is around 10-20% (D'Hont et al. 1996; Piperidis et al. 2010; Hoang et al. 2015).

Modern cultivars have limited genetic variation. Fewer than 20 *S. officinarum* clones are involved in the genealogy of sugarcane cultivars with only a few being used extensively (Raboin et al. 2008). Basic crosses can be made with *S. spontaneum*, *S. robustum*, and species of other genera within the *Saccharum* complex to broaden the genetic base (Ming et al. 2006; Moore et al. 2013; Todd et al. 2014).

Sugarcane has a high linkage disequilibrium (LD), thus giving genome wide association studies (GWAS) an advantage in sugarcane over traditional biparental mapping for the identification of trait-specific molecular markers. High levels of LD can be attributed to relatively few generations between modern cultivars and the limited number of initial clones used in hybridization (Debibakas et al. 2014). In a biparental population, a limited number of recombination events are present potentially increasing the size of linkage blocks (Gouy et al. 2015). Large linkage blocks would make a quantitative trait locus (QTL) difficult, if possible, to detect without a very large trait effect (Zhu et al. 2008). An association panel, on the other hand, has more genetic variation with smaller linkage blocks.

*Saccharum* spp. and related genera for introgression have been collected into the “World Collection of Sugarcane and Related Grasses” (WCSRG) at the National
Germplasm Repository of the USDA-ARS Subtropical Horticulture Research Station, Miami, FL. Various studies have described the diversity in the WCSRG (Tai and Miller 2001, 2002; Nayak et al. 2014; Todd et al. 2014). A total of 342 S. spontaneum clones were studied to designate a 75-clone core collection by Tai and Miller (2001). They used stratified random sampling over geographical origins and principal component cluster groups to select their core collection. Tai and Miller (2002) also evaluated diversity based on sugar composition of 32 S. officinarum, 30 S. barberi, 28 S. sinense, and 27 S. robustum. Cluster analysis was performed using principal component analysis. Nayak et al. (2014) created a 300-clone diversity panel based on genetic diversity among the clones in the WCSRG that was phenotypically characterized by Todd et al. (2014). However, this panel did not include clones outside of the world collection, i.e., from the basic breeding program at the USDA-ARS Sugarcane Research Unit in Houma, Louisiana (USDA-Houma) or the elite cultivars and parents used in breeding programs in Louisiana. Moreover, an additional ~250 clones have also been included into the WCSRG in the last 4 years (Parco et al., 2017).

Other core collections previously developed (Tai and Miller 2001, 2002; Nayak et al. 2014) may not account for the breadth of subtropic sugarcane genotypes currently being used in Louisiana. A Saccharum diversity panel developed from WCSRG including clones in Louisiana breeding programs would facilitate GWAS studies for identification of trait-specific markers for use in marker-assisted breeding in Louisiana and other sugarcane industries, as applicable. The present study was conducted with an objective to develop an inclusive sugarcane diversity panel (SDP1) for its use in GWAS of different agronomic traits.
4.2 MATERIALS AND METHODS

4.2.1 Plant material

The study included 1,485 *Saccharum* complex clones from the genera *Saccharum, Miscanthus, Coix, Imperata,* and *Sorghum* (Table A.3, Figure 4.1).

*Saccharum* spp. previously classified as *Erianthus* spp. including *S. arundinaceum,*

**Figure 4.1.** Frequency of species groups for both the full population (1,485 clones) and the selected diversity panel (309 clones). The diversity panel clones consisted of 238 of the total 309 clones. An additional 57 commercial cultivars, and 14 basic-cross f1 clones were selected by the breeders but not represented in the population. The two axes are proportional based on set size for comparison. *Erianthus*-like *Saccharum* spp. included *S. arundinaceum,* *S. bengalense,* *S. ravennae,* *S. rufipilum,* *S. brevibarbe,* *S. kanashiroi,* *S. procerum,* and unknown species previously identified as *Erianthus. bengalense,* *S. ravennae,* *S. rufipilum,* *S. brevibarbe,* *S. kanashiroi,* and *S. procerum* were grouped together as *Erianthus*-like *S.* spp. (ELSS) for analysis. Of these, 1,236 were clones from the WCSRG; 113 clones were elite and historic breeding clones from
the Louisiana sugarcane breeding program; and, 119 were clones of wild/exotic species, and 17 were hybrids from the base broadening program of the USDA-ARS Sugarcane Research Unit, Houma, LA.

