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ANALYSIS OF *STARCH BRANCHING ENZYME 1 (SBE1)* GENE IN MAIZE

BY

ABISKAR GYAWALI

A thesis submitted in partial fulfillment of the requirements for the

Master of Science

Major in Biological Sciences

Specialization in Biology

South Dakota State University

2016

ANALYSIS OF *STARCH BRANCHING ENZYME 1 (SBE1)* GENE IN MAIZE

This dissertation is approved as a creditable and independent investigation by a candidate for the Master of Science in Biological Science degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Abiskar Gyawali

Brookings, SD

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ABSTRACT

ANALYSIS OF *STARCH BRANCHING ENZYME 1 (SBE1)* GENE IN MAIZE

ABISKAR GYAWALI

2016

A previous study revealed a quantitative trait locus (QTL) in maize on the short arm of chromosome 5 (5S) for endosperm amylose content. In that original study, both low and high amylose parental lines, H99ae and GEMS-0067 respectively, were homozygous recessive for *amylose extender 1 (ae1)* and the polymorphism responsible for this QTL was additive (semi-dominant). Located within the QTL interval is *starch branching enzyme 1 (sbe1)*, which makes it a candidate gene. In order to test whether a polymorphism in *sbe1* is the source of this QTL, we crossed a plant homozygous for *ae1* and *sbe1-Mu* onto a GEMS-0067/H99ae hybrid to test whether this allele would eliminate additivity in the progeny. The *sbe1-Mu* allele is null and acts as a simple recessive against a functional *Sbe1* allele. PCR markers were used to distinguish homozygous wild (*Sbe1-G/Sbe1-G* or *Sbe1-H/Sbe1-H*), heterozygous (*Sbe1-G/sbe1-Mu* or *Sbe1-H/sbe1-Mu*) and homozygous mutant (*sbe1-Mu/sbe1-Mu*). Furthermore *Alu1* restriction digestion was done to distinguish GEMS-0067 from H99ae. A dual wavelength iodine-binding assay was used to determine relative amylose/amylopectin content from these segregated populations. The amylose assay showed that the presence of *sbe1-Mu* eliminated additivity and dominance relationship was revealed. This establishes that allelic differences of *sbe1* between H99ae and GEMS-0067 as the source of the QTL. The

gene for *starch branching enzyme 1 (sbe1)* in a high amylose line, GEMS-007, would translate into a protein with six amino acid polymorphisms relative to a lower amylose line, H99ae. A review of the published *sbe1* sequence data indicates that most varieties of maize are remarkably uniform, i.e., they have the same amino acid usage as found in H99ae. In *Zea mays* L., we studied the phylogenetic and selection analysis of *starch branching enzyme 1 (sbe1)*, a candidate gene for high amylose QTL. The main objective of this study was to know whether or not *sbe1* was subjected to selection. We compared 2797 bp of the *sbe1* coding region of 17 accessions of maize and teosinte. Very low proportion of single nucleotide polymorphisms were observed relative to other genes in maize. Comparison of synonymous and nonsynonymous polymorphism revealed the effect of purifying selection in the whole species. Phylogenetic analysis of *sbe1* revealed that *sbe1* in a high amylose line, GEMS-007, is ancestral as it lies together in group with teosintes.

Chapter 1 Introduction

1. Purpose

The project is focused in confirming two hypotheses, which are described in chapters two and three. Those chapters in this thesis are written in manuscript format. Chapter one is a general introduction of *sbe1* and its effects upon endosperm amylose content. Chapter two describes confirmation that *starch branching enzyme 1 (sbe1)* is the source of a high endosperm amylose content QTL in maize. Chapter three elaborates about the phylogenetic analysis of *sbe1*. The last chapter is about the summary and future work on both projects.

2. Maize kernel structure and composition

The maize grain is composed of the same basic structures that are found in major cereals: endosperm (82-83 %), germ (10-11 %), pericarp (5-6 %) and tip cap (0.8-1 %) (SINGH, *et al.*, 2014). Pericarp is the outermost layer consisting most of the cellulose, hemicellulose and lignin with a lesser proportion of lipids. Endosperm is the major portion of the maize kernel with large number of cells and each cell is composed of densely packed starch granules (MIAO, *et al.*, 2014). Germ contains the living part of the maize kernel and stores the genetic information along with vitamins, enzymes and other nutrients that helps the kernel to grow into whole plant. Tip cap is the point of attachment of kernel to maize ear and it is the only structure that is not covered with pericarp.

2.1. Molecular and granular composition of maize starch

The major component of endosperm dry matter is starch and starch is present in two forms: amylose, the linear form, and the amylopectin which is highly branched. The normal amylose content in maize is 20-25% which are glucose polymers linked by α -D-1, 4-glucosidic bonds. Maize amylose is composed of not only the straight chains of glucose but they also have few branching points (TAKEDA, *et al.*, 1988). The majority of maize endosperm is composed of amylopectin, which is about 75% of total starch. Straight chains of glucose in amylopectin, joined with α -D-1, 4-glucosidic bonds, are branched with α -D-1, 6-glucosidic bonds.

Three levels of starch structure have been observed. At first, many unbranched glucose monomers are linked together to form an A chain. One or more glucose molecules connect to each other to make branch linkage known as a B chain. In the second level, A chains and B chains link together to form crystalline and amorphous layer. The major difference between crystalline and amorphous layer is based on their subjection to acid hydrolysis. The crystalline layer is resistant to acid hydrolysis whereas amorphous layer is more susceptible to acid hydrolysis. The third level is mainly about the blocklet structure made of crystalline and amorphous layer and the starch granules are made of these blocklets, which are organized to form different rings.

2.2. Starch Biosynthesis

Starch biosynthesis in the endosperm of cereal is a coordinated activity of several enzymes, including adenosine 5' diphosphate-glucose (ADP-Glc) pyrophosphorylase (AGPase), granule-bound starch synthase (GBSS), soluble starch synthase (SS), and starch branching enzyme (SBE) and starch debranching enzyme (DBE). Seven genes are specifically involved in the starch synthesis pathway (Figure 1.1): *shrunken1* (*sh1*), *shrunken2* (*sh2*), *brittle2* (*bt2*), *waxy1* (*wx1*), *ae1 amylose extender* (*ae1*), *starch branching enzyme1* (*sbe1*), *starch branching enzyme3* (*sbe3*), *sugary1* (*su1*) (MYERS, *et al.*, 2000). Several steps are involved in this pathway. The first step involves the synthesis of UDP-glucose which is catalyzed by sucrose synthase that is encoded by *sh1*. Two genes; *sh2* and *bt2* encode ADP-glucose pyrophosphorylase (AGPase) which assists in conversion of UDP-glucose to ADP-glucose. The enzymes of starch synthesis are encoded by *wx1*, *ae1*, *sbe1*, *sbe3* and *su1* to produce amylose and amylopectin. single mutants of *wx1* and *ae1* decrease and increase the amylose content in the starch respectively (TSAI, 1974). In case of homozygous *wx1* mutant, the endosperm starch granule produces 100% amylopectin. The *wx1* gene has a epistatic gene interaction that cause the mutants to resist amylose accumulation (YEH, *et al.*, 1981).

3. Enzymes involved in amylose and amylopectin synthesis

3.1 Starch Synthase

Starch synthase catalyzes the elongation of linear glucose chain by transferring the glucosyl unit of ADP-glucose to the non-reducing end of glucose

chain. Various forms of starch synthase identified so far are GBSS, SSI, SSII, SIII, SSIV (JAMES, *et al.*, 2003)

3.2 Granule bound starch synthase (GBSS)

Two isoforms of GBSS has been identified; GBSS I and GBSS II. In cereal endosperm, GBSSI is found in endosperm and is encoded by *waxy* locus (*wx*) whereas GBSSII is predominant in non-storage plant tissue. Maize *wx1* mutants in maize have either low or no amylose starch content, however these mutants do not show difference in starch content (TSAI, 1974). Single *waxy* mutant in barley contains between 0.4% and 9% amylose (1:3 ratio of amylose and amylopectin present in wild barley) in starch (PATRON, *et al.*, 2002).

3.3 Branching Enzyme

Branching enzyme (BE) is the class of enzyme that catalyzes the formation of branch point by cleaving α -1, 4-glucosidic bonds and attaching it again through α -1, 6-glucosidic bonds. Based on biochemical and physiochemical properties, two isoforms of BE are known; BEI and BEII. BEI differs from BEII in terms of amino acid composition, enzyme kinetic properties, immunological reactivities, peptide maps, optimal reaction conditions and substrate specificity (FISHER, *et al.*, 1983, STINARD, *et al.*, 1993). In addition, BEII also possess two isoforms; BEIIa and BEIIb (HAN, *et al.*, 2007). BEIIa and BEIIb are not distinct in biochemical and immunological properties (BOYER, *et al.*, 1978, FISHER, *et al.*, 1983). However they showed difference in the branching linkage assay (STINARD, *et al.*, 1993) and optimum temperature.

