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REVIEW ARTICLE

Nutritional enhancement and genetic innovations in sweet corn: unlocking super sweetness and health benefits through modern breeding technique- A review

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Abstract

Sweet corn originated from Mesoamerica around 10,000 years ago; sweet corn's distinctiveness lies in its genetic mutations *sugary1* (*su1*), *shrunken2* (*sh2*) and *sugary enhancer1* (*se1*) that enhance kernel sweetness by inhibiting the average sugar-to-starch conversion. This transformation from an ancient staple to a globally beloved vegetable highlights sweet corn's adaptability, high yield potential and nutritional benefits, including its role as a source of carbohydrates, proteins, vitamins and minerals. Advances in biofortification and genetic research have further enriched its nutritional profile, positioning sweet corn as a nutraceutical crop capable of addressing global nutritional deficiencies. Modern breeding techniques, including marker-assisted selection and omics technologies, have significantly accelerated the development of varieties with improved traits such as disease resistance, stress tolerance and enhanced nutritional quality. Additionally, it is important to conserve sweet corn's genetic diversity for future crop improvement and adaptation. High-throughput phenotyping and genome-editing tools such as CRISPR/Cas9 have further accelerated sweet corn breeding, offering a sustainable solution to enhance yield and quality. This exploration shows sweet corn's agricultural importance, its potential to fight nutritional challenges and the role of scientific advancements in securing its future as a valuable and versatile crop. This detailed review explores the history, genetic diversity, nutritional value and modern advancements in the cultivation and breeding of sweet corn.

Keywords

Biofortification; genetic diversity; marker assisted selection; omics technology

Introduction

Sweet corn originated in Central America and was domesticated between 5000-8000 BC (1). It represents a distinct variant of corn with its noticeable sweetness, slender pericarp, endosperm of a fine texture and high nutritional value. It is classified as a vegetable due to its carbohydrate content supreme that of standard sweet corn varieties (2,3). It has a higher sugar content, has less total carbohydrate in the kernels and therefore is lower in calories and higher in protein concentration (4). Exposure to the super-sweet phenotype in corn is associated with unfavourable traits, such as lower germination rates and decreased persistence against pests and diseases (3). The contrast between sweet and normal corn stems from genetic mutations that alter carbohydrate biosynthesis in the corn's endosperm, preventing the usual conversion of sugars into starch.

Sweet corn has a higher sugar content due to mutations such as *sugary-1* (*su1*), which reduces starch and increases phytoglycogen and *shrunken-2* (*sh2*), leading to even higher sugar levels in super sweet corn varieties. These genetic modifications are crucial for sweet corn's distinctive sweetness compared to normal corn (5-7). The kernels possess an endosperm abundant in amylopectin, contributing to their sweetness (8). The genetic components include *shrunken-2* (*sh2*), *brittle* (*bt*), *Amylose Extender* (*ae*), *sugary enhancer* (*se*), *sugary* (*su*), *Brittle-2* (*bt2*), "*Dull*" (*du*) and *Waxy* (*wx*), each being monogenic and recessive (3). Among this recessive gene in the genetic basis of super sweet corn results in sugar levels in the endosperm, (SU type) contains 4-6% sugars in the fresh kernel mass, while sugary enhanced varieties (SE type) contain 6-8% and super-sweet shrunken varieties (SH type) contain 8-12% (9). The homozygous varieties (sese su1su1) have higher sugar (20% to 35%) in 100% of their kernels. While the heterozygous varieties (Sese su1su1) have lower sugar (14% to 25%) and only 25% of the se type kernels and 75% of the su1 type therefore, homozygous varieties are usually sweeter than heterozygous varieties (10).

Sweet corn kernels are rich in essential nutrients and health-promoting components. The increasing popularity of corn is attributed to its gluten-free nature and the presence of zein, a protein located in the endosperm of caryopses, which is utilized in pharmaceuticals and the production of nutraceuticals (11-13). Sugar corn caryopses serve as a rich source of carbohydrates (simple sugars, starch), proteins, vitamins, minerals, phenolic acids, carotenoids and dietary fiber. Since sugar corn kernels are gluten-free, the plant holds significant importance in human nutrition and contributes to reducing the risk of various chronic diseases, such as cardiovascular diseases, eye disorders, obesity, type 2 diabetes and digestive issues. It is also recognized as a valuable product in the food industry. The rising demand and popularity of sweet corn can be attributed to increased consumption and the growing availability of food-processing industries (14). However, sweet corn breeding is a pretty different practice from field corn breeding because of the highly spoilable nature of its end product. However, sweet corn varieties with extended shelf-life, enhanced consistency and improved flavor have been developed using various breeding techniques. While yield potential gains in sweet corn have been lower compared to field corn, this is because the primary focus of sweet corn breeding programs has been on improving ear appearance and quality rather than enhancing reproductive potential (15).

In recent years, genetic research advancements have led to the development of biofortified sweet corn hybrids enriched with essential nutrients such as lysine, tryptophan and provitamin-A, enhancing health benefits and addressing nutritional deficiencies (16). The overall approach of biofortification in agriculture, including through breeding, agronomy and transgenic methods, offers a sustainable, cost-effective means to deliver essential micronutrients, thereby addressing global nutritional challenges (17). Breeding methods in sweet corn have evolved significantly, focusing on the growth of desirable traits such as enhanced sweetness, improved texture and greater nutritional profiles. Through careful genetic selection and hybridization techniques, researchers have successfully identified and manipulated genes responsible for these key characteristics, such as *su* (*sugary*), *se* (*sugary enhancement*) and *sh2* (*shrunken 2*). These advances in breeding strategies not only defer to consumer preferences but also contribute to the agricultural and nutritional value of sweet corn (18). Omics technologies, containing genomics, transcriptomics, proteomics and metabolomics are increasingly integrated into sweet corn research and breeding programs. These technologies offer time and cost efficiencies, aiding in the improvement of abiotic and biotic stress tolerance and agronomic traits in sweet corn. High-throughput sequencing technologies (HSTs) have been highly transformative, facilitating the identification of beneficial quantitative trait loci (QTL), genes and alleles for crop enhancement under diverse stress conditions (19). This review aims to examine the integral role of genetic diversity, advanced breeding techniques and omics technologies in enhancing sweet corn's nutritional value, yield potential and flexibility to environmental challenges, securing its future as a nutritionally rich and globally significant crop.