### 4.2.2 Simple sequence repeat (SSR) markers and genotyping

Leaf tissue samples were harvested, placed directly on ice, and stored in -80 °C until DNA extraction. Genomic DNA was extracted from ~100 mg leaf tissues using the CTAB miniprep method as described previously (Parco et al. 2017). The DNA was checked for quality and quantity using a ND-100 spectrophotometer (Nanodrop Technologies Inc, Wilmington, DE).

The present study used 11 SSR markers from the sugarcane microsatellite consortium that have been mapped to 9 chromosomes of the *Sorghum bicolor* (Cordeiro et al. 2000; James et al. 2011) (Table 4.1). These markers were selected based on their high polymorphic index among the 113 Louisiana clones (Parco et al. 2011). The polymerase chain reaction (PCR) was performed in a 10 µL reaction mixture containing 1X reaction buffer, 2.5 mM MgCl₂, 0.4 unit GoTaq Flexi DNA Polymerase, 200 µM dNTP mix (all PCR reagents from Promega, Madison, WI), 0.5µM each of forward and reverse primer and 50 ng of genomic DNA. The thermal cycler program used was: (i) an initial denaturation at 95°C for 5 min; (ii) amplification for 36 cycles at 95°C for 45 s, 58°C for 45 s, 72°C for 1 min, and (iii) a final extension at 72°C for 5 min. Amplification products were electrophoresed in a 6% polyacrylamide gel using a high efficiency gel electrophoresis system (HEGS, Nihon Eido, Tokyo, Japan) according to the manufacturer’s instructions. The gel was stained with ethidium bromide, and visualized and documented in a Kodak Gel Logic 200 documentation system (Kodak Inc, New York, NY).
Table 4.1. Statistics of the 11 sugarcane SSR markers used to genotype 1,485 clones used in the study.

<table>
<thead>
<tr>
<th>SSR Name</th>
<th>Sorghum bicolor chromosome</th>
<th>Number of alleles</th>
<th>Major allele frequency</th>
<th>PIC&lt;sup&gt;a&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>SCESSR1299</td>
<td>4</td>
<td>65</td>
<td>0.796</td>
<td>0.268</td>
</tr>
<tr>
<td>SCESSR1296</td>
<td>6</td>
<td>41</td>
<td>0.869</td>
<td>0.286</td>
</tr>
<tr>
<td>SCESSR1023</td>
<td>2</td>
<td>47</td>
<td>0.884</td>
<td>0.293</td>
</tr>
<tr>
<td>SCESSR0909</td>
<td>5</td>
<td>58</td>
<td>0.576</td>
<td>0.375</td>
</tr>
<tr>
<td>SCESSR0616</td>
<td>1</td>
<td>55</td>
<td>0.730</td>
<td>0.240</td>
</tr>
<tr>
<td>SCESSR1773</td>
<td>7</td>
<td>33</td>
<td>0.348</td>
<td>0.205</td>
</tr>
<tr>
<td>SCESSR2275</td>
<td>8</td>
<td>43</td>
<td>0.599</td>
<td>0.235</td>
</tr>
<tr>
<td>SCESSR0835</td>
<td>3</td>
<td>22</td>
<td>0.925</td>
<td>0.203</td>
</tr>
<tr>
<td>MOLSSR2961</td>
<td>4</td>
<td>13</td>
<td>0.934</td>
<td>0.238</td>
</tr>
<tr>
<td>MOLSSR2770</td>
<td>9</td>
<td>18</td>
<td>0.858</td>
<td>0.212</td>
</tr>
<tr>
<td>LAPSSR0733</td>
<td>4</td>
<td>28</td>
<td>0.788</td>
<td>0.172</td>
</tr>
</tbody>
</table>

<sup>a</sup> Average of allele polymorphic information contents

Brokhaven, CT). Amplified fragments (alleles) were manually scored as “1” (present, dominant) and “0” (absent). Alleles occurring in less than 1% (15 clones) of the clones were discarded prior to downstream statistical analysis to reduce false similarity between clones due to shared absence of alleles while still capturing rare alleles.