4 Genetic approach to altering amylose content

There are specific genes that are known to regulate the amylose content. However there are also some unknown factors. Amylose content in rice is predominantly controlled by *wx* gene on chromosome 6 (TSAI, 1974). In wheat, there are three waxy loci located on the short arm of chromosome 7A (CHAO, *et al.*, 1989). Wheat lines lacking one or two GBSS isoforms produce low amylo-starch. Although increasing the *waxy* protein can lead to higher amylose but this cannot exceed 40% (FASAHAT, *et al.*, 2014). Altering the branching enzyme activity can also increase the amylose proportion in starch. Three isoforms of starch-branching enzymes, SBEI, SBEIIa and SBEIIb, have been identified in maize (DANG, *et al.*, 1989). These enzymes are responsible for formation of amylopectin. Amylose is a linear chain consisting α -1, 4 glycosidic linkage and amylopectin also had the branched form of α -1,6 linkages. The properties of SBEI differ significantly from SBEIIa and SBEIIb. SBE I is active in branching amylose, whereas SBE II is active in branching amylopectin (GUAN, *et al.*, 1993). BLAUTH, *et al.* (2002) found that single mutant of *sbe1* does not affect the endosperm starch structure, whereas a deficiency of SBEIIb in *amylose extender1 (ae1)* mutants increases the amylose content.

4.1 High amylose and amylopectin in mutant maize

Normal amylose content in maize is around 25% and the rest is amylopectin. The proportion of amylose in maize endosperm can be increased if the kernels are homozygous for the recessive allele of *ae1* (VINEYARD AND BEAR, 1952) which encodes SBEIIb. One maize inbred line GEMS-0067, (Reg. no GP-550, PI 643420),

derived from the pedigree of [GUAT209:-S13 × (OH43ae × H99ae)], is the only publicly available source of high amylose maize in the US (CAMPBELL, *et al.*, 2007). H99ae is a Midwestern dent that was converted to being homozygous *ae1*; it yields about 50% amylose

4.2 Breeding for high amylose corn

High amylose starch has been previously used to make gums, candies and adhesive for cardboard (Ferguson, 1994). However in recent times amylose has been used for the manufacturing the biodegradable plastic and has been found to be good source of 'resistant starch' that lowers the glycemic index when added in the food (BEHALL, *et al.*, 2002). Isolating amylose from normal maize is quite costly. Therefore high amylo-maize breeding can be economically significant and also can be useful in expanding the application of maize starch and starch based maize industry (SLATTERY, *et al.*, 2000). Previously little was known about the inheritance of *ae1* and its complementary interaction with other regulating genes. Subsequent work on the interaction of *ae1* with other endosperm mutants revealed much variation in amylose content (BEAR, *et al.*, 1958, KRAMER, *et al.*, 1958, ZUBER, *et al.*, 1958). Amylose content ranging from 36.5 to 64.9 was reported from cross between 135 inbreds in *ae1* background (VINEYARD, *et al.*, 1958). This variation in the amylose content is the result of different modifier genes that interacted with the *ae1* (VINEYARD, *et al.*, 1958, ZUBER, *et al.*, 1958). Different breeding procedures have been proposed to develop agronomically adapted amylo-maize hybrids (BEAR, *et al.*,

1958, HELM, *et al.*, 1967). Some of these include three cycles of alternate backcrossing and selfing sequence for development of high amylose inbred lines.

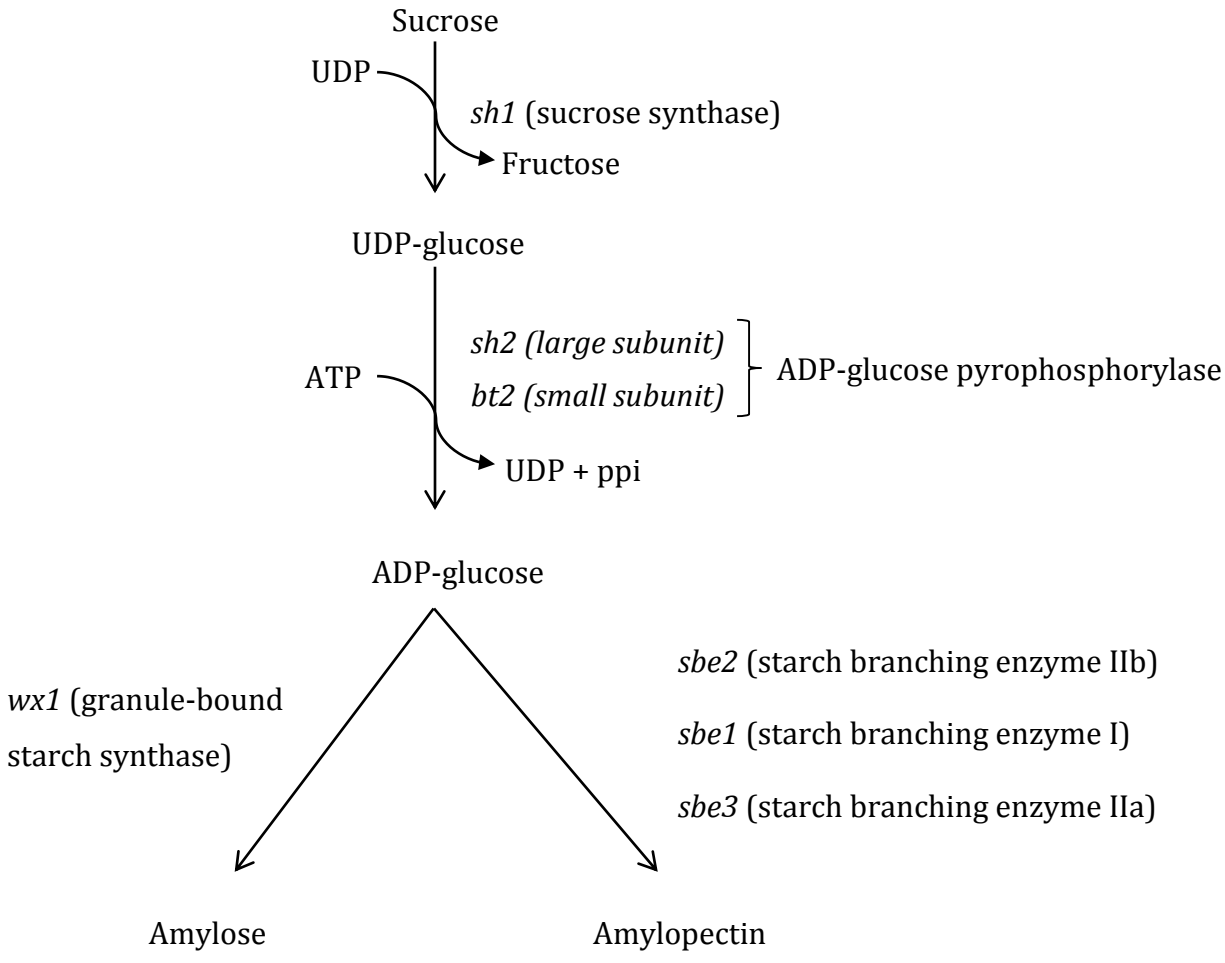


Figure 1.1 A pathway of starch synthesis in maize

Chapter 2 Confirmation that *starch branching enzyme 1 (sbe1)* is the source of a high endosperm amylose content QTL in maize

Introduction

Starch is composed of two forms; straight chained amylose and highly branched amylopectin (BANKS, 1975). Generally, maize endosperm starch is composed of about 25% amylose and 75% amylopectin (NELSON, *et al.*, 1995). High amylose starch has been of great benefit in making gums candies and adhesive (FERGASON, 2000). High amylose foods is also found as a source of resistant starch which helps in lowering the risk of colon cancer (BEHALL, *et al.*, 2002).

The ratio of amylose increases to over 50% in maize kernels homozygous for the null allele of the *amylose extender1 (ae1)* gene, which encodes starch branching enzyme 2b (SBE2b) (VINEYARD, *et al.*, 1958). In the GEMS-0067 maize line, which is homozygous for *ae1*, the proportion of amylose is over 70% (CAMPBELL, *et al.*, 2007). A strong quantitative trait locus (QTL) on the short arm of chromosome 5 (5S) was identified using an F2 population from a cross of GEMS-0067 and H99ae, a lower amylose line (WU, *et al.*, 2009).

Even though *starch branching enzyme1 (sbe1)* is located within this QTL, there is no direct evidence that allelic segregation of *sbe1* contributes to this QTL. To test if an allelic difference of *sbe1* is the cause of this QTL we contrasted two known facts: the QTL is additive (WU, *et al.*, 2009), and a null allele of *sbe1* (*sbe1-Mu*) acts as

a simple recessive (BLAUTH, *et al.*, 2002). If the amylose trait continues to demonstrate additivity in endosperm that is heterozygous for *sbe1-Mu*, it would indicate that some other closely linked locus, is responsible for the QTL. If the amylose trait demonstrates simple dominance when heterozygous for *sbe1-Mu*, it would indicate that *sbe1* is responsible for this QTL.

Materials and methods

In order to examine dominance relationship, plant homozygous for *sbe1-Mu* was crossed with a GEMS-0067/H99ae. The *sbe1-Mu* plant was in a W64A background and homozygous for *ae1*; it was obtained from Mark Campbell, Truman State University. The GEMS-0067 and H99ae stocks were the same as were used by Wu *et al.*, (2009). Several progeny of this cross were selfed, which produced kernels of five different genotypes (Figure 2.1).