Origin of sweet corn

In the late 1940s and early 1950s, John R. Laughnan, a geneticist at the University of Illinois, studying alleles related to the coloration of corn kernels and was initially focused on the *anthocyanin 1* (*Al*) locus, a gene associated with the pigmentation of corn kernels. In his interest in understanding this gene's variations, he acquired a corn stock from E. B. Mains of the University of Michigan. This particular stock carried a recessive allele tightly linked to a gene known as *sh2* (20,21). During his studies, Laughnan made a spontaneous discovery that kernels containing the *sh2* gene were abnormally sweet and had a pleasant malty flavour. He dug into extensive research on its biochemical impact on endosperm carbohydrates. He found that *sh2* endosperms stored less starch but had significantly higher sugar levels compared to normal and *sugary* (su1) types, with sucrose levels approximately ten-fold and four-fold higher respectively (Fig.1). And identified sweet corn with the *sh2* gene could offer higher sugar content and longer shelf-life traits highly desirable for the sweet corn industry. Laughnan initiated his breeding program. He carefully backcrossed the *sh2* allele into established sugary inbreeds, creating hybrids like 'Golden Cross Bantam' and 'lochief'. His efforts advanced in the development of commercially viable super sweet hybrids, such as 'Illini Chief' and 'Illini Xtra Sweet', which were rapidly received by home gardeners and the canned and frozen food markets (22). Meanwhile, in Florida, Emil Wolf recognized the potential of super sweet corn (*sh2*) to address the declining consumption of fresh sweet corn. Through his breeding program (back cross) Wolf developed super sweet hybrids like 'Early Xtra Sweet' and 'Florida Sweet'. These varieties showed improved storage quality and consumer preference over traditional sugary corn, despite initial challenges with seed emergence and disease resistance (23,24).

Phylogeny of sweet corn

The genome of sweet corn, particularly the inbred line Ia453 with the mutated *shrunken2*-reference allele (Ia453-*sh2*), has been extensively studied, revealing robust aspects of sweet corn's evolution and genetic composition (25). The “de novo” assembly of Ia453-*sh2* has explained the structural variation responsible for the mutant *sh2*-R allele, which is key to its higher sugar

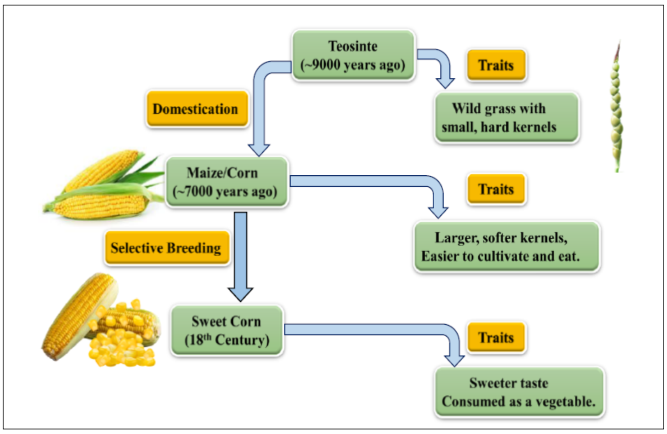

Fig. 1. Evolution of corn from teosinte to sweet corn.

accumulation. Comparative analysis of field corn genomes underscores variations in single-nucleotide polymorphisms, structural variations and transposon composition. The phylogenetic analysis incorporates a wide range of maize and teosinte accessions points to a common origin for modern sweet corn in northern Mexico, with population genomic analysis identifying genome regions under selection and genes linked to sweet corn traits (25). The *sh2*-R allele's origin was found to be due to a complex chromosomal rearrangement, involving multiple breaks in chromosome 3 and an intra-chromosomal inversion, providing insights into unusual recombination rates in this region (26). The *sh2* gene's molecular evolution, crucial in endosperm starch biosynthesis, shows signs of purifying selection preceding domestication, with very few nucleotide polymorphisms compared to other maize genes, suggesting a long-term maintenance of effective *Sh2* alleles by natural selection (27). The diversity of sweet corn germplasm, especially its derivation from the Northern Flint race, has been extensively examined using RFLPs, isozymes and morphology. A key study involving 43 significant sweet corn inbreeds and three dent corn inbreeds used these methods to maintain that most publicly available inbreeds originated from three cultivars Stowell's Evergreen, Country Gentleman and Golden Bantam, highlighting the Northern Flint race's major influence on sweet corn germplasm (28). Isozyme studies revealed a significant genetic divergence between Northern Flint and Southern Dent maize landraces, with Midwestern Dents similar to Southern Dent (29). Northern Flint differentiated notably from other North American maize landraces, likely due to genetic drift and environmental selection (30). RFLP analysis showed high allelic richness and variability in European maize, particularly in Southern Europe, aiding in understanding European maize's role in global corn germplasm (31).