4.2.3 Genetic diversity analysis

GeneAlEx 6.502 (Peakall and Smouse 2006, 2012) was used to compute gene diversity (h), Shannon’s information index (I), Nei’s distance, a principal coordinate analysis (PCoA), and an analysis of molecular variance (AMOVA). The AMOVA was done for species groups by recorded names: S. spontaneum, S. officinarum, hybrid cultivar, S. robustum, ELSS, S. sinense, S. barberi, Miscanthus spp., and other (Peakall and Smouse 2006, 2012). Analysis of molecular variance was also conducted on species groups devised from the neighbor-joining analysis, and on groups devised from the population structure analysis (described below). Also, the polymorphic information
content (PIC) for each SSR marker was calculated by averaging the PIC of each allele. The allele PIC was calculated using the formula:

$$PIC = 1 - \sum f_i^2,$$

where \(f_i^2\) is the frequency of the \(i^{th}\) allele presence or absence (Weir 1990).

Genetic diversity was also analyzed using DARwin 6.0.12 (Perrier and Jacquemoud-Collet 2006). In DARwin, a present/absent dissimilarity matrix was calculated using Dice dissimilarity scores (Perrier et al. 2003). Weighted neighbor-joining algorithms were used to construct a phylogenetic tree, which was evaluated for robustness with 1000 bootstrap repetitions.

Population structure was determined using STRUCTURE 2.3.4 (Pritchard et al. 2000). The number of populations, \(K\), was expected to be 6 or more based on the number of species. Therefore, models were run for \(K = 2 - 10\), and \(K = 8\) was selected as per the software’s documentation. The eight species groups used as priors were \(S.\) spontaneum, \(S.\) officinarum / robustum / hybrid cultivar, ELSS / \(Miscanthus\) spp., \(S.\) sinense, \(S.\) barberi, unknown species, and other species. A standard admixture model was used with an inferred alpha. Due to the importance found in minor alleles, lambda was evaluated at different levels and a lambda of 0.5 yielded the best models based on the log of the probability of the data. The Markov chain Monte Carlo program converged well before 50,000 iterations, so 50,000 iterations were used for ‘burn-in’, and 25,000 subsequent iterations were used for model parameter estimation. Ten model runs were used to check for non-symmetric modes, and two modes were found. One mode occurred seven times and the other was less consistent and occurred three times. An average of the seven runs from the first mode was used for the final result.
4.3 RESULTS

4.3.1 SSR genotyping

The 11 SSRs resulted in a total of 423 polymorphic alleles (Table 4.1). The number of alleles per SSR ranged from 13 to 65 with an average of 38. Four sugarcane SSRs on Sorghum bicolor chromosome 4 generated 106 alleles. All other chromosomes were represented by a single SSR producing 18 (chromosome 9) to 58 (chromosome 5) alleles. The average number of alleles per clone-SSR pair was 8.01 with the maximum being 30. The maximum average number of alleles per clone for an SSR was 16.28. This indicated that more than one loci were represented by each SSR, as the basic chromosome number of the species in the population ranges from \( x = 7 \) to \( x = 19 \) (Moore et al. 2013). S. spontaneum, representing one-third of the population, has a basic chromosome number of 8.

The low frequency of S. sinense, and S. barberi, and Miscanthus spp., necessitated maintaining minor alleles. Thus, alleles with frequencies between 0.990 and 0.010 were retained for analysis. These bounds were equivalent to the frequency of Miscanthus spp. in the population, which was 0.009. All SSR primers produced at least one polymorphic allele with a frequency at or above 0.348, higher than the average allele frequency (0.210).

4.3.2 Gene diversity and allele polymorphism by species

GeneAlEx measures of gene diversity (h), Shannon’s information index (I), and allele polymorphism within species are provided in Table 4.2. The h ranged from 0.162 for Miscanthus spp. to 0.241 for S. spontaneum indicating that Miscanthus spp. was the
least diverse and *S. spontaneum* the most diverse. The overall average gene diversity was 0.213.

**Table 4.2.** Gene diversity (h), Shannon’s information index (I), and the percentage of polymorphic alleles within species groups.

