International Journal of Plant Breeding ©2007 Global Science Books

Breeding for Increased Sweetness in Sweet Corn

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ABSTRACT

Sweetness, a creamy texture and aroma, along with desirable kernel color, good germination, and high yield, are the important traits for sweet corn. Various recessive mutants in corn expressed in the endosperm e.g. sugary1 (su_1), sugary enhancer (*se*), shrunken2 (sh_2), brittle1 (*bt*) etc., which improve quality traits such as sweetness, flavor and nutritive value have been used either singly or in combination for developing new commercial hybrids. In single mutant varieties, at harvest (20 days after pollination), the sugar (sucrose) concentration in su_1 and sh_2 sweet corn is 3 and 8 times higher than wild type, respectively. For *se*-type when in combination with su_1 the sucrose level is as high as that in sh_2. After harvest, the sugar in kernels of su_1 and *se* types is rapidly converted to starch, but this conversion occurs more slowly in sh_2 type. However, both su_1 and *se* sweet corn have more phytoglycogen or creamy texture, than sh_2 variety without difficulties in germination. The details of breeding methods using a combination of endosperm genes for sweetness improvement are disclosed in the U.S. Patents Nos. 3,971,161 and 4,630,393. To date, two new high sugar types of commercial sweet corn, synergistic and augmented sweet varieties have been developed and released by U.S. seed companies. Synergistic has a combination of su_1, *se*, and sh_2 kernels on each ear. It carries the seed quality and vigor of su_1 varieties, the enhanced sweet corn flavor of *se* and harvest-ability and shelf life approaching supersweet (sh_2) type. Augmented sweet varieties, sh_2 type, carry *se* modifier genes for tenderness and sweetness and the sh_2 gene for high sugars and long shelf life.

Keywords: augmented shrunken, eating quality, endosperm mutants, flavor improvement, quality improvement, supersweet corn, synergistic, triple sweet

Abbreviations: WSP, water soluble polysaccharide

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INTRODUCTION

Sweet corn (*Zea mays* L. var. *rugosa* Bonaf.) eaten in the immature stage, is widely used for human consumption throughout the world. It is an important source of fiber, minerals, and certain vitamins. It is produced for three distinct markets; fresh, canning, and freezing. Production within these markets is largely independent of each other. Newly developed products such as sweet corn milk and soups are gaining popularity in many countries. New varieties of sweet corn have been developed with improved consistency, taste and shelf life. The adoption of newer "high sugar or sweeter" varieties with longer shelf life and new sweet corn products have increased sweet corn consumption and have helped to further expand the market.

Sweet corn eating quality of fresh or processed whole-kernels, canned or frozen, is determined by its unique combination of flavor, texture, and aroma. Sweetness is the most important factor in consumer satisfaction with sweet corn (Evensen and Boyer 1986). It makes up most of flavor and depends largely on kernel sucrose content. Texture is determined primarily by pericarp tenderness, levels of water soluble polysaccharides (phytoglycogen), and kernel moisture content.

The contents of this mini-review are about the economic value of sweet corn, types of important endosperm mutants, and the development of sweet corn breeding for sweetness.

ECONOMIC VALUE OF SWEET CORN

According to the Food and Agriculture Organization of the United Nations statistic data, in 2005 the world's sweet corn production for the fresh, frozen and canned food industries by harvested area is about 1.06 million ha. In 2004, the world's top four leading producers were the US (4.12 million MT), Mexico (0.63 million MT), Nigeria (0.58 million MT) and France (0.50 million MT). The world's top four leading exporters of canned sweet corn are the US (0.14

Received: 28 February, 2007. Accepted: 9 April, 2007.

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million MT), Hungary (0.13 million MT), France (0.11 million MT), and Thailand (0.10 million MT). And the world's top four leading exporters of frozen sweet corn are the US (0.07 million MT), Hugary (0.04 million MT), New Zealand (0.03 million MT), and Belgium (0.02 million MT). Global imports of canned sweet corn are valued over $468 million in 2004. The top five importing countries are the Russian Federation (0.09 million MT), Germany (0.06 million MT), the UK (0.05 million MT), Japan (0.05 million MT), and the Republic of Korea (0.04 million MT). The global imports of frozen sweet corn were valued over $218 million. And, the top five importing countries for frozen sweet corn are the UK (0.07 million MT), Japan (0.05 million MT), Belgium (0.02 million MT), the U.S. (0.02 million MT), and China (0.01 million MT). In terms of per capita consumption sweet corn, the US currently consumes 2.5 kg per year higher than the EU (1.5 kg per year). And, French per capita consumption is one of the highest in Europe (Hénard 2003).