Sample kernels were randomly selected from five selfed ears. These sample kernels were sliced horizontally to separate the endosperm distal to the scutellum (Figure 2.2). The distal portions were used to assay for relative amylose content; the proximal portions were germinated to produce leaf tissue that was used to obtain DNA for genotyping. DNA extraction was done with a Genomic DNA Mini Kit (IBI Scientific, Peosta, IA) using their protocol. Genotyping of each kernel was done in two-steps. Primer pairs 1A4/1A5 and 1A4/*Mu*TIR (Table 2.1) were used to distinguish the null *Mutator* allele from the alleles found in GEMS-0067 and H99ae (BLAUTH, *et al.*, 2002). Although both primer sets yield 500 bp products, 1A4/1A5 amplifies only wild-type alleles of *sbe1* while 1A4/*Mu*TIR amplifies only the null

allele (Figure 2.3). In the second step, the *sbe1* alleles from GEMS-0067 (*Sbe1-G*) and H99ae (*Sbe1-H*) are distinguished by restriction digest of a 906 bp PCR product that is produced with a different primer pair (sixth SNP forward and reverse, Table 2.1). The *Sbe1-H* product has an *AluI* restriction site, whereas the *Sbe1-G* product does not. Figure 2.4 shows the PCR products from *Sbe1-H* are cut into two smaller fragment of 617 and 289-bp by *AluI* digestion, but the *Sbe1-G* products are not. We tested a total of 71 individual kernels of which 10 were *Sbe1:G/Sbe1:G*, 16 were *Sbe1:G/sbe1:Mu*; 10 were *Sbe1:H/Sbe1:H*, 12 were *Sbe1:H/sbe1:Mu* and 23 were *sbe1:Mu/sbe1:Mu*.

The amylose assay was performed by the dual wavelength iodine-binding method (KNUTSON, *et al.*, 1994). The isolated endosperm from each individual kernel was crushed using a mortar and pestle. Approximately 10 mg of the endosperm sample was placed in a 1.5 mL centrifuge tube and mixed with 100 μ L of 3M CaCl_2 and vortexed for 60 s. After standing for 10 min, 900 μ L of 6.7×10^{-3} M iodine diluted in dimethyl sulfoxide (DMSO) was added. The iodine-starch samples were heated to 70°C for 15 min and a 100 μ L aliquot of the heated starch suspension was combined with 900 μ L of DMSO 6.7×10^{-3} M iodine in a 15 mL tube. A volume of 8 mL of deionized water was added to the starch-DMSO-iodine solution to form an amylose-iodine complex. One milliliter of the amylose-iodine complex was placed in the cuvette and absorbance was measured at 550 nm and 620 nm using Thermo Scientific Genesys-20 spectrophotometer (Thermo Fisher Scientific, Waltham, MA). In the presence of iodine, the peak absorbance of amylose and amylopectin occurs at 620 nm and 550 nm respectively (FAJARDO, *et al.*, 2013). Three technical replicates

were measured for each sample. The A_{620}/A_{550} ratios for each kernel was recorded and assigned to its corresponding genotype. Because the samples were from non-inbreds, care was made to insure that kernels of similar genotypes came from multiple ears. Duncan's multiple range test was done using R version 3.2.3 (R Core Team 2013).

Results

It was previously demonstrated that the null *sbe1:Mu* allele acts as a simple recessive as a heterozygote and results in a lower amylose ratio when homozygous in an *ae1* background (Blauth et al., 2002) This is in contrast to the QTL affecting amylose content, which is additive (WU, et al., 2009). If the amylose trait continues to demonstrate additivity in endosperm that are heterozygous for *sbe1-Mu*, it would indicate that some other locus, not *sbe1*, is responsible for the QTL. If the amylose trait demonstrates simple dominance when heterozygous for *sbe1-Mu*, this would indicate that *sbe1* is responsible for this QTL.

The mean A_{620}/A_{550} ratios for each genotype are portrayed in Figure 2.5. The mean A_{620}/A_{550} ratios of *Sbe1:G/Sbe1:G* and *Sbe1:G/sbe1:Mu* are equal to each other and are significantly higher ($P \leq 0.01$) than the other genotypes. The mean A_{620}/A_{550} ratios of *Sbe1:H/Sbe1:H* and *Sbe1:H/sbe1:Mu* are lower than those involving *Sbe1:G* ($P \leq 0.01$) but are equal to each other. The mean A_{620}/A_{550} ratios of *sbe1:Mu/sbe1:Mu* are significantly lower ($P \leq 0.01$) than the other four genotypes. Heterozygosity of *sbe1:Mu* with either the GEMS-0067 or H99ae *sbe1* alleles resulted in a dominance relationship relative to this trait rather than additivity.

Discussion

WU, *et al.* (2009) used the triploid model of inheritance to show that the variation in amylose content in endosperm starch between H99ae and GEMS-0067 was highly heritable. Furthermore, their models suggested a strong additive with lesser dominant component. However they were unable to explain the cause of high amylose QTL. Therefore we tried to explain whether or not *Sbe1* is the source of 5S QTL. Statistical analysis of our result shows that both *Sbe1:H* (allele associated with lower amylose) and *Sbe1:G* (allele associated with higher amylose) acts as simple dominants to the null *Sbe1:Mu* allele.

Two main pathways are involved in the production of amylose and amylopectin (JAMES, *et al.*, 2003, TETLOW, *et al.*, 2004). Granule-bound starch synthase helps in synthesis of amylose (DENYER, *et al.*, 2001, NELSON, *et al.*, 1962) and different isoforms of starch synthase, branching and debranching enzymes synthesize amylopectin. Three isoforms of starch branching enzymes have been recorded in maize: *Sbe1a*, *Sbe2a* and *Sbe2b* (DANG, *et al.*, 1989). These are encoded by *Sbe1*, *Sbe3* and *ae1* respectively. *Sbe2b*, predominates in maize endosperm and *Sbe2a* is inhibited by functional *Sbe1a* (YAO, *et al.*, 2004). During endosperm development, *Sbe1* mRNA expression peaks later than the other two isoforms of *Sbe2* (both *Sbe2a* and *Sbe2b*) mRNA (GAO, *et al.*, 1996). This differential expression suggests that *Sbe1* plays more important role in the later stage of endosperm starch synthesis. Synthesis of starch in endosperm is the result of protein-protein

interaction between starch synthesizing enzyme (JAMES, *et al.*, 2003). Zymogram analyses of maize *ae1* suggest that the interdependence of branching enzyme is a result of protein-protein interaction (COLLEONI, *et al.*, 2003). A similar result was shown in the endosperm amyloplasts of *T. aestivum*, which explains that Sbe1 and Sbe2 form phosphorylation-dependent protein complexes (TETLOW, *et al.*, 2004). However there were studies that showed that no any protein complexes were formed between Sbe1a and Sbe2b. HENNEN-BIERWAGEN, *et al.* (2009) explained that Sbe1a functioned independently and no other interaction was observed in either wildtype or mutant *ae1*.

In maize, the homozygous null allele of *sbe1* results in reduced amylose in the endosperm starch (BLAUTH, *et al.*, 2002), however the branching pattern has been changed comparison to wild type (XIA, *et al.*, 2011). It was consistent with another study done in rice where an *sbe1* null allele resulted in increased proportion of amylopectin (SATO, *et al.*, 2003). Paradoxically a double mutant of *sbe1a* and *ae1* results in decreased amylose content in the endosperm starch (YAO, *et al.*, 2004). If this proposition holds true, then the Sbe1 protein either solely or interacting with Sbe2 should have some effect in increasing amylose in *ae1* background.

Table 2.1 Primers for genotyping sbe1 alleles.

Name of Primers	Sequence
1A4	5'-TGGGATGCGATTTGCCGGGAAATACAG-3'
1A5	5'-CTCTGGAAGCTTTGACGTCGATGCTC-3'
<i>Mu</i> TIR	5'-AGAGAAGCCAACGCCA(AT)CGCCTC(CT)ATTTTCGTC-3'
Sixth SNP Forward	5'-GTACACATTTAAGCATCCTCGGC-3'
Sixth SNP Reverse	5'-CTGATCATGGCTCTCAGCATATG-3'

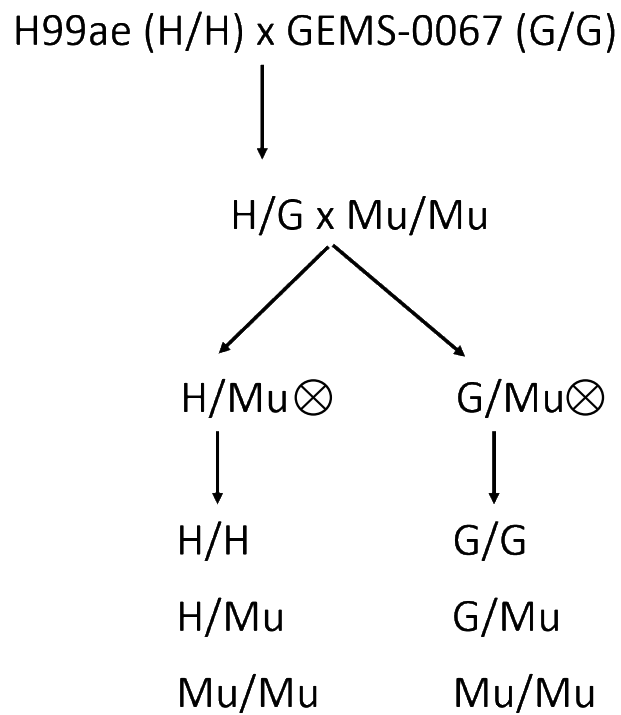


Figure 2.1 Generation of segregating population.