Botanical description of sweet corn

Sweet corn is scientifically named as (*Zea mays ssp. saccharata*), has diploid structure with a chromosome number of 20 ($2n = 2x = 20$). It is classified under the family Gramineae, within the sub-family Panicoideae and the tribe Maydeae, it can grow up to 4 meters in height. The kernels of sweet corn are characterized by their wrinkled and translucent appearance when dry, which is a result of a single recessive gene (32). Sweet corn produces male flowers in the tassel and female flowers in rows on a thick cob. The variety is known for its distinct sweetness and comes in three primary colors - yellow, white and bicolor. The sweetness is due to the presence of certain recessive genes, *su1*(*sugary*), *sh2* (*shrunken*) and *se* (*sugary enhancer*) genes that control the sweetness levels in different cultivars of sweet corn (Fig. 2) (33). The fruit of the sweet corn plant is called a caryopsis. The corn ear, an associate of kernels on the cob, always has an even number of rows because the plant is a monocot. The ear is included in leaves known as the husk, with the pistillate flowers, called silk, emerging from it. Before cooking, particularly boiling, the husk and silk are typically removed by hand in a process known as husking. Sweet corn is not only genetically distinct from field maize but is also popular for its tender, flavour kernels, which have made it a popular vegetable worldwide. Unlike field corn, sweet corn is harvested when the ears are in the milky stage. The cobs are used immediately or stored frozen, as the sugar content in the kernels rapidly converts to starch. The time to harvest can vary between early varieties (70-80 days), medium early varieties (85-90 days) and late varieties (95-110 days) depending on the cultivar. Harvesting is typically timed when the silk end of the ear is full, the silk has browned and the kernels are firm yet milky (9,34). The diversity of sweet corn is significant, with variations in flavour, texture, nutrition and metabolic profiles among different cultivars. Sweet corn kernels contain carbohydrates, organic acids, amino acids, phenylpropanoids and alkaloids, contributing to their nutritional value. The metabolites vary significantly among cultivars, making sweet corn a diverse and nutritionally rich crop (35).

Growth, development and agronomic attributes

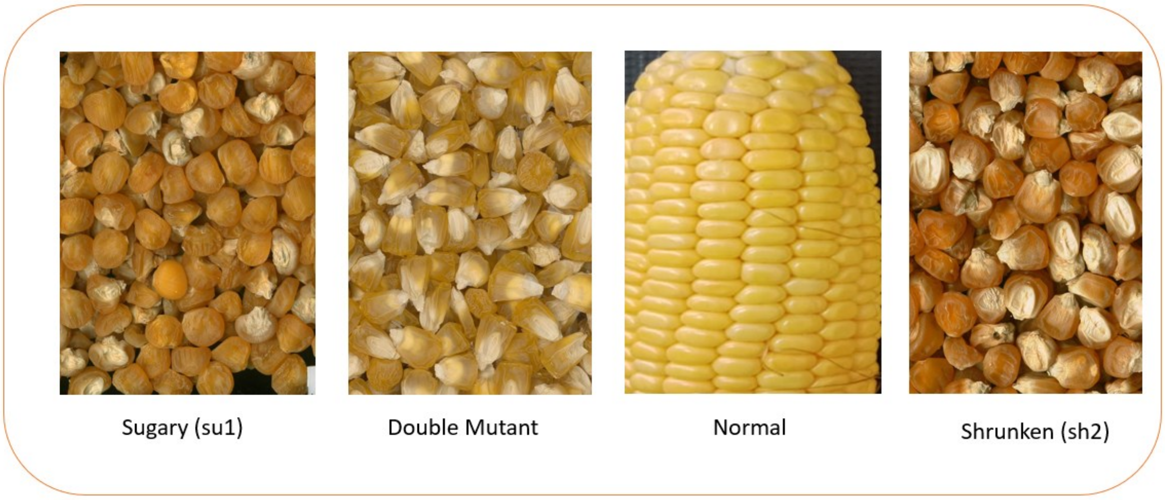
Sugary (su1)
Double Mutant
Normal
Shrunken (sh2)

Fig. 2. Sweet corn difference based on kernel.

Sweet corn has undergone selective breeding to enhance its qualities such as taste, short growth period and high yield. This has led to the development of various sweet corn varieties with improved quality features. A soil pH between 5.8 and 6.2 is adequate for sweet corn production (34) and it performs best in neutral, well-drained, well-aerated and moderately heavy, deep fertile soils. It can be grown on a wide range of soils, but optimal yield is often achieved in soils that provide good drainage and adequate fertility. Peat soils, for instance, have been shown to produce high yields under the right plant density and planting distance conditions (36). The optimal temperature range for sweet corn cultivation is from 22°C to 33°C. Sweet corn requires moderately high temperatures for optimal growth and development. The base temperature for germination of corn is approximately 10°C, which highlights the importance of warm soil temperatures for successful germination and early growth and it needs adequate and well-distributed rainfall of not less than 200 mm during the growing season (37). Sweet corn's growth and nutrient accumulation occur in three distinct phases, each approximately a month long: from planting to the five-leaf stage, from the five-leaf stage to silk emergence and from silk emergence to harvest. Notably, the period between the ten-leaf stage and silk appearance is critical for nitrogen uptake, essential for robust growth (38). Fertilization, especially with nitrogen, significantly impacts the dried matter mass and ear yield of sweet corn (39). Optimal harvest occurs when kernels are in the 'milk stage,' about 20 to 24 days after the first silks appear, marking peak sugar content. Throughout the season, maintaining optimum temperature (15.5°C to 30°C) and moisture, especially during flowering and ear development, is crucial to conflict with water stress and ensure high-quality yield (40). Inoculation with specific bacteria such as *Burkholderia cepacia* can promote plant growth and increase yield in sweet corn. This approach can be an alternative to synthetic chemical fertilizers (41). The diversity of sweet corn is significant, with variations in flavour, texture, nutrition and metabolic profiles among different cultivars. This diversity contributes to the broad use of sweet corn in human diets, animal feed and industrial materials (42).

Global production trends

Leading producers

Sweet corn is grown across various regions worldwide, with significant production occurring in North America, Europe and parts of Asia. The largest producers of sweet corn are the United States, China and Brazil. Sweet corn is primarily cultivated for both fresh market consumption and processing (canning, freezing).

United States: The U.S. is the largest producer of sweet corn, with significant production in states like California, Florida and Washington. It is a major exporter of processed sweet corn and also grows a large volume for domestic consumption.

China: While China is a major producer of field corn, sweet corn production has increased in recent years due to rising consumer demand for fresh produce and processed corn products.

Brazil: Brazil has emerged as a growing producer of sweet corn, with increased exports to global markets. The country benefits from its tropical climate, which allows year-round cultivation.

In Europe, sweet corn production is concentrated in countries like France, Hungary and Spain, where it is mainly grown for the canning industry.