TYPES OF IMPORTANT ENDOSPERM MUTANTS

Sweetness is affected by the amounts of sugar and starch in the endosperm. One of the areas of genetic improvement of sweet corn has involved the selection of mutants that produce high sugar levels in the kernel endosperm. To date, starch biosynthesis and the genetic modification of endosperm carbohydrates have been researched and reviewed. Several endosperm genes used in sweet corn improvement to increase sugar content and decrease starch content have been identified (Creech 1965; Boyer and Shannon 1984; Tracy 1997). Four most useful mutants are shrunken2 (sh_2), brittle1 (*bt*), sugary1 (su_1), and sugary enhancer1 (*se*).

The sh_2 and *bt* located in chromosome 3 and 5, respectively are classified as class 1 mutants involved in large reductions in starch and large increase in sugar. Mature dry kernels of both mutants are collapsed, angular, opaque and brittle. While the su_1 and *se* located in chromosome 4 and 2, respectively are the class 2 mutants occurred later in the starch biosynthesis pathway and changed types and proportion of types of polysaccharides stored in the endosperm. Mature dry kernels of the su_1 are wrinkled and translucent. While *se*'s kernels observed only in su_1 lines, were inflated, light colored, slow drying, color varies with background, collapsed, angular, opaque and brittle. The class 1 mutants are epistatic to class 2 mutants (Boyer and Shannon 1984; Tracy 1997).

THE DEVELOPMENT OF SWEET CORN BREEDING FOR SWEETNESS

Standard or conventional sweet corn breeding method has been used to develop commercial hybrids by breeders for more than century. This method involves the development of homozygous inbred lines by selfing and selection of desired phenotypes using pedigree selection from broad-based breeding populations, the crossing of these inbred lines, and the evaluation of the hybrids from the crosses to determine which have commercial potential. The most efficient method used for flavor screening is bite taste at marketing stage.

Sweet corn breeders have been extensively and successfully used 4 mutants, sh_2, *bt*, su_1, and *se*, singly or in combination in modern breeding to create new "high sugar" commercial sweet corn varieties. The breeding work has been centered on manipulation of these endosperm genes which control the level of sugar found in the corn kernel. As a results, 4 groups of sweet corn: standard, supersweet, sugary enhanced, and high sugar sweet corn, have been developed and successfully used for commercial production.

Standard sweet corn varieties

Standard or traditional sweet corn varieties are su_1 mutants. The su_1 varieties, at immature milky stage (20 days after pollination), contain 10.2% of sucrose and 22.8% of water soluble polysaccharide (WSP), a creamy texture, about 3 and 8 times the sugar and WSP contents of field corn, respectively (Creech 1965). The sugary varieties have a creamy texture and good corn flavor and are known for their good germination and seedling vigor. But their kernels can lose their sucrose from 14.4% to 5.7% (about 2.5 times) at room temperature (27.0°C) 24 hours after harvest due to sucrose rapidly converting to starch (Garwood *et al*. 1976). These losses greatly affect the eating quality. As a result, the harvest and storage periods for the su_1 varieties are short. These varieties are suitable for processing, e.g., canning and freezing.

Most of sugary-type sweet corn breeding works for temperate region have been done in the US. Dantings Early was one of the first named sweet corn varieties that appeared in 1844 (Galinat 1971) while Golden Bantam, released in 1902, became one of the most important open-pollinated varieties. Many new hybrid varieties such as Jubilee, Silver Queen (the most popular roadside market sweet corn variety in the US), Golden Cross Bantum, Early Sunglow, Merit, Seneca Chief, Bonanza and Earlivee have been developed and marketed.

Sugar-enhanced sweet corn varieties

The *se* type varieties have a sugar content twice as much as normal sweet corn, extremely tender kernels, creamy texture and good corn flavor. Sugar conversion occurs at the same rate as for the su_1 type since the kernels contain more sugar, their sweet taste retain longer after harvest. There are two distinct groups within the varieties containing the *se* gene: homozygous and heterozygous. The homozygous varieties (*sese* su_1su_1) have higher sugar (20% to 35%) in 100% of their kernels. While the heterozygous varieties (*Sese* su_1su_1) have lower sugar (14% to 25%) and only 25% of the *se* type kernels and 75% of the su_1 type therefore, homozygous varieties are usually sweeter than heterozygous varieties (Tracy 1997).