<table>
<thead>
<tr>
<th>Species</th>
<th>Gene diversity</th>
<th>I</th>
<th>Polymorphic alleles (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. spontaneum</em></td>
<td>0.241</td>
<td>0.386</td>
<td>99.29</td>
</tr>
<tr>
<td><em>S. officinarum</em></td>
<td>0.209</td>
<td>0.332</td>
<td>92.43</td>
</tr>
<tr>
<td>hybrid cultivar</td>
<td>0.218</td>
<td>0.345</td>
<td>92.20</td>
</tr>
<tr>
<td><em>S. robustum</em></td>
<td>0.223</td>
<td>0.355</td>
<td>89.36</td>
</tr>
<tr>
<td><em>Erianthus</em>-like(^a)</td>
<td>0.195</td>
<td>0.315</td>
<td>82.51</td>
</tr>
<tr>
<td><em>S. sinense</em></td>
<td>0.206</td>
<td>0.324</td>
<td>78.25</td>
</tr>
<tr>
<td><em>S. barleri</em></td>
<td>0.213</td>
<td>0.331</td>
<td>75.65</td>
</tr>
<tr>
<td>Miscanthus spp.</td>
<td>0.162</td>
<td>0.252</td>
<td>54.37</td>
</tr>
</tbody>
</table>

\(^a\) *Erianthus*-like *Saccharum* spp. included *S. arundinaceum*, *S. bengalense*, *S. ravennae*, *S. rufipilum*, *S. brevivarbe*, *S. kanashiroi*, *S. procerum*, and unknown species previously identified as *Erianthus*.

The entropy measured by Shannon’s information index followed the same trend with those species having higher gene diversity also had higher entropy (Table 4.2). The only exceptions were *S. officinarum* and *S. barleri*, where *S. officinarum* had h = 0.209 but a I = 0.332, and *S. barleri* had h = 0.213, but I = 0.331. The I value ranged from 0.252 (Miscanthus spp.) to 0.386 for (*S. spontaneum*), with an average of 0.338.

The percentage of polymorphic alleles within a species was directly proportionate to its population size (Figure 4.1, Table 4.2). The percentage of polymorphism by species were 99.29, 92.43, 92.20, 89.36, 82.51, 78.25, 75.65, and 54.37 for *S. spontaneum*, *S. officinarum*, hybrid cultivar, *S. robustum*, *ELSS.*, *S. sinense*, *S. barleri*, and Miscanthus spp., respectively.
4.3.3 Genetic distance between species

Nei’s pairwise genetic distance (D) was calculated to evaluate the genetic distance between species (Table 4.3). The greatest distance was between the Miscanthus spp. and hybrid cultivar groups at 0.105, while the shortest distances were between the S. officinarum and hybrid cultivar. Miscanthus spp. was closest to ELSS and S. spontaneum at D = 0.038 and D = 0.49, respectively. The D value between the rest of the species groups and Miscanthus spp groups (0.009).

Table 4.3. Nei’s genetic distance between species groups

<table>
<thead>
<tr>
<th>Species</th>
<th>S. spont.</th>
<th>S. offic.</th>
<th>hybrid cultivar</th>
<th>S. robustum</th>
<th>Erianthus-like a</th>
<th>S. sinense</th>
<th>S. barberi</th>
<th>Miscanthus</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. spontaneum</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. officinarum</td>
<td>0.055</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>hybrid cultivar</td>
<td>0.060</td>
<td>0.009</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. robustum</td>
<td>0.032</td>
<td>0.011</td>
<td>0.019</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Erianthus-like a</td>
<td>0.032</td>
<td>0.074</td>
<td>0.086</td>
<td>0.051</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. sinense</td>
<td>0.049</td>
<td>0.032</td>
<td>0.036</td>
<td>0.024</td>
<td>0.077</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. barberi</td>
<td>0.049</td>
<td>0.034</td>
<td>0.042</td>
<td>0.024</td>
<td>0.067</td>
<td>0.029</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Miscanthus spp.</td>
<td>0.049</td>
<td>0.093</td>
<td>0.105</td>
<td>0.069</td>
<td>0.038</td>
<td>0.101</td>
<td>0.090</td>
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a Erianthus-like Saccharum spp. included S. arundinaceum, S. bengalense, S. ravenae, S. rufipilum, S. brevibarbe, S. kanashiroi, S. procerum, and unknown species previously identified as Erianthus.

followed by the D between S. officinarum and S. robustum (0.011). Miscanthus spp. was the farthest from the other species groups. ranged from 0.069 to 0.105. The next farthest from the others was ELSS followed by S. spontaneum.
4.3.4 Phylogeny and population structure

Neighbor joining on a Dice dissimilarity matrix was also used to evaluate genetic diversity (Figure 4.2). ELSS, *Miscanthus* spp., and *S. spontaneum* each showed distinct separation from other species. *S. robustum*, *S. officinarum*, hybrid cultivars, and *S. edule* grouped together in a major cluster with sub-clusters concentrated independently with *S. robustum*, and of hybrid cultivars. *S. sinense* and *S. barberi* also showed distinction between species, but overall had very little diversity. *Miscanthus* spp. were most distant from other clones followed by ELSS and *S. spontaneum*.