H/H: Plants homozygous for H99ae allele of *sbe1*; G/G: Plants homozygous for GEMS-0067 allele of *sbe1*; H/G: Plants heterozygous for H99ae and GEMS-0067 alleles of *sbe1*; H/Mu: Plants heterozygous for H99ae and null allele of *sbe1*; G/Mu: Plants heterozygous for GEMS-0067 and null alleles of *sbe1*; Mu/Mu: Plants homozygous for null allele of *sbe1*.

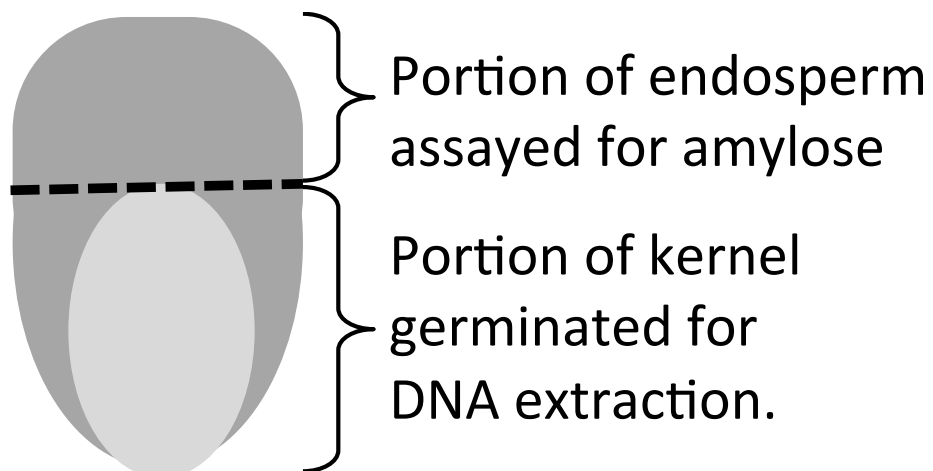


Figure 2.2 Diagram showing how kernels were separated for phenotyping and genotyping.

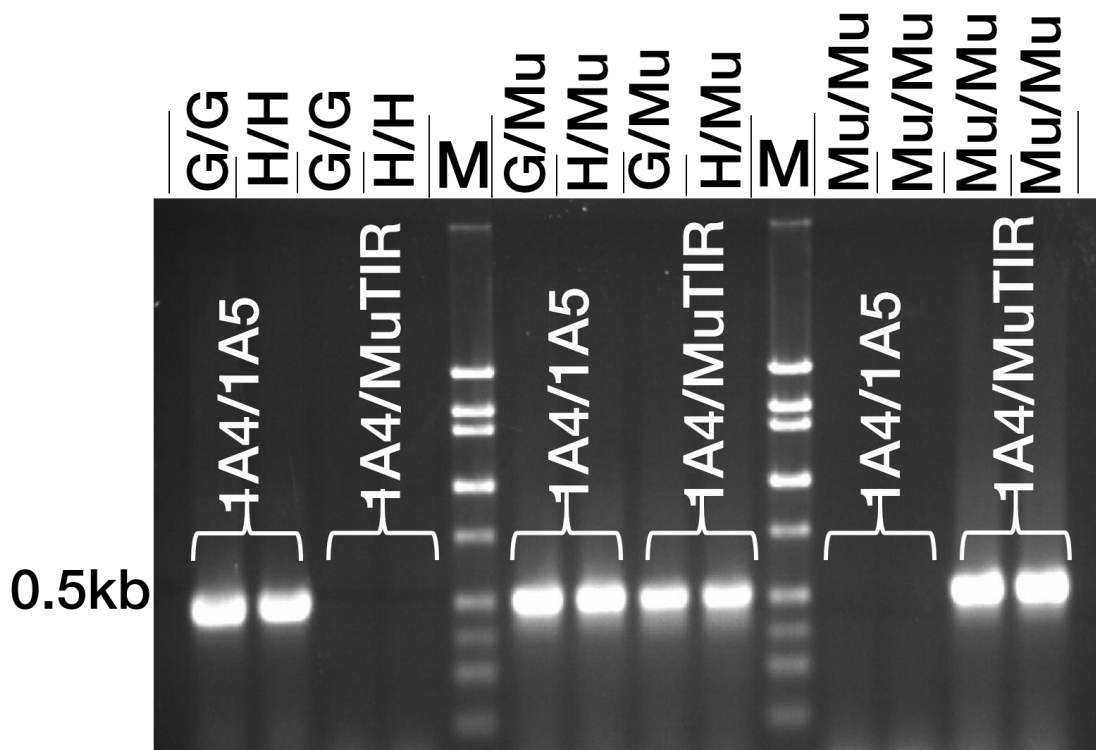


Figure 2.3 PCR genotyping of maize kernels for *sbe1-Mu* versus the wild-type alleles. First two lanes of each group of four show the products of primer set 1A4 and 1A5, which produces a 0.5 kb band only from wild-type alleles of *sbe1*. The latter two lanes of four show products from primer set 1A4 and MuTIR, which also amplifies a 0.5 kb product, but only from the *sbe1-Mu* allele. The genotypes are indicated above each lane. G/G: homozygous for GEMS-0067 alleles (*Sbe1:G/Sbe1:G*); H/H: homozygous for H99ae alleles (*Sbe1:H/Sbe1:H*); G/Mu; heterozygous *Sbe1-G/sbe1:Mu*; H/Mu heterozygous *Sbe1:H/sbe1:Mu*; and Mu/Mu homozygous *sbe1:Mu/sbe1:Mu*. MW = 100-bp low scale DNA ladder (Thermo Fisher Scientific, Waltham, MA).

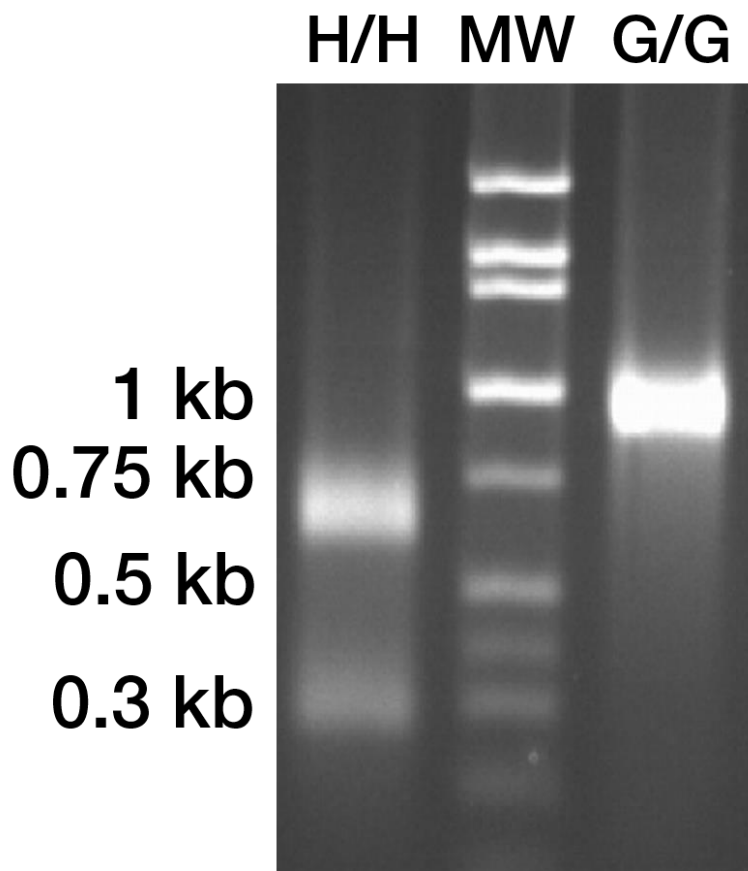


Figure 2.4 Distinguishing *sbe1* alleles originating from H99ae and GEMS-0067.