High quality commercial *se*-hybrids have been developed and commercialized such as Seneca Arrowhead and Temptation from Seminis Seeds; Sugar Buns and Miracle from Crookham, Co.; and Spring Treat and Merlin from Mesa Maize, Inc.

However, progress in developing *se* hybrids has been relatively slow due to the difficulty in identifying its presence in dry seeds and its undesirable pale yellow kernel color. Also, it appears that a number of recessive modifiers are required to attain high quality su_1se hybrids (Tracy 1997).

Supersweet or extrasweet corn varieties

The sh_2 mutants at the immature milky stage (20 days after pollination) contain 29.9% sucrose, the highest amount, about 3 and 8 times the sugar content of the su_1 (10.2%) and field corn (3.5%), respectively. And it retains this level longer and has less starch than su_1, but has a less creamy texture due to very little WSP (Creech 1965). From Nelson's study in 1980, at 21 days after pollination the *bt* kernels contain 19.3% less sucrose than the sh_2 kernels (22.5%) but higher than field corn (2.9%). The texture of supersweet corn is crispy rather than creamy as with the standard and enhanced varieties. The fresh market shelf life is extended because of the slower conversion of sugars to starch after harvest. Seed kernels are lighter in weight, shrunken in appearance and difficult to germinate under cold soil temperature.

Supersweet corn sh_2-type in the US was firstly developed by Professor John Laughnan, University of Illinois in the 1950's. Illinois Foundation Seeds Inc. (IFSI) is the first seed company to release a supersweet corn and it is called "Illini Xtra Sweet". In the early 1980s a widespread use of the supersweet corn hybrid, from 2 to over 90% within five years, has started in the Florida growing area after a successful marketing campaign by Abbott and Cobb Inc., to educate wholesale buyers, consumers and growers about the superior qualities of supersweet corn. And the same trend occurred throughout the US for all sweet corn grown for long-distance shipping. Simultaneously, the introduction of new supersweet hybrids with necessary processing traits marked the beginning of canned supersweet corn industry (Pataky 2003).

Supersweet corn varieties, both sh_2- and *bt*-types for the tropic were developed by Professor James Brewbaker, University of Hawaii in the 1960's. Seventeen populations of sweet (su_1 gene) and supersweet corn (*bt*, bt_2 and sh_2 genes) have been bred in Hawaii for quality, yield, and tolerance to maize mosaic virus and other diseases. These populations offer tropical breeders some of the best germplasm for sweet and supersweet corn improvement. Several of the varieties are in commercial use internationally, as they have been informally released during earlier cycles of breeding since 1968 (Thailand, sh_2 COMP 1). All have a foundation in Hawaiian Sugar (tracing to Cuban × Golden Bantam), with inputs from many different sources. The most widely grown OP populations are "Hawaiian Supersweet #9", *bt* and "Thai Supersweet", a yellow sh_2 population. Collaborative studies in Hawaii, Australia and Thailand have led to the development of commercially successful hybrids of these sweet corns, which have expanding importance for fresh and processing markets in Asia. Widely grown supersweet hybrids include "Hawaiian Supersweet #10", a 3-way *bt* hybrid, Australia's "H5", a singlecross sh_2 hybrid, and Thailand's sh_2 hybrids: ATS-5, Sugar-75, Hibrix3; *bt*: ATS-8. Several companies now market tropical supersweets, the most extensive being that of Pulam's "Sweet Seed Co." in Thailand, and the products are well accepted by public (Brewbaker *et al*. 2006).

These newer supersweet varieties are becoming the dominant type in all major US sweet corn production regions and many countries in Asia, Europe, South America and Africa. It is popularly known due to its higher sugar content and long shelf life, suitable for long-distance shipping. And it has enabled manufacturers to can sweet corn without adding sugar.

High sugar sweet corn varieties

Although there are many commercial varieties of sweet corn containing an individual gene of su_1, *se*, sh_2, or *bt*, which provide a number of useful traits, these varieties are not without their problems. Sugary varieties lose their sweetness rapidly after maturity. Supersweet (sh_2, or *bt*) varieties have a tough pericarp, lack creaminess, poor corn flavor and poor germination. Sugary enhanced varieties still have lost their sweetness faster than in supersweet varieties. For this reason, breeders have developed new varieties with a high sugar content, good germination and superior agronomic traits by using genetic combinations of other endosperm genes with the sugary allele. Details of the breeding methods are disclosed in the U.S. Patents Nos. 3,971,161 and 4,630,393.