Sweet corn plays a significant role in Indian agriculture, with an area of approximately 1.5 million hectares dedicated to its cultivation. The production of sweet corn in India is about 5.2 million metric tons, resulting in a productivity rate of around 3.47 metric tons per hectare (Fig. 3). These figures highlight the importance of sweet corn as a crop, although specific values can vary slightly depending on the source (43,44).

In Maharashtra, sweet corn is cultivated over an area of approximately 0.45 million hectares, yielding around 1.5 million metric tons with a productivity rate of about 3.33 metric tons per hectare. Karnataka follows with an area of roughly 0.35 million hectares dedicated to sweet corn, producing about 1.2 million metric tons and achieving a productivity of approximately 3.43 metric tons per hectare. Uttar Pradesh also contributes significantly, with around 0.3 million hectares under sweet corn cultivation, resulting in a production of about 1.0 million metric tons and a productivity rate of 3.33 metric tons per hectare (Fig. 4). These figures underscore the importance of sweet corn in these states' agricultural landscapes.

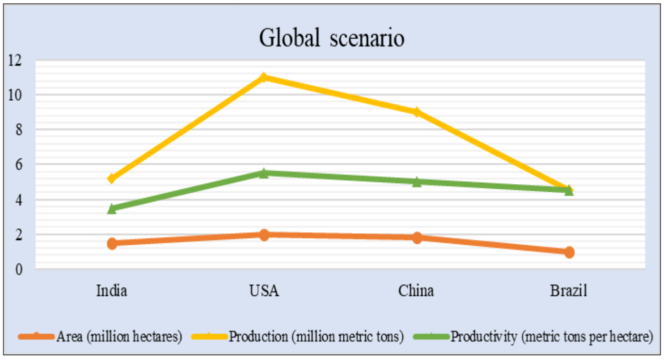

Fig. 3. Global trends in agricultural area, production and productivity of sweetcorn. (44)

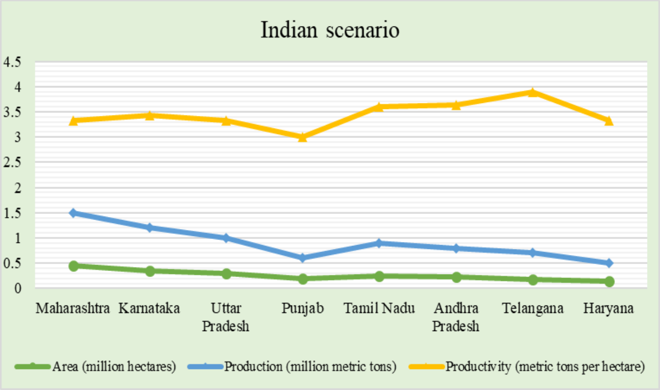

Fig. 4. State-Wise Agricultural Area, Production and Productivity in India (43)

Biochemical and cellular effects of sweet corn endosperm

The biochemical effects associated with the *su* locus in maize lead to significant alterations in kernel carbohydrate composition. In sweet corn, the *su* locus mutation results in reduced starch content and an accumulation of higher sugar levels, primarily sucrose, along with glucose, fructose and maltose. This mutation also causes an increase in the concentration of phytoglycogen, a highly branched polysaccharide made up of glucose molecules, which accumulates to more than 25% of the kernel's dry weight in sweet corn, in contrast to normal maize where it is virtually absent. The decreased amylopectin levels in sweet corn, due to the *su* locus mutation, contribute to the lower overall starch content compared to normal maize. This mutation has a deep impact on the starch biosynthesis process, affecting the balance and composition of storage carbohydrates in the maize kernels (5,45).

The development of the endosperm in sweet corn involves cellular changes that significantly impact kernel carbohydrate composition. During the growth of *su* maize kernels, a variety of plastid types are observed, ranging from amyloplasts with compound starch granules to those containing only phytoglycogen. This diversity is attributed to the different physiological ages of the cells within the endosperm. As the endosperm cells mature, especially in the central top region, the initially formed starch granules are mobilized and replaced with phytoglycogen. This process results in older cells predominantly filled with phytoglycogen rather than starch, following the typical developmental sequence of normal kernels but with a distinct end product. This cellular-level approach to understanding endosperm development in *su* maize highlights the complex interaction between genetics and metabolism (Fig. 5). The *su* gene is suggested to play a regulatory role, potentially consisting of a multiple allelic series, influencing the timing and extent of starch granule mobilization and phytoglycogen accumulation (6,46).

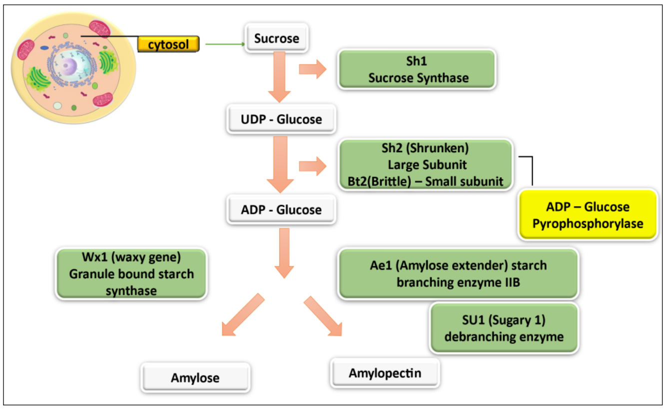

Fig. 5. Pathway of starch biosynthesis in plants highlighting key enzymes and genetic controls.