Lanes under H/H and G/G show PCR products using “Sixth SNP” primers (Table 2.1) that amplify an internal segment of *sbe1*. The left lane (H/H) was from a kernel that was homozygous for the H99ae *sbe1* allele and the right lane (G/G) was from a kernel that was homozygous for the GEMS-0067 *sbe1* allele. Both PCR products were digested with AluI restriction endonuclease. The 906-bp products from G/G were not cut, whereas the H/H products were cut into two smaller fragments of 617 bp and 289-bp. MW = 100-bp low scale DNA ladder (Thermo Fisher Scientific, Waltham, MA);

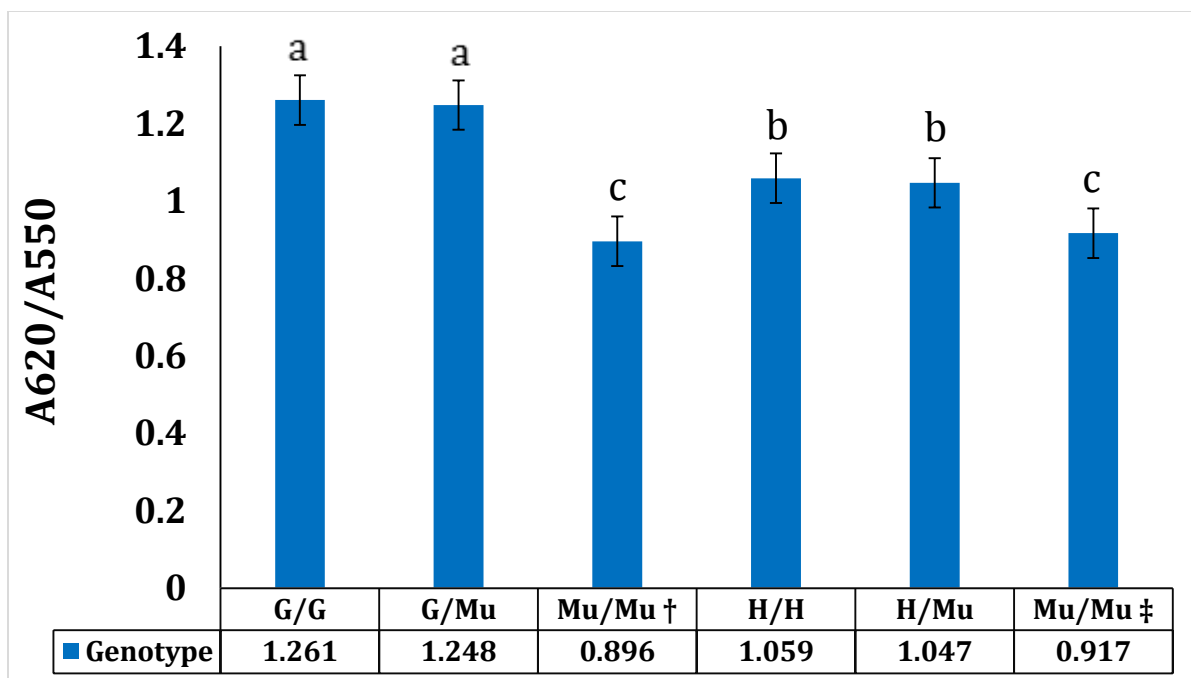


Figure 2.5 Absorbance ratios of 620 nm/550 nm per genotype. The means with the same letter are not significantly different, otherwise they are significantly different ($P < 0.01$).

†: Mu/Mu plants from G/Mu self progeny. ‡: Mu/Mu plants from H/Mu self progeny.

Chapter 3 Phylogenetic analysis of *sbe1* in maize

Introduction

Maize (*Zea mays mays*) was domesticated from Mexican teosinte (*Zea mays parviglumis*) about 5000 to 10,000 year ago (MATSUOKA, *et al.*, 2002). Molecular diversity in maize is around two to five fold higher compared with other grass crops (BUCKLER, *et al.*, 2001). During domestication, much of the transformation took place in the ear (DOEBLEY, 1992). This observation was consistent with BEADLE (1939) who suggested that differences between maize and teosinte is controlled by five key traits.

Among all the traits that differ between modern maize and teosinte, kernel weight shows significant variation and it directly depends on the amount of starch that accumulates in the endosperm. Starch is composed of two forms; straight chained amylose and highly branched amylopectin (BANKS, 1975). Generally, maize endosperm starch is composed of about 25% amylose and 75% amylopectin (NELSON, *et al.*, 1995). More than 20 genes have been identified that are involved in starch synthesis (MYERS, *et al.*, 2000, NELSON, *et al.*, 1995). Enzymes encoded by *sbe1*, *ae1*, *su1* and *wx1* collectively participate in starch synthesis (FISHER, *et al.*, 1983, JAMES, *et al.*, 1995). Strong selection has been reported in *ae1* and *su1* but no evidence of selection has been demonstrated for *wx1* (WHITT, *et al.*, 2002), which may indicate that high amylopectin was the target of selection.

The published *sbe1* sequence data indicate that commercial dents are remarkably uniform (HUANG, 2012). We studied the phylogenetics and selection of *sbe1* using synonymous and nonsynonymous changes in the sequence from 17 different samples.

Methods

Sequencing of alleles

For this study we sequenced 17 varieties (Table 3.1), including two teosinte genotype; *Zea diploperennis*, *Zea mays ssp. parviglumis*. The seventeen varieties were chosen to represent modern commercial variety belonging to different heterotic group. Sorghum was used as an out group for analysis (GenBank accession: EF089838). Seeds were germinated and around 1 g of leaf tissue was taken from each seedling. DNA extraction was done with a Genomic DNA Mini Kit (IBI Scientific, Peosta, IA) using their protocol.

Polymerase chain reaction (PCR) was carried out using genomic DNA as the template. Thirteen primer sets were used to sequence the transcribed region of the *sbe1* gene (Table 3.2). B73 was used as the reference genome for the design of these primers

(http://popcorn.maizedb.org/search/project_search/project_search.php?record=1232999). Each reaction mixture contained 10ul of GoTaq Green Master Mix (Promega, Madison, WI), 0.5 μ M each of forward and reverse primer, 50 ng of DNA sample and sufficient water to make a final volume of 20 μ l. All the amplification were conducted with initial denaturation at 95°C for 5 min., followed by denaturation at 94 °C for 30 sec., annealing at 60 °C for 30 sec., extension at 72 °C for

1 min. and a final extension at 72 °C for 7 min. Denaturation, annealing and extension were repeated for 35 cycles. The PCR product was loaded onto a 0.6% general purpose agarose (MIDSCI, St. Louis, MO) gel with TAE buffer with a 100bp Low Scale DNA Ladder (Fisher BioReagents, Pittsburgh, PA). After running, the gels were stained with ethidium bromide. The amplicon of expected size was excised with razor under UV light and the gel fragment was cleaned following the protocol of the Gel/PCR DNA fragment extraction kit (IBI Scientific, Peosta, IA). The extracted DNA was then sent to Nevada Genomics Center (University of Nevada, Reno) for Sanger sequencing.

Data Analysis

The sequences were analyzed visually using Chromas v 2.0.0 software and whenever required, edited using chromatogram. Nucleotide and derived amino acid polymorphisms were detected by aligning sequences with CLUSTALW using MEGA version 7 (KUMAR S, 2016). We tested for neutrality of polymorphism using Tajima's D test (TAJIMA, 1989) and (FU, *et al.*, 1993) *F* tests as applied in DNA-SP (LIBRADO, 2009) with *S. bicolor* as outgroup. The neighbor joining (NJ) was used for tree construction and *Z* test of selection analyses were conducted using MEGA version 7 using bootstrap method with 1000 bootstrap replications.

Results

Nucleotide and amino acid polymorphisms

Out of a total 8550 bp DNA sequence (not shown), 174 single nucleotide polymorphisms (SNPs) (2.03 %) are observed. Most of these (79.31%) are found in

the noncoding region including 5' untranslated region (UTR) and introns. Excluding sorghum, 36 SNPs were observed in the open reading frame (ORF) (Table 3.3). Of these 36, 15 translated into amino acid polymorphism (Table 3.4).

Phylogenetic Analysis

Three phylogenetic trees of *sbe1* in genus *Zea* are constructed using *Sorghum bicolor* as the outgroup. Neighbor joining trees with 1000 bootstrap replications were made using DNA sequences (Fig 3.1), the open reading frames (Fig 3.2) and the amino acid sequences (Fig 3.3). Based upon analysis of protein domains (not shown) and SNPs in those domain, each tree can be divided into five clades. Clade I (Nueta Sweet, Mandan Black, M162W, CML 247, NC 358 and B73) share same amino acid at position 211 which is the Carbohydrate Binding Module (CBM). Mo18W and CML 277 at clade II share same amino acid at 213 (CBM), Ree Flint and Mandan Yellow Flint at clade III have same amino acid at position 70 and 490 (catalytic domain). Clade IV (*Parviglumis*, *Diploperennis*, NC 350 and GEMS-0067) share same amino acid at position 30 and 444 (catalytic domain) and the remaining (Mandan Yellow Flour, Mandan Red Clay and Bear Island) are assigned to clade V as no such significant SNPs were discovered.

Test for Selection

We used Tajima's *D* test to evaluate the role of selective process. Both coding and non-coding regions were used for this test. *D* (-1.63) was not found significant ($P > 0.05$) for whole DNA sequence meaning that the hypothesis of neutrality cannot be rejected. A similar result was found in Fu and Li's test (-2.02) with *S. bicolor* as

the outgroup. However, statistically it is very hard to detect a deviation from neutrality from these tests with the size of the sample used in this study.

We compared the synonymous and nonsynonymous polymorphism in the ORF of *sbe1* having 2474 nucleotides and 824 codons. Codon based Z test of selection indicated that the null hypothesis of strict neutrality ($d_N = d_S$) was rejected ($P = 0.00055$) in favor of the alternate hypothesis of purifying selection.

Discussion

We are interested in whether *sbe1* has been subjected to selection. For this study we used sequences of *sbe1* from 17 different genotype and SNPs detected among these seventeen genotypes are similar to the ones seen in CHEN, *et al.* (2013) and WU, *et al.* (2015).