The eight sub-populations delineated by the structure analysis had near direct correspondence to species groups (Figure 4.3). The first two sub-populations corresponded to both *S. officinarum* and *S. robustum* with no clear distinction between them. Other sub-populations corresponded to hybrid cultivars, *S. sinense*, and *S. barberi*. ELSS and *Miscanthus* spp comprised one sub-population, whereas *S. spontaneum* was delineated by two sub-populations.

Principal coordinate analysis (PCoA) showed definite variance between species groups (Figure 4.4). The coordinates cumulatively accounted for 12.8% of the total variation, with the first three accounting for 8.04, 2.55, and 2.21%, respectively. *Saccharum spontaneum* grouped by itself with some outliers that grouped with the cluster comprising ELSS and *Miscanthus* spp. *Saccharum officinarum*, *S. robustum*, and hybrid cultivars grouped together but with distinct centroids. *Saccharum sinense* and *S. barberi* formed separate clusters but close to each other bordering the clusters of the *S. officinarum* and *S. robustum* clones.

Analysis of molecular variance (AMOVA) was conducted on the 1485 clones with
Figure 4.2. Phylogenetic tree of the *Saccharum* complex showing clear species differentiation. Neighbor-joining tree of a Dice dissimilarity matrix of 1,485 clones using 423 SSR alleles. *Erianthus*-like *S.* spp. included *S. arundinaceum*, *S. bengalense*, *S. ravennae*, *S. rufipilum*, *S. brevibarbe*, *S. kanashiroi*, *S. procerum*, and unknown species previously identified as *Erianthus*. Other species included *Coix lacryma-jobi*, *Imperata* sp., *Sorghum polumosum*, *Saccharum edule*, and unknown.

the sub-populations derived from three independent diversity analysis-based divisions (Table 4.4). The first division was based on the recorded name of the clones with nine groups consisting of *S. spontaneum*, *S. officinarum*, hybrid cultivar, *S. robustum*, ELSS, *S. sinense*, *S. barberi*, *Miscanthus*, and other, which included *Coix lacryma-jobi*,
Figure 4.3. Population structure of 1,485 clones using 423 SSR alleles using eight subpopulations. Species groups *Saccharum officinarum* / *robustum*, and *S. spontaneum* were each represented by two groups. Clones are in the order of the clones in the neighbor joining analysis for comparison (Figure 2). *Erianthus*-like *S.* spp. included *S. arundinaceum*, *S. bengalense*, *S. ravenae*, *S. rufipilum*, *S. brevibarbe*, *S. kanashiroi*, *S. procerum*, and unknown species previously identified as *Erianthus*. The values in the vertical axis represent the likelihood in percent of an individual belonging to one of the eight colored subpopulations. *Imperata sp.*, *Sorghum polumosum*, *Saccharum edule*, and unknown species (Figure 4.1). The second division was based on the DARwin neighbor-joining on Dice dissimilarities. Here clones grouping together were considered part of the same species groups. This eliminated the ‘other’ group and combined *S. officinarum* and *S. robustum* leaving 7 groups. Clones falling in the *S. officinarum* / *S. robustum* / hybrid cultivar complex that were not hybrid cultivars were considered part of the *S. officinarum* / *S. robustum* group. The third grouping was based on STRUCTURE model estimates using the group that was estimated to contribute the largest proportion to the genome. All three AMOVA showed significant differences within sub-populations with p-values ≤ 0.001 (Table 4.4). Genetic variation within a sub-population was high (85 – 91%), whereas 9, 14, and 15% of the variance was attributable to between sub-population
Figure 4.4. Principal coordinate analysis (PCoA) of 1,485 clones showing species differentiation with 423 SSR alleles. *Erianthus*-like *Saccharum* spp. included *S. arundinaceum*, *S. bengalense*, *S. ravennae*, *S. rufipilum*, *S. brevibarbe*, *S. kana shiroi*, *S. procerum*, and unknown species previously identified as *Erianthus*. Other species included *Coix lacryma-jobi*, *Imperata* sp., *Sorghum polumosum*, *Saccharum edule*, and unknown.

variance in the name-based division (groups by species), the DARwin and the STRUCTURE divisions, respectively.