Nutraceutical values of super sweet corn

Sweet corn stands out as a highly nutritious and beneficial food, rich in essential nutrients and boasting a diverse nutrient profile. It is particularly high in moisture, especially in baby corn, which contains about 90.03% moisture. Protein is another significant component of sweet corn, with levels ranging from 12.08% to 17.96%, while its fat content remains relatively low at around 2.13% to 6.66% (47). In terms of carbohydrates, sweet corn contains about 11.98% soluble carbohydrates and is also high in dietary fiber, contributing significantly to its dietary benefits (48). Sweet corn has emerged as a significant crop in nutraceutical research, pesenting a rich profile with high water (72.7%) and total solids (27.3%) content. The solid portion primarily consists of carbohydrates (81%), proteins (13%), lipids (3.5%) and other elements (2.5%), with starch being the dominant carbohydrate (9,49) (Fig. 6). It offers a wide range of health benefits. Light-germinated sweet corn sprouts have shown increased Total phenolic content (TPC) and Total flavonoid content (TFC),

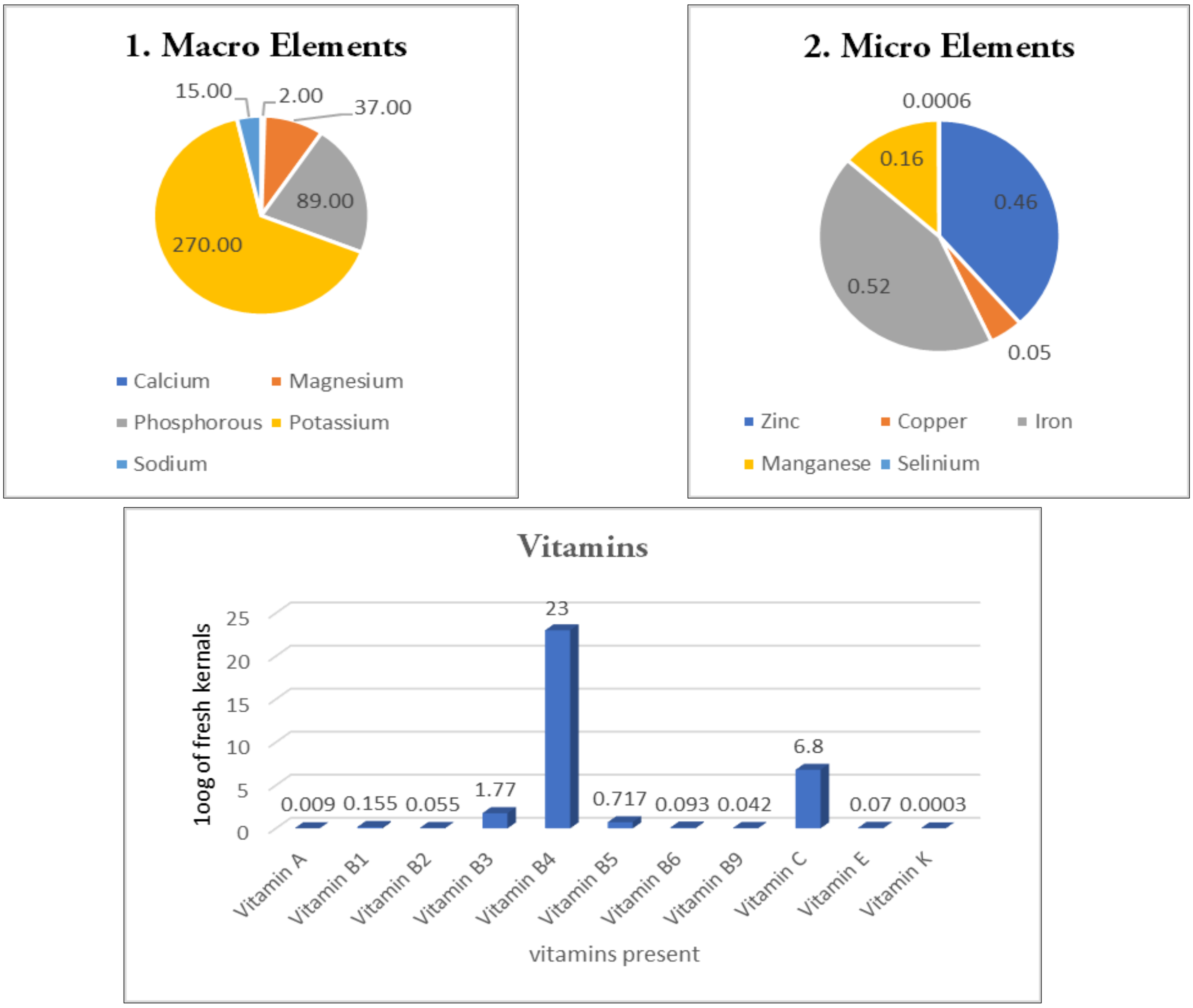

Fig.6. Pie chart 1,2 & Bar diagram. The content of major nutrients in 100g of fresh sweet corn kernal in (mg)(14).

leading to enhanced antioxidant activities, as revealed by (50). Bio-organomineral fertilizer (combines mineral, organic and biological elements including microorganisms) application on sweet corn significantly improves plant growth and nutrient uptake, contributing to sustainable agriculture practices for the availability of nutrients needed by sweet corn plants (51). Genomic advancements have enabled the development of sweet corn hybrids enriched with essential nutrients such as lysine, tryptophan and provitamin-A, enhancing the crop's nutritional value (52).

(53) found that cooking increases total carotenoids and alters tocopherol content, highlighting the impact of cooking methods. (42) used HPLC-MS/MS to identify significant metabolic differences across sweet corn cultivars, including 262 differential metabolites crucial for quality and breeding. (54) showed regional variations in sweet corn's fatty acid profiles suggest potential health benefits related to heart disease prevention. (55) demonstrated that zinc and selenium foliar applications boost yield and nutrient content, highlighting micronutrient fertilization's role in nutritional quality improvement.

Genetic resources of sweet corn

The genetic makeup of sweet corn is enriched by various alleles contributing to its sweet phenotype. (56) have identified multiple alleles in Brazilian corn varieties, providing insight into the genetic bases of sweet corn's distinct characteristics. Morphological traits such as ear and kernel size are key in characterizing sweet corn varieties. This morphological variation is critical for breeders aiming to enhance specific traits (57). In situ, conservation maintains genetic diversity within the natural environment, while ex-situ conservation involves preserving genetic material in controlled environments like gene banks. (58) highlight the matching of these two methods in preserving the genetic diversity of maize germplasm. Ex-situ conservation in gene banks is essential for safeguarding genetic diversity against potential losses due to environmental changes or cultural shifts. These gene banks act as warehouses for genetic material, available for future breeding and research purposes (59). Core collections represent a manageable subset of the genetic range of the base collection, enabling focused and efficient evaluation of traits. This approach is essential in identifying trait-specific accessions for breeding programs. Despite the extensive diversity in gene banks, the actual use of these resources in breeding programs remains limited, often due to challenges in accessing and evaluating the large volume of stored material. One of the primary challenges is the potential loss of genetic diversity termed genetic erosion which can be caused by environmental changes, shifts in agricultural practices or cultural factors. Modern biotechnological tools and techniques offer opportunities to enhance the preservation and management of sweet corn genetic resources. Advanced methods such as cryopreservation and *in vitro* storage can improve the longevity and quality of conserved germplasm (60). Till 2023, the germplasm of maize and the number of accessions conserved under the NBPGR will be 11,911 (61,62) (Table 1, 2 and Fig.7).