Phylogenetic analysis reveals that clades are consistent in all three neighbor joining tree constructed using transcribed DNA, ORF and amino acid sequences (Fig 3.1, 3.2 and 3.3). Analysis of the clades, suggests that the *sbe1* alleles present in the maize lines GEMS-0067 and NC 350 are more ancestral because they occur in clade IV with teosintes. If we compare the amino acid (AA) polymorphism among the 17 varieties, we observed five polymorphic sites in the α -amylase catalytic domain of SBEI protein. Among those five AA polymorphism, a polymorphism at position 444; aspartic acid (D) is observed in all four varieties in clade IV; GEMS-0067, *Diploperennis*, *Parviglumis*, NC 350. A similar result was observed by (HUANG, 2012), when comparing *sbe1* transcripts from GEMS-0067, H99ae and B73. CHAW,

et al. (2004) and GAO, *et al.* (1996) reported that SBEI evolved prior to the divergence of monocots and dicots and is highly conserved for 140 million years.

Codon based *Z* test, which compares the polymorphisms that result in synonymous and non-synonymous changes in the coding sequence, indicates purifying selection in whole coding sequence of *sbe1*. A similar result has been observed with another gene involved in starch biosynthesis: *sh2*, which is indicated to be involved in a purifying selection in both cultivated and wild forms of maize (MANICACCI, *et al.*, 2007). Analyzing the maize subgenomes, (SCHNABLE, *et al.*, 2011, SCHNABLE, *et al.*, 2011) predicted that genes of subgenome 1 are subjected more to purifying selection than subgenome 2. WHITT, *et al.* (2002) proposed that because of the positions of *bt2*, *su1* and *ae1*, the selection process for these genes is still continuing for increased yield and increasing amylopectin content. Maize farmers and breeders in the past bred for high yield and increased starch content. However grain quality is also an important feature while breeding for high yield. We can see the evidence from gluten level in wheat and stickiness in rice. In maize, high amylopectin in starch influenced the pasting and gelatinization properties that could affect tortilla and porridge texture (CHEN, 1992, JANE, *et al.*, 1999, KLUCINEC, *et al.*, 2002). Therefore the selection for amylopectin would have been favored over amylose. This may be the reason why the modern maize varieties have low amylose level in the starch. Therefore we can propose that purifying selection evident in *sbe1* is turning into stabilizing selection. However this still needs to be confirmed.

Table 3.1. Name and source of all the seventeen genotypes used in our study

Name	Source
Ree Flint	PI 213764
<i>Z. m. parviglumis</i>	Ames 21894
Neuta Sweet	PI 213796
NC 358	Ames 27175
NC 350	Ames 27171
Mo 18W	PI 550441
M 162W	Ames 27134
Mandane Yellow Flour	PI 213794
Mandane Yellow Flint	PI 213800
Mandane Red Clay	PI 213807
Mandane Black	PI 213806
GEMS-0067	PI 643420
<i>Z. diploperennis</i>	PI 462368
CML 277	PI 595550
CML 247	PI 595541
Bear Island	PI 213801
B73	Transcript ID: GRMZM2G088753_T01

Table 3.2 Primers sets used for PCR amplification and their amplicon size

Primer Name	Sequence	Size
1A1 F	CCCGATGAAGTCAAGGATAGTG	572
1A1R	CCTAGCTGTCACTCCCTAGTAA	
1A2F	ATTGATGATCCGCTCCTGAAC	688
1A2R	GCTTTCTCAAGGAActCTCGAA	
1A3F	TGCCGTGCCACTCTATTT	992
1A3R	GATTGGCCTTTGGGCTTG	
1B3F	TGTTCATTCTAAGGCCGTTGTC	708
1B3R	CTCTCACTGTCCACCTCACTAA	
1C3F	CCGCATGTTCAATTCATCACTTT	844
1C3R	TATATCGGGTGCCGGACT	
1A4F	AACCTATAAGCAGGACACATGAA	615
1A4R	CACTGGACAGACAACACACT	
1A5F	TCTTCTGTACTGATGGTTCATAGTT	786
1A5R	CGGAAATGTTGATGATGCAGATAA	
1A6F	GCAGAAAGGATCAATTGAAGAA	945
1A6R	CTTAAATGTGTACCTGCAAACC	
1B6F	AAATGAGGGAAGTCTTGAATCT	623
1B6R	CGACCAAACAACCAAATTTATCC	
1C6F	GTCATGTCTTAGCTGAGGAG	684
1C6R	GCTCCATAACTGCCATCAA	
1A7F	AGCAATAGACCTTAGCAGACAAA	687
1A7R	ACAGCTGTGTCCAAACTGAA	
1A8F	GGCTTCCGATTTGATGGAGTTA	802
1A8R	CCAGGTTCAACCAGAActTGA	
1A9F	ACTATTGCATTTCTCCTGATGGA	909
1A9R	CCTAGAATGGTGCCAGAACAA	
1A10F	CACTGATCACTTGCCGTACA	739
1A10R	AAGAAAGAAACGTCGCAACAC	
1A11F	CGTTTGACCAAGCGATGAATG	751
1A11R	CGGAGAAAGGACTTTGAACGA	
1A12F	ATCATATCAGGCTGTCTGTTT	856
1A12R	GCTGAACAGCTGGAATCAAATG	
1B13F	CGAAAGCAGAGACAGGAAAGA	877
1B13R	TGACATTCAGCCACACACA	

Table 3.3 Single nucleotide polymorphism (SNP) of *Sbe1* ORF among 17 alleles from different *Zea mays*. Numbers on the top of each column shows the position of SNPs.

	88*	117	208*	413*	443*	450	504	597	627	632*	638*	692*
Ree Flint	C	C	C	G	C	G	G	A	A	G	G	G
Parviglumis	A	T	G	G	T	A	G	A	T	G	G	G
Neuta Sweet	C	C	G	G	C	G	G	A	A	T	G	G
NC 358	C	C	G	G	C	G	G	A	A	T	G	G
NC 350	A	T	G	G	C	A	G	A	T	G	G	T
Mo 18W	C	C	G	G	C	G	G	A	A	G	A	G
M 162W	C	C	G	G	C	G	G	A	A	T	G	G
M Y Flour	C	C	G	G	C	G	G	A	A	G	G	G
M Y Flint	C	C	C	G	C	G	G	A	A	G	G	G
M R Clay	C	C	G	G	C	G	G	A	A	G	G	G
M Black	C	C	G	G	C	G	G	A	A	T	G	G
GEMS-0067	A	T	G	A	T	A	G	A	T	G	G	T
Diploperennis	A	T	G	G	T	G	G	G	T	G	G	G
CML 277	C	C	G	G	C	G	A	A	A	G	A	G
CML 247	C	C	G	G	C	G	G	A	A	T	G	G
Bear Island	C	C	G	G	C	G	G	A	A	G	G	G
B73	C	C	G	G	C	G	G	A	A	T	G	G

	897	912	1210	1220*	1287	1290	1331*	1438*	1470*	1476	1542	1626
Ree Flint	G	C	T	T	G	G	C	C	A	C	G	T
Parviglumis	G	C	T	T	G	G	A	C	C	T	A	T
Neuta Sweet	G	C	T	T	G	G	C	T	C	C	G	T
NC 358	G	C	T	T	G	G	C	C	C	C	G	T
NC 350	G	C	C	T	G	A	A	C	C	T	A	T
Mo 18W	G	C	T	T	G	G	C	C	C	C	G	C
M 162W	G	C	T	T	G	G	C	C	C	C	G	T
M Y Flour	G	C	T	T	G	G	C	C	C	C	G	T
M Y Flint	G	C	T	T	G	G	C	C	A	C	G	T
M R Clay	A	T	C	T	G	G	C	C	C	C	G	T
M Black	G	C	T	T	G	G	C	C	C	C	G	T
GEMS-0067	G	C	T	C	G	A	A	C	C	T	A	T
Diploperennis	G	C	C	T	A	G	A	A	C	C	G	T
CML 277	G	C	T	T	G	G	C	C	C	C	G	T
CML 247	G	C	T	T	G	G	C	C	C	C	G	T
Bear Island	G	C	T	T	G	G	C	C	C	C	G	T
B73	G	C	T	T	G	G	C	C	C	C	G	T

	1716	1945*	1971	1980	1983	1986	1998	2186*	2238	2314*	2325	2450*
Ree Flint	T	G	G	G	C	C	C	C	G	C	G	C
Parviglumis	C	G	G	G	C	A	C	C	G	C	G	C
Neuta Sweet	T	G	G	G	C	C	C	C	G	C	G	C
NC 358	T	G	G	A	C	C	C	C	G	C	G	C
NC 350	C	G	G	G	C	A	C	C	G	C	G	A
Mo 18W	T	G	G	G	C	C	C	T	G	C	G	C
M 162W	T	A	G	G	C	C	C	C	A	C	G	C
M Y Flour	T	G	G	G	C	C	C	C	G	C	G	C
M Y Flint	T	G	G	G	C	C	C	C	G	C	G	C
M R Clay	T	G	G	G	C	C	C	C	G	C	G	C
M Black	T	G	G	G	C	C	C	C	G	C	G	C
GEMS-0067	C	G	G	G	C	A	C	C	G	C	G	C
Diploperennis	T	G	A	G	A	A	T	C	G	G	C	C
CML 277	T	G	G	G	C	C	C	C	G	C	G	C
CML 247	T	G	G	G	C	C	C	C	G	C	G	C
Bear Island	T	G	G	G	C	C	C	C	G	C	G	C
B73	T	G	G	G	C	C	C	C	G	C	G	C

* Nonsynonymous substitution

Table 3.4 Amino acid polymorphism of SBEI among 17 genotypes from different *Zea mays*. Numbers on the top of each column shows the position of AA polymorphism.