4.3.5 Sugarcane diversity panel 1 (SDP1) selection

A 309-clone SDP1 was selected by the Louisiana sugarcane breeders based on the diversity analysis where clones were picked from different subclusters maximizing the clones existant in Louisiana to minimize the number of clones to be imported from WCSRG, Miami, FL. SDP1 consisted of 284 clones from Louisiana that represent clones within WCSRG, Miami, FL and Louisiana breeding programs. The remainder 25
Table 4.4. Analysis of molecular variance (AMOVA) with population division by clone-recorded name, DARwin neighbor-joining on Dice dissimilarities, and STRUCTURE estimates using Markov chain Monte Carlo.

<table>
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<th>Division method</th>
<th>Source</th>
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<th>SS</th>
<th>MS</th>
<th>Est. var.</th>
<th>% variation</th>
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<td>Among pops</td>
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<td>6611.129</td>
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<td>91</td>
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<td>82656.980</td>
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<tr>
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<td>Total</td>
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<td>82656.032</td>
<td>57.919</td>
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a The nine species groups from clone-recorded names were *Saccharum spontaneum*, *S. officinarum*, hybrid cultivar, *S. robustum*, *Erianthus*-like *S. spp.*, *S. sinense*, *S. barberi*, *Miscanthus* spp., and other.

b The seven species groups from DARwin were *S. spontaneum*, *S. officinarum* / *robustum*, hybrid cultivar, *Erianthus*-like *S. spp.*, *S. sinense*, *S. barberi*, and *Miscanthus* spp.

c The eight species groups from STRUCTURE were combined into six (Figure 4.3): *S. spontaneum*, *S. officinarum* / *robustum*, hybrid cultivar, *Erianthus*-like *S. spp.* / *Miscanthus* spp., *S. sinense*, and *S. barberi*.

clones are being imported from the WCSRG. In the SDP1, Louisiana clones had some clustering, but were fairly well dispersed across the entire study population (Figure 4.5). The *S. spontaneum* clones’ representations in the SDP1 were minimized since wild clones cannot be grown in the field. Instead, hybrids x *S. spontaneum* F1s developed by the base broadening breeding program of the USDA-ARS, Houma were included in the panel. Over 100 of the SDP1 clones were hybrid cultivars that consisted of both historic and current clones. Representation of the ELSS and *Miscanthus* spp. from the WCSRG were, intentionally, kept to minimum. The remainder of SDP1 was proportionally distributed over other species groups (Figure 4.1).
Figure 4.5. Neighbor-joining tree of 238 of the 309 clones selected by the breeders. An additional 57 commercial cultivars, and 14 basic-cross F₁ clones were not represented in this study. Seven basic-cross F₁ clones not originally represented are included as their non-cultivar parent.

4.4 DISCUSSION

The present study developed an SDP1 with breeder input based on the diversity analysis of the WCRG plus additional clones from Louisiana (Figure 4.1, Figure 4.5). Other core collections previously developed (Tai and Miller 2001, 2002; Nayak et
al. 2014) did not account for all subtropic-specific sugarcane genotypes, which may limit its applications for GWAS in Louisiana. For instance, the 300-clone core collection developed by Nayak et al. (2014) include 228 S. spontaneum, other S. spp., other genera, and unknown spp., potentially all needing to be maintained as wild-types in pots on concrete. This hinders the phenotypic characterization of the panel under natural field conditions. But, SDP1 contains less than 50 wild-type clones, all of which are already maintained in Louisiana.