Table 2. Current biological status of various Germplasm (61)

Biological status	Number
Wild	216
Semi natural	371
Landrace	27827
Breeding material	831
Breeders line	111
Synthetic population	935
Hybrid	3
Inbreed line	1409
Segregating population	1040
Clonal selection	77
Cytogenetic stocks	169
Improved cultivar	1377

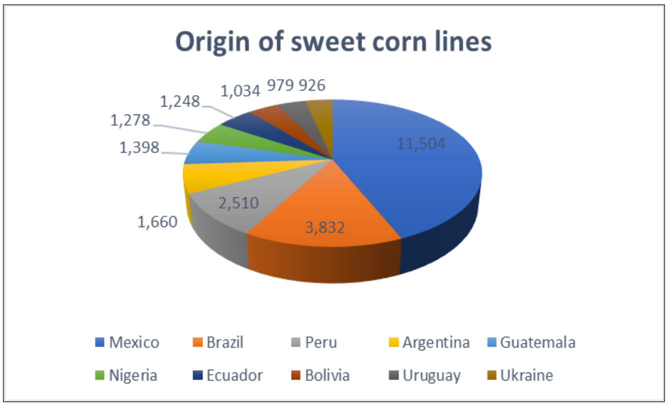

Fig. 7. Origin of Sweet corn lines (61).

Genetic elements in super sweet corn

Sweet corn, a staple food worldwide, has its unique qualities due to a series of key genetic factors. These genes *ae1, bt1, bt2, du1, sh2, su1, se1* and *wx1* play pivotal roles in the development and quality of sweet corn kernels. Each gene influences specific aspects such as *su* (*sugary*) gene is pivotal in granting the kernel's sweetness and soft texture, while additional genes have been identified that further develop sweetness, taste and overall quality (Table 3). These include the *se* (*sugary enhancement*) gene and the *sh2* (*shrunken 2*) gene. Genetic combinations between the *su* and *sh2* genotypes have promoted the development of abnormally sweet varieties.

Table 1. Corn germplasm holding under international institutes (61)

Holding institute	Acessions
CIMMYT - International Maize and Wheat Improvement Center, Mexico	32,086
IITA - International Institute of Tropical Agriculture, Nigeria	2446
GeRRI - Genetic Resources Research Institute - Kenya	1827
NPMS - National Plant Materials System - Brazil	1298
IK - Institute of Kyiv - Ukraine	579
IK - Ukraine	536
NOODiK - National Office of Developed Cultivars - Hungary	146
NC7 - North Central Regional Plant Introduction Station - United States	99
OPGR - Official Plant Genetic Resources - Bulgaria	93
IPK - Leibniz Institute of Plant Genetics and Crop Plant Research - Germany	91

Table 3. Genetic elements in sweet corn

Genes	Chromosome location	Primary function	Mutation effects	Impact on sweet corn	Citation
ae1	Long arm - 5	Encodes starch-branching enzyme *IIb (SBEIIb)*	Alters starch composition, affecting amylose and amylopectin ratios	Improves blood sugar responses, contributes to digestive fitness	(63,64,65)
bt1	4	Regulates starch metabolism, influences kernel quality and seed vigor	Affects kernel weight, density and starch content	Enhances overall sweetness and texture	(66)
bt2	4	Affects endosperm development, influences sucrose and starch composition	Variations can lead to differences in seedling vigor and germination efficiency	Crucial for eating quality, impacts carbohydrate profile and flavour	(67,68)
du1	2	Encodes a unique starch synthase	Leads to significant changes in physical and cooking properties	Determines agronomic and consumer quality, affecting texture and flavour	(69)
sh2	Long arm - 3	Encodes ADP glucose pyrophosphorylase, a key enzyme in starch biosynthesis	Increases sucrose levels in seeds, decreases starch content	Revolutionized industry with enhanced sweetness and eating quality	(26,70)
su1	Short arm - 4	Encodes the *SU1* isoamylase, a starch-debranching enzyme	Alters starch composition, leading to higher sugar content	Increases sweetness and palatability, affects texture	(70,71)
se1	2	Acts as a recessive modifier of the su1 gene	Enhances accumulation of water-soluble polysaccharides and sugars	Improves kernel sweetness and eating quality, maintains creamy texture	(72)
wx1	9	Encodes granule-bound starch synthase, synthesizing amylopectin	Associated with a waxy, glutinous texture due to high amylopectin content	Influences texture and flavour, affects agricultural traits and processing	(73)
Opaque-2(o2)	7	Regulates the synthesis of storage proteins, leading to improved nutritional quality.	Mutation in *o2* leads to a decrease in zein protein content, resulting in softer, more digestible kernels with higher lysine and tryptophan content.	Increases lysine and tryptophan content, used for nutritional enhancement	(52,71)
opaque16 (o16)	Long arm of 8	Further increases nutritional quality, especially lysine content.	Enhances lysine and tryptophan content beyond *o2* mutation alone.	Genes enhance sweet corn's nutritional value by increasing essential amino acids like lysine and tryptophan, making it healthier for consumption.	(74,75)
ZmVTE-4	10	Involved in the biosynthesis of tocopherols, contributing to antioxidant properties.	Mutations can affect tocopherol levels, potentially impacting the antioxidant capacity and nutritional value of the corn.	Increases vitamin E (tocopherols) content, important for antioxidant activity	(76)