Bonucci, US Patent Nos. 3,971,161 and 4,630,393 has developed two new sweet corn hybrids, "Sweet Gene hybrid" and "Sweetie". The first hybrid or the sugary-shrunken hybrid, having the genotype $su_1su_1Sh_2sh_2$ is derived from a cross between sugary-shrunken inbred (su_1su_1 sh_2sh_2) as female with sweet corn male inbred ($su_1su_1Sh_2Sh_2$). The F_1 is normal appearing sweet corn seed and produced F_2 ears characterized by a 3:1 segregation of sugary (su_1su_1) kernels to shrunken (sh_2sh_2) kernels. The hybrid has very high in both sugars (approximately 50% more sucrose, 33% more total sugars) and WSP. The second hybrid, "Sweetie" or "Improved Supersweet" hybrid, having the genotype Su_1su_1 sh_2sh_2 is derived from a cross between sweet corn inbred (Su_1Su_1 sh_2sh_2) as female with sugary-shrunken male inbred (su_1su_1 sh_2sh_2).

After breeders have been "stacking" the endosperm genes, new varieties contain a number of different combinations of the three major genes and their modifier genes have been released. These new types can be divided into two pollination groups as a supersweet or sugary variety (Tracy 2005).

Improved sh_2 varieties (Augmented: Xtra-Tender Brand®, Gourmet Sweet Brand®, and Multisweets®) have recently appeared. They have a sh_2 endosperm that has been successfully combined with *se* genes and modifier genes. The kernels of these ears are more tender than those of ordinary sh_2 varieties. They are also very sweet (over 30% sugars), have a good corn flavor, good longevity and are more robust in the field than the sh_2 varieties. Newly improved sh_2 hybrids varieties have been developed and commercialized such as Xtra-Sweet and Xtra-Tender from Illinois Foundation Seeds Inc., Mirai® from Siegers Seed Co. and Optimum and Holiday from Crookham, Co.

Synergistic varieties (Sweet Breed™ and Triple Sweet®) have been created by combining su_1 gene with *se* and sh_2 genes. They are homozygous for the su_1 gene but heterozygous for the other genes. The ear therefore contains different types of kernels.

Sweet Breed™ such as Sweet Chorus, Sweet Rhythm, and Sweet Ice developed by Harris Moran Seeds are based on a *se* heterozygous background have about 25% *se* kernels, 25% sh_2 kernels and 50% su kernels. These varieties have good seed quality combined with higher sugar content than the su_1 varieties.

Triple Sweet® varieties such as Avalon, Serendipity, Honey select developed by Rogers seed, are based on a se homozygous background have an ear composed of 75% sugary enhancer kernels and 25% sh_2 kernels. This type of corn combines the outstanding tenderness and flavor of the *se* type with higher sugar content and an extended longevity of the sh_2 type. It also has good field robustness. Tablesweet® varieties such as Parfait TSW®, and Welcome TSW® developed by Mesa Maize, Inc. are the newly improved homozygous *se* varieties with high sugar contents and long shelf life.

CONCLUSION

Because of the importance of sweet corn, breeders have been devoted to the improvement of sweetness and others valuable characteristics, such as yield, disease and insect resistance, and tolerance of environmental stress. By developping new genetic combinations of four important endosperm genes which are shrunken2 (sh_2), brittle1 (*bt*), sugary1 (su_1), and sugary enhancer1 (*se*), new high sugar sweet corn varieties of great texture and taste with long shelf life have been developed and marketed. These high sugar sweet corn with extending postharvest quality hybrid varieties are well accepted by consumers both in the US and Japan. The worldwide expansion of using the high sugar sweet corn hybrids especially for fresh market can be anticipated. However, better varieties with an emphasis on superior kernel quality and agronomic requirements such as ear size and shape, kernel color and size unique to each specific market is required. The sweet corn breeding program must go on and need more support.

ACKNOWLEDGEMENTS

We would like to sincerely thank Professor James Brewbaker from the University of Hawaii in the United States for laying the foundation for sweet corn breeding in Thailand and for providing the valuable information used in this review.

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