*Saccharum* spp. genome size and complexity creates challenges to evaluating genome-wide genetic diversity. The 11 SSR primers generated a total of 423 alleles with an average of ~38.45 alleles per locus. While 423 alleles cannot cover all of over 100 chromosomes in the *Saccharum* complex, a random distribution of the alleles over the genome was possible by the multiallelic nature of the SSR primers as well as their coverage of 9 out of the 10 sugarcane homeologous groups based on their location on the sorghum genome. Previous studies have used fewer total alleles and a lower average number of alleles per SSR for diversity analysis, such as 261 alleles with 7.35 per locus (Banumathi et al. 2010), 209 alleles with 5.8 per locus (Nayak et al. 2014), and 205 alleles with 13.67 per locus (You et al. 2016). With nearly twice the number of alleles and more than twice the number of alleles per locus than in previous studies, the present study is expected to capture a more significant proportion of the genetic diversity.

Bootstrapping failed to show robustness in the neighbor-joining tree due to the combination of varying number of clones within a species in the population and the use of minor alleles. Each bootstrap replication takes a random sample with replacement
from the alleles used while retaining a sample size equal to the original number of variables (Perrier et al. 2003). The nature of our population meant alleles primarily present in *S. spontaneum*, in particular, or in *S. robustum*, *S. officinarum*, or hybrid cultivars required little representation within their primary species to be included at higher frequencies under bootstrapping, while alleles primarily present in species with less clones needed more representation. The cut off allele frequency of 0.01 used in our study was 15 clones, which make up 3% of *S. spontaneum*, but 107% of *Miscanthus* spp. Thus, each species did not have equal representation among the alleles used, which resulted in changes in the diversity-based tree when different samples were selected. Nevertheless, the genetic diversity is expected to be well represented despite low bootstrap values as described in section 4.2.3.

The clusters generated by neighbor-joining analysis, structure analysis and PCoA were very similar. The species groups described by neighbor-joining were *S. spontaneum*, *S. officinarum / robustum*, hybrid cultivars, ELSS, *S. sinense*, *S. barberi*, and *Miscanthus* spp. The only difference was that, unlike the neighbor-joining analysis, neither the structure analysis nor the PCoA produced a *Miscanthus* spp. cluster separate from ELSS. Principal coordinate analysis also showed hybrid cultivars and *S. officinarum / robustum* clustering together. Additionally, the first two coordinates of PCoA explained 10.59% of the total variance, which was close to 9, 14, and 15% found by the AMOVA between groups. Thus, it is likely that the PCoA provides visualization for the majority of the variance between populations.

Results of the diversity analysis of the WCSRG from the present study and that of Nayak et al. (2014) were in agreement. In the present study, overall averages were
0.213 and 0.338 for gene diversity and Shannon’s information indexes, respectively as compared to 0.310 and 0.438, respectively observed by Nayak et al. (2014). The percentage of polymorphic alleles in the present study ranged from 54.37 to 99.29, while theirs ranged from 75.6 to 99.52. The genetic distances reported by Nayak et al. (2014) were larger. For example, their distance between S. spontaneum and S. officinarum was 0.79 compared to ours at 0.55. The lower averages in the present study could be due to the retention of minor alleles.

Clustering analysis conducted by Nayak et al. (2014) produced results similar to the present study. Three main clusters: 1) S. spontaneum; 2) S. officinarum, hybrid cultivars, S. robustum, S. edule, S. barberi, and S. sinense; and 3) other species were described. More distinction between species within these groups were found in the present investigation as compared to that of Nayak et al. (2014). Seven clusters in the neighbor-joining analysis (S. spontaneum, S. officinarum / robustum, hybrid cultivar, ELSS, S. sinense, S. barberi, and Miscanthus spp.), and six clusters with the structure analysis and the PCoA (S. spontaneum, S. officinarum / robustum, hybrid cultivar, ELSS / Miscanthus spp., S. sinense, and S. barberi) were identified in the present study. Nayak et al. (2014) did not consider ELSS as a species group, but left Erianthus and Saccharum synonyms as found in the WCSRG database. They used non-Saccharum species as a group, grouping Erianthus spp. (which has been reclassified under Saccharum) with Miscanthus spp. Thus, it is difficult to comprehend if their analysis found the same distinction that was observed in the present study between ELSS and Miscanthus spp. The results from the genetic diversity study of 1,485 clones helped Louisiana breeders in the selection of 309 clones to serve as the SDP1 for future
research, especially in GWAS to identify markers associated with different agronomic
trait(s) of interest.