Sweet corn improvement through traditional and modern breeding approaches

Sweet corn breeders have used a traditional breeding approach to produce commercial hybrids for over a hundred years. This process involves creating pure inbred lines through self-pollination and selecting preferred traits within a wide-ranging breeding pool. These inbred lines are then crossbred and the resulting hybrids are assessed for their commercial viability. Taste testing at the point of sale is considered the most effective way to screen for flavour. In recent years, sweet corn breeding has significantly advanced through the use of four key genetic mutations: *sh2, bt, su* and *se*. These mutations, used individually or in various combinations, have been pivotal in developing new varieties of sweet corn with enhanced sugar content. This genetic manipulation focuses on altering the genes responsible for the corn kernel's sugar levels. Consequently, four distinct categories of sweet corn have emerged: standard, super sweet, sugary enhanced and high sugar sweet corn, all of which are now widely cultivated for commercial purposes (77).

Traditional breeding methods

Traditional breeding methods in plant cultivation, including the development of crops like super sweet corn, generally involve the following techniques:

Recurrent Selection and Participatory Plant Breeding

Participatory Plant Breeding (PPB) engages farmers, breeders and stakeholders to develop crops adapted to organic agriculture's demands. Research in Minnesota and Wisconsin (2008-2013) led to significant enhancements in crop traits, particularly in a sugary-enhancer sweet corn variety noted for superior flavour, tenderness, taller growth and larger ears assisting weed management. The 2014 release of 'Who Gets Kissed?' a sugary-enhanced, open-pollinated sweet corn was commercialized through High Mowing Organic Seeds without intellectual property rights, encouraging broad adoption and further breeding innovations (78,79).

Pure line selection

Innovations in sweet corn breeding (80), have significantly advanced the development of sweet corn varieties with enhanced traits. A modified backcross breeding method was introduced to integrate the *shrunken2* (*sh2*) gene into elite field corn lines, enhancing sugar content and sweetness, key traits for consumer appeal. This approach exploits the visual distinction of *sh2* kernels for foreground selection, streamlining breeding by bypassing complex molecular techniques. The strategy effectively incorporates the recessive allele that alters carbohydrate storage to improve kernel sweetness.

A tetraploid sweet corn collection based on Baksanskaya Sugary var. (VIR catalog no. k-23426) was created from the MRPP-20 dent corn tetraploid population known for high grain yield. The collection, developed through inbreeding of caryopses homozygous for su1 and su2 genes and subsequent selection, includes over 300 specimens, with traits such as 17.0-18.0% high and 11.0-12.0% low protein content, 9.0-10.0% high and 5.0-6.0% low oil content and 66.0-67.0% high and 60.0-61.0% low starch content. Specimens like C-1042 combine high starch with low oil content, while C-1114 and C-1116 combine high oil with low starch and C-1180 and C-1370 have low protein and oil with high starch content. Comparative studies with diploid sweet corn (cv. 'Rannyaya Lakomka', c-1775) showed tetraploid varieties have superior ear structure, higher protein and oil content, increased synthesis of organic acids, amino acids, fatty acids and enhanced taste qualities due to improved biochemical composition (8,81).

Pedigree breeding

Pedigree breeding in corn germplasm development relies on progenitor lines like B73 (yield potential, disease resistance, adaptability), LH82 (standability, reduced lodging) and PH207 (grain quality), which form the foundation of modern germplasm. New corn lines are primarily developed by recycling elite inbred lines through two-parent crosses and pedigree selection. The evolution of inbred lines, including sweet corn, has been extensively documented, highlighting their development through various pedigree linkages to enhance elite line recycling and create new lines (82). Pedigree breeding in sweet corn, particularly focusing on the *sugary1 (su1), shrunken2 (sh2)* and *su1/sh2* double mutant lines, involves a careful process of analyzing genetic diversity, developing inbred lines and understanding gene effects for effective hybrid breeding. Microsatellite markers have revealed significant diversity within these inbreeds, indicating their potential for creating novel breeding populations (18). Furthermore, understanding gene effects and the combining ability of these lines is crucial. Studies using line × tester mating designs have highlighted significant genetic variance components and combining abilities in sweet corn lines, with specific lines showing positive general combining ability effects for traits like grain yield, underscoring their importance in forming high-yielding sweet corn hybrids (83).

Mass selection

(84) improved tenderness in 'Hawaiian Super-sweet No. 9' corn through mass selection, achieving 9.2% genetic advance per cycle via pericarp thickness and 3.9% improvement via bite test. Significant correlations between bite-test scores and immature pericarp thickness, highlighted the approach's effectiveness. (85) demonstrated the effectiveness of mass selection in enhancing ear length and yield in sweet corn populations. The research involved two cycles of mass selection on populations BC2-10 and

BC1-10 × Syn-Ⅱ, incorporating exotic germplasm. The study revealed varied responses to mass selection among the populations, with significant improvements in ear length and yield. Selection for ear length, which showed high heritability, proved more effective than direct yield selection. This approach led to populations with longer ears and increased fresh ear yield compared to base populations, underscoring the potential of mass selection in sweet corn breeding for traits with high heritability.

Hybrid Breeding

In 1934, a quantitative method for assessing pericarp tenderness was introduced, advancing sweet corn breeding by aligning hybrids with consumer preferences (86). Breeding work in 2019-2020 found non-additive gene action influencing carotenoid content, with line L20 and tester T2 showing high general combining ability (GCA) for carotenoids; T2 × L20 excelled in lutein, zeaxanthin and total carotenoids, while T2 × L9 was high in β-carotene (87). By doing a molecular analysis of 48 genotypes, the research uncovered a remarkable 213 alleles across markers, on an average of 3.8 alleles per locus that highlight the rich genetic diversity present. The Polymorphism Information Content (PIC) stood at an average of 0.50, indicating a moderate polymorphism among the markers, while a genetic dissimilarity score of 0.73 pointed to the extensive genetic variance within these inbreeds. Crucially, cluster analysis organized the inbreeds into three primary groups according to their mutation types - su1su1, sh2sh2 and su1su1/sh2sh2 - thereby facilitating the identification of heterotic groups essential for effective hybrid breeding (18). The National Institute of Crop Science, Korea, developed hybrids Godangok 1 (20.8 Brix sugar, superior lodging tolerance) and Baekgeumok (39 μm pericarp thickness, 19.5 Brix sugar) with high sugar content and disease resistance (88). Both require isolation from other corn types to maintain their unique properties.