	30	70	138	148	211	213	231	407	444	480	490	649	729	772	817
Ree Flint	P	H	G	A	W	R	W	F	A	R	E	D	T	R	P
Parviglumis	T	D	G	V	W	R	W	F	D	R	D	D	T	R	P
Neuta Sweet	P	D	G	A	L	R	W	F	A	W	D	D	T	R	P
NC 358	P	D	G	A	L	R	W	F	A	R	D	D	T	R	P
NC 350	T	D	G	A	W	R	L	F	D	R	D	D	T	R	Q
Mo 18W	P	D	G	A	W	H	W	F	A	R	D	D	M	R	P
M 162W	P	D	G	A	L	R	W	F	A	R	D	N	T	R	P
M Y Flour	P	D	G	A	W	R	W	F	A	R	D	D	T	R	P
M Y Flint	P	H	G	A	W	R	W	F	A	R	E	D	T	R	P
M R Clay	P	D	G	A	W	R	W	F	A	R	D	D	T	R	P
M Black	P	D	G	A	L	R	W	F	A	R	D	D	T	R	P
GEMS-0067	T	D	E	V	W	R	L	S	D	R	D	D	T	R	P
Diploperennis	T	D	G	V	W	R	W	F	D	R	D	D	T	G	P
CML 277	P	D	G	A	W	H	W	F	A	R	D	D	T	R	P
CML 247	P	D	G	A	L	R	W	F	A	R	D	D	T	R	P
Bear Island	P	D	G	A	W	R	W	F	A	R	D	D	T	R	P
B73	P	D	G	A	L	R	W	F	A	R	D	D	T	R	P

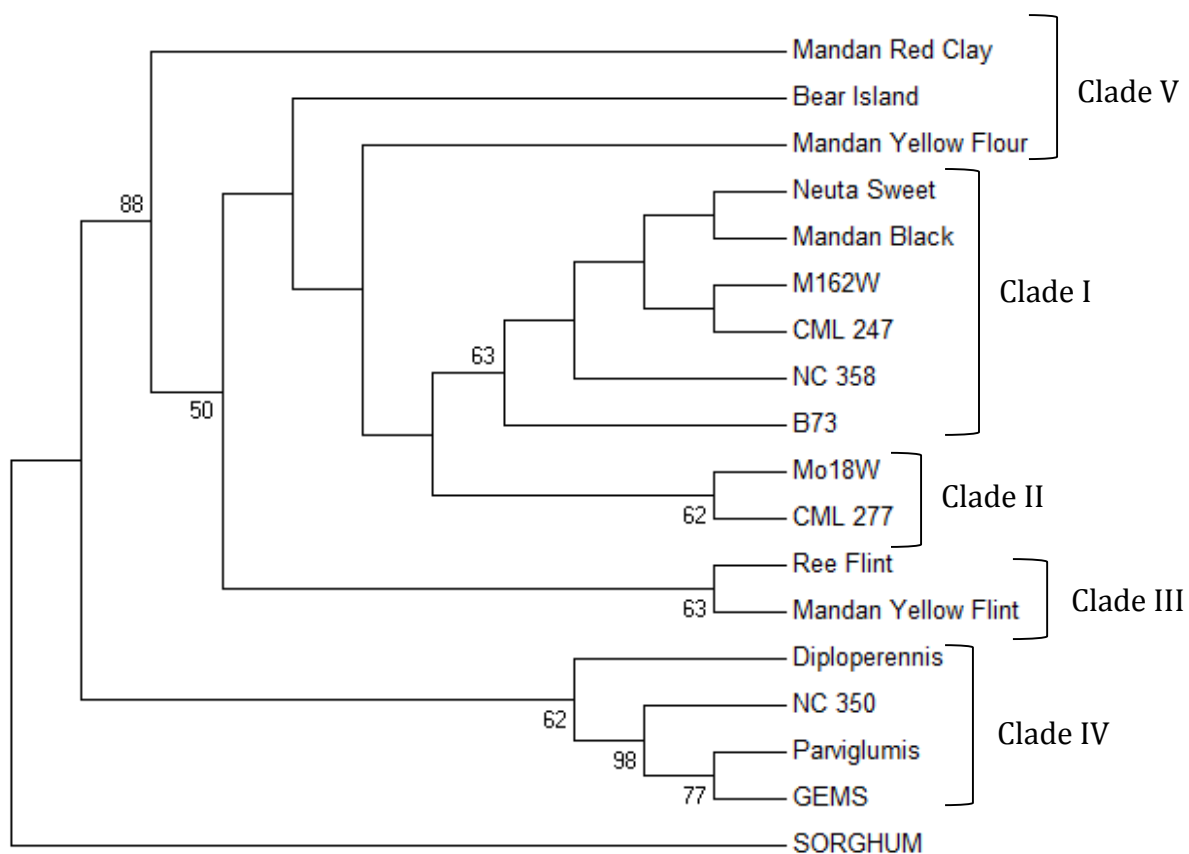


Figure 3.1 Neighbor joining tree based *sbe1* DNA sequence from 17 *Zea* accessions with *S. bicolor* as outgroup. The values above the branches are the bootstrap support of 1000 replications.

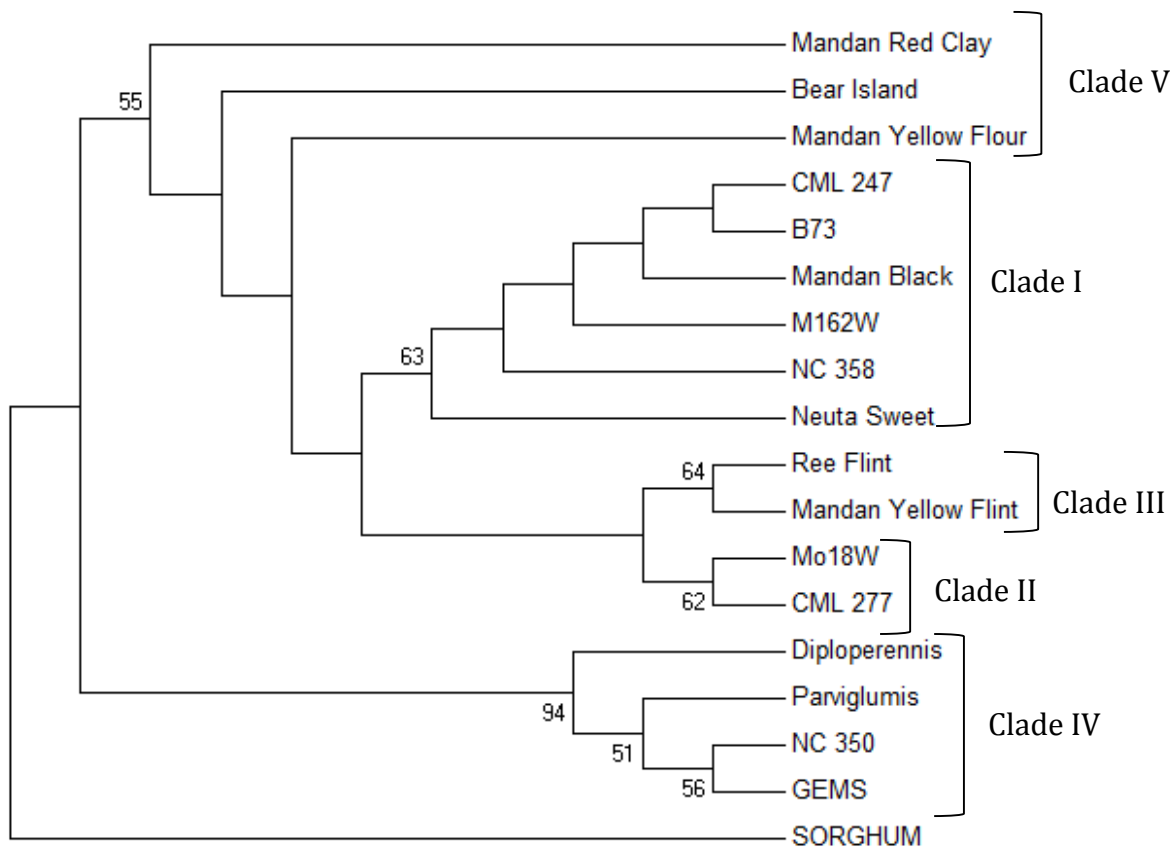


Figure 3.2 Neighbor joining tree based *sbe1* reading frame from 17 *Zea* accessions with *S. bicolor* as outgroup. The values above the branches are the bootstrap support of 1000 replications.