4.5 REFERENCES

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CHAPTER 5. GENERAL CONCLUSIONS AND FUTURE RESEARCH

5.1 GENERAL CONCLUSIONS

- Model comparison between TASSEL 5.1 and JMP Genomics 8.0 showed very similar results and suggested that the same results could be achieved with minor changes to menu options in the software. The differences found included JMP Genomics using a square root matrix for a kinship (K) matrix, TASSEL using covariance and JMP Genomics using correlation when computing principal component analysis (PCA) to obtain a population structure (Q) matrix, and JMP Genomics not forcing imputation of missing marker data (resolved in JMP Genomics 9.0).

- For genetic diversity analysis, the Dice dissimilarity matrix from DarWIN, the Q-matrix from STRUCTURE 2.3.4, and the PCA from GeneAlEx were all comparable in the representation of the population structure.

- TASSEL and JMP Genomics identified potential marker trait associations (MTA) with sucrose traits. Three markers, each representing 15 to 20 % of the phenotypic variance, were consistent across models.

- The first genome wide association study using genotyping by sequencing data was performed with single nucleotide polymorphisms (SNPs) and insertions-deletions (InDels) for cane yield-component and sucrose traits. Significant MTAs (P-value > 0.05) were found for all traits: stalk counts, stalk height, stalk diameter, stalk weight, total recoverable sugar, Brix, percent sucrose, fiber, Pol, and purity. Due to high correlation between traits, many of the markers were common between different traits.
An inclusive sugarcane diversity panel (SDP1) was developed using simple sequence repeat (SSR) markers to facilitate Louisiana sugarcane breeding programs. The markers used were able to show clear structure in the population of clones coming from the World Collection of Sugarcane and Related Grasses, and from Louisiana breeding programs. The diversity analysis informed the breeders in the selection of 309-clone SDP1 that captured the diversity found in the population.

5.2 FUTURE RESEARCH

- Markers from the Chapter 2 and Chapter 3 need to be validated using biparental populations involving multiple crosses before they can be used for marker-assisted selection in Louisiana sugarcane breeding programs.
- MTAs for brown rust disease with the markers from Chapter 3 need to be carried out in the population for which phenotypic data is already available.
- High-quality GBS data on the new SDP1 will be needed for use in GWAS. As new reference genomes for sugarcane are developed, SNP-calling can be performed using the same GBS data allowing for their locations in sugarcane genome.
- The non-wild type clones within SDP1 have already been planted at the Sugarcane Research Station of the Louisiana State University Agricultural Center, St. Gabriel, Louisiana. The wild-type clones are being maintained in pots in the USDA-ARS in Houma, Louisiana. The 25 clones from the USDA Agricultural Research Station (ARS) in Canal Point, Florida are being imported.
Phenotyping of SDP1 for traits of agronomic importance need to be conducted for GWAS studies.
APPENDIX. SUPPLEMENTARY DATA

Table A.1. Phenotypic data of 48 elite and historic Louisiana sugarcane clones.

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TRS, Total recoverable sugar
### Table A.2. Phenotypic data of 97 elite and historic Louisiana sugarcane clones.

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TRS, Total recoverable sugar
Table A.3. Clone species and presence in selected diversity panel (SPD1) for 1485 clones of sugarcane and related species.

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*a Order of clones based on the neighbor joining tree from Dice dissimilarities*
Nathanael Fickett was born in Albuquerque, New Mexico and moved to Pennsylvania when he was six and a half. He is the second born of seven brothers. During high school he volunteered at Faith Ranch in Jewitt, Ohio, where he learned and taught horsemanship. He completed his undergraduate degrees in Pennsylvania at Messiah College where he dual majored in Mathematics and Computer Science, with a minor in Statistics. During high school and college he travelled to 17 countries including eight months volunteering at Grace Farm and Orphanage in Malawi. His volunteer experience gave him interest in agriculture leading him to complete a Master’s degree in Agronomy from the University of Wisconsin–Madison. He continued to pursue his quantitative and agronomic interests at LSU earning a Master of Applied Statistics and planning on finishing a Doctoral degree in Agronomy. Towards the end of his Doctoral work, Nathanael was also able to complete training as a data scientist at the Data Incubator in New York City, New York.

During Nathanael’s time in graduate school he married Sarah Fickett and has had three children, all of whom bring him lots of joy. He also enjoys gardening, ties exquisite fly fishing flies, is an avid fly fisherman, plays the fiddle, loves photography, bakes pastries, and likes making whistles. He aspires to be a farming data scientist with his own stream to fish.