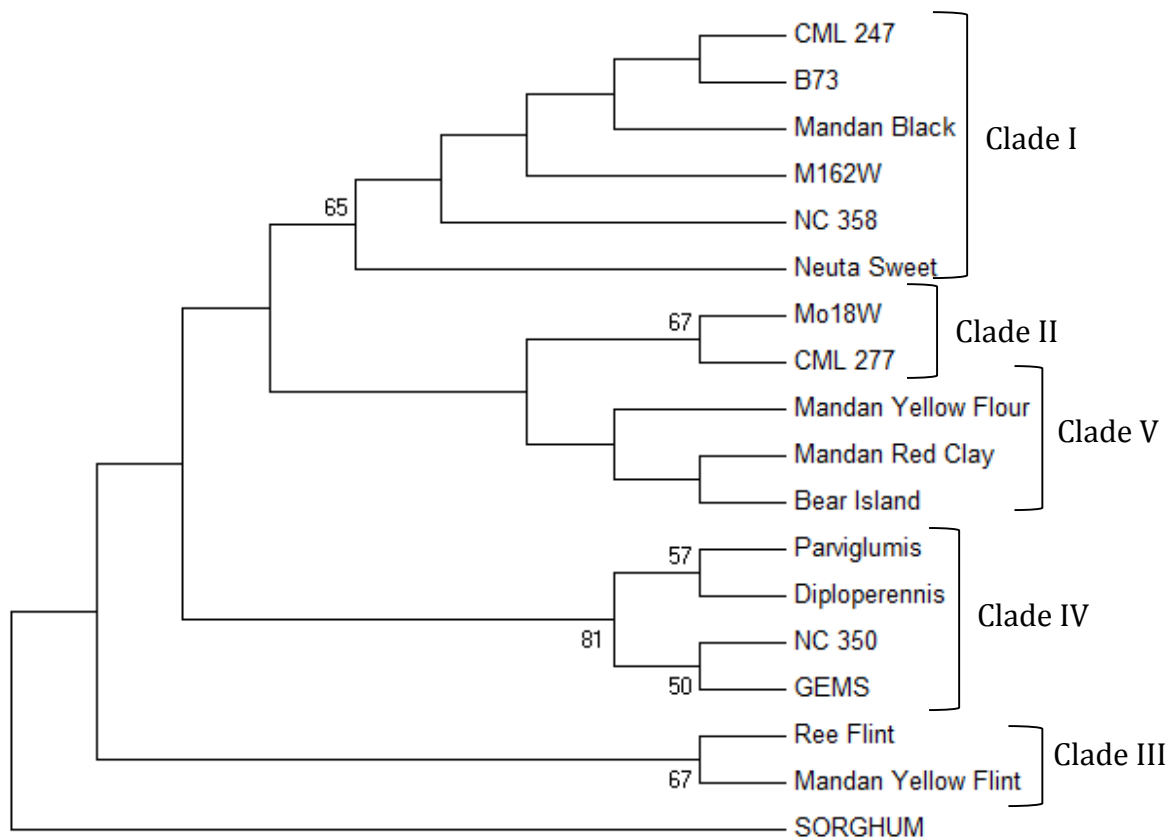


Figure 3.3 Neighbor joining tree based *sbe1* amino acid sequence from 17 *Zea* accessions with *S. bicolor* as outgroup. The values above the branches are the bootstrap support of 1000 replications.

Chapter 4 Summary and future work

Previously our lab proposed *starch branching enzyme 1 (sbe1)* as a candidate gene for high amylose endosperm starch QTL. So we were interested in knowing whether this particular enzyme is actually the source of high amylose or not. For this we introduced null allele of *sbe1* against the two wild type alleles of *sbe1* that are found in GEMS-0067 and H99ae, ultimately to produce five segregated population; G/G, G/mu, H/H, H/mu and mu/mu. Estimating the amylose content revealed that G/G and G/mu; H/H and H/mu had similar amylose content and higher than mu/mu. This was the result of dominance relationship between the wild and the mutant which led us to conclude that allelic segregation of *sbe1* is the basis for the QTL.

In most maize, amylopectin content is much higher than amylose, but GEMS-0067 is the only publicly available inbred having higher amylose than amylopectin. A previous study suggested that *sbe1* in GEMS-0067 may be more ancestral and proposed that *sbe1* in modern maize may have been selected during the improvement of maize. To validate this proposition we used *sbe1* sequence from seventeen varieties including two teosinte; *parviglumis* and *diploperennis* in our study. Phylogenetic analysis of these 17 genotypes validated that *sbe1* in GEMS-0067 along with NC 350 is ancestral as it is grouped together with *parviglumis* and *diploperennis*. We compared the synonymous and nonsynonymous polymorphism *sbe1* ORFs having 2474 nucleotides and 824 codons. Codon based *Z* test of selection

indicated that the null hypothesis of strict neutrality ($d_N = d_S$) was rejected ($P = 0.00055$) in favor of the alternate hypothesis of purifying selection.

Since we have now established that *sbe1* is the source of amylose QTL, future direction of this project can be focused in determining which amino acid polymorphism or combination of polymorphism is responsible for the trait. One strategy for achieving the goals would be comparing the amino acid sequence in maize varieties of high and low amylose content. Having larger sample for comparing the polymorphisms and amylose contents, we gain confidence as to what polymorphisms are important for increasing amylose content.

Another question that we could address is the relationship between amylose content and yield. During the field trial, we have observed that high amylose corn have small size kernel, which may affect the overall productivity of crop. Therefore unveiling the correlation between yield and amylose would encourage breeder to work on increasing amylose content without reduction in the yield.

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Appendix

Appendix 1. Absorbance at 550 nm and 620 nm

Genotype	Source	620/550	Genotype	Source	620/550
G/G	G/Mu x G/Mu	1.265051	H/H	H/Mu x H/Mu	1.045089
G/G	G/Mu x G/Mu	1.28621	H/H	H/Mu x H/Mu	1.019286
G/G	G/Mu x G/Mu	1.253089	H/H	H/Mu x H/Mu	1.030357
G/G	G/Mu x G/Mu	1.231185	H/H	H/Mu x H/Mu	1.087193
G/G	G/Mu x G/Mu	1.28391	H/H	H/Mu x H/Mu	1.079758
G/G	G/Mu x G/Mu	1.267436	H/H	H/Mu x H/Mu	1.064552
G/G	G/Mu x G/Mu	1.252882	H/H	H/Mu x H/Mu	1.061153
G/G	G/Mu x G/Mu	1.261297	H/H	H/Mu x H/Mu	1.067246
G/G	G/Mu x G/Mu	1.272921	H/H	H/Mu x H/Mu	1.073904
G/G	G/Mu x G/Mu	1.236246	H/H	H/Mu x H/Mu	1.065122
G/Mu	G/Mu x G/Mu	1.257426	H/mu	H/Mu x H/Mu	1.039941
G/Mu	G/Mu x G/Mu	1.242699	H/mu	H/Mu x H/Mu	1.02637
G/Mu	G/Mu x G/Mu	1.264357	H/mu	H/Mu x H/Mu	1.012863
G/Mu	G/Mu x G/Mu	1.264706	H/mu	H/Mu x H/Mu	1.081569
G/Mu	G/Mu x G/Mu	1.23945	H/mu	H/Mu x H/Mu	1.029377
G/Mu	G/Mu x G/Mu	1.244009	H/mu	H/Mu x H/Mu	1.019777
G/Mu	G/Mu x G/Mu	1.249462	H/mu	H/Mu x H/Mu	1.060144
G/Mu	G/Mu x G/Mu	1.238901	H/mu	H/Mu x H/Mu	1.096954
G/Mu	G/Mu x G/Mu	1.230723	H/mu	H/Mu x H/Mu	1.059343
G/Mu	G/Mu x G/Mu	1.266304	H/mu	H/Mu x H/Mu	1.034157
G/Mu	G/Mu x G/Mu	1.256987	H/mu	H/Mu x H/Mu	1.044248
G/Mu	G/Mu x G/Mu	1.242849	H/mu	H/Mu x H/Mu	1.059524
G/Mu	G/Mu x G/Mu	1.274676	mu/mu	H/Mu x H/Mu	0.927031
G/Mu	G/Mu x G/Mu	1.212166	mu/mu	H/Mu x H/Mu	0.898392
G/Mu	G/Mu x G/Mu	1.253968	mu/mu	H/Mu x H/Mu	0.870982
G/Mu	G/Mu x G/Mu	1.238271	mu/mu	H/Mu x H/Mu	0.939048
Mu/Mu	G/Mu x G/Mu	0.903191	mu/mu	H/Mu x H/Mu	0.933836
Mu/Mu	G/Mu x G/Mu	0.917277	mu/mu	H/Mu x H/Mu	0.927176
Mu/Mu	G/Mu x G/Mu	0.867851	mu/mu	H/Mu x H/Mu	0.938621
Mu/Mu	G/Mu x G/Mu	0.923111	mu/mu	H/Mu x H/Mu	0.93626
Mu/Mu	G/Mu x G/Mu	0.899613	mu/mu	H/Mu x H/Mu	0.922838
Mu/Mu	G/Mu x G/Mu	0.912054	mu/mu	H/Mu x H/Mu	0.902868
Mu/Mu	G/Mu x G/Mu	0.898408	mu/mu	H/Mu x H/Mu	0.908517
Mu/Mu	G/Mu x G/Mu	0.862646	mu/mu	H/Mu x H/Mu	0.912213
Mu/Mu	G/Mu x G/Mu	0.869996	mu/mu	H/Mu x H/Mu	0.905512
Mu/Mu	G/Mu x G/Mu	0.913892			

Appendix 2. DNA sequence from seventeen varieties

>B73

GTCGACTGCCCTCTAGACCCCGATGAAGTCAAGGATAGTGAGCGCCCAACCAAGTTTAGGCTCCCCAGCCAGATGATCATGTTA
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 GAAGGGAAAGAGGAAAACGAATGATGATAGCTGCATCAGTTCACCAACATCCTTGACCAGGGTCATCAGTGGGATTGATGATCC
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Appendix 3. ORF from seventeen varieties

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