Backcross breeding

Efficient backcross breeding method is used to transfer the *shrunken2 (sh2)* gene, known for its high sugar content, into superior field corn lines, aiming to create high-yielding sweet corn hybrids. This innovative approach has the advantage of the distinctive shrunken kernel trait for direct selection, alongside phenotypic similarity to the recurrent parent for background selection. The process involves selecting BC1F1 plants that closely match the recurrent parent for selfing and backcrossing, followed by harvesting BC2F1 kernels that exhibit expected segregation. The final selection phase involves identifying and selfing BC2F1 plants that most closely resemble the recurrent parent to obtain BC2F2, where shrunken kernels are selected as indicators of *sh2* homozygosity. This method stands out for its speed, cost-effectiveness and the advantage of not requiring practical marker-assisted selection technologies (80).

Outcrossing

The study utilized North Carolina Design II and ear-to-row breeding, crossing *Ga1-s* popcorn and *sh2* sweet corn inbred lines, producing homozygous *Ga1-s sh2* inbred lines. Five hybrids were evaluated across diverse environments, demonstrating *Ga1-s*'s efficacy in safeguarding *sh2* genetic integrity while showing a need for enhanced agronomic traits. *Ga1-s* presents a promising strategy for mitigating outcrossing and preserving genetic purity in sweet corn breeding (89).

Modern breeding methods

Marker-assisted pyramiding and selection

Genotyping-by-sequencing (GBS) has altered the Marker Assisted Selection (MAS) in plant breeding by offering a cost-effective means for sequencing large genomes like maize and wheat and facilitating both molecular marker discovery and genotyping (90). This advancement is particularly advantageous for largescale breeding programs aiming to develop new crop varieties with desired traits such as disease resistance, grain yield and seed characteristics more efficiently and precisely (91). Additionally, Simple Sequence Repeats (SSRs), also known as microsatellites, are widely utilized for their ease of use and cost-effectiveness, further enhancing the MAS process (92).

MAS was used to develop biofortified sweet corn hybrids, focusing on vitamin E and folic acid enhancement. Key genes identified for vitamin E synthesis include *ZmHPT* and *ZmTC*, with *ZmVTE4* genes playing a pivotal role in γ-tocopherol methyltransferase activity for vitamin E content. For folic acid enhancement, *DHAR, TMT* and *GTPCH* genes were significant in biosynthesis pathways during seed germination. This led to the selection of 15 inbred lines, high in biofortified hybrids rich in vitamin E and folic acid (93). (94) identified SSR markers bnlg1721 and umc1042 on chromosome 2, linked to the *Ht1* gene, crucial for NCLB resistance. (95) demonstrated the practical use of these SSR markers in breeding, underlining their role in enhancing NCLB resistance. (96) discovered three significant QTLs on chromosomes 2, 5 and 8 for NCLB resistance, with a major QTL on chromosome 8. (97) identified an *Ht3*-like locus associated with NCLB resistance, presenting a new genetic resource for resistance improvement. Additionally, (98) found 11 QTLs, with qNCLB 7.02 as the most significant, illustrating the genetic complexity in NCLB resistance. These studies collectively advance MAS's role in developing disease-resistant maize varieties.

Quantitative Trait Loci (QTL) Mapping

In super-sweet corn, a genetic linkage map was constructed using SSR markers across a population of 208 F2 individuals derived from a cross between Ji557 (*sh2*) and Ji165 (*sh2*) varieties. This map covers 1470.9 cM with marker density ranging from 2.2 cM to 65.3 cM, average at 13.0 cM between adjacent markers. Through the use of Mapmaker/QTL, 11 quantitative trait loci (QTLs) were identified for kernel soluble sugar content, explaining between 3.5% to 20.3% of the variance in this trait and together explain for 63.7% of the total trait variance. These QTLs exhibited a range of genetic effects on kernel soluble sugar content, including additive, partially dominant, dominant and over-dominant effects, highlighting the complexity of genetic influences on this trait (99). And another study delves into the genetic foundations underlying quality traits in sweet corn, using 63 microsatellites (SSR) markers across 39 inbred lines. Key focus areas include traits such as pericarp thickness and soluble components like sugar, dextrose, sucrose, amylose, total soluble solids (TSS) and reducing sugar. Out of these markers, 30 exhibited polymorphisms with a subset significantly associated with TSS and reducing sugar levels specifically markers phi027, umc2056, umc1633, bnlg1265, umc1031 for TSS and umc1465, umc1633, umc1492, bnlg1079, umc1320 for reducing sugar. Marker umc1633 emerged as a common link between both traits underscoring its potential in sweet corn breeding enhancements (100-103). Researchers advanced the genetic understanding of zeaxanthin concentration in sweet corn by mapping eight QTLs critical for zeaxanthin content, notably in the umc1632-umc1401 region on chromosome 7. This finding is pivotal for breeding strategies aimed at increasing zeaxanthin levels thereby enhancing dietary health benefits. The identification of major QTLs like *qZeax7* opens up new possibilities for genetic improvement and requires further investigation (104). Additionally, the genetic architecture of pericarp thickness, crucial for sweet corn's sensory quality, was explained through QTL mapping studies by (105,106). They identified three pivotal QTLs located in bins 3.01, 6.01 and 8.05, which collectively account for a significant portion of the phenotypic variance in pericarp thickness. (106) advanced this understanding by integrating genetic mapping with transcriptome analysis in a BC4-F3 population, leading to the identification of fourteen QTLs for pericarp thickness, including a stable QTL, qPT10–5 on chromosome 10. This approach pinpointed 42 candidate genes, with three-GRMZM2G143352, GRMZM2G143402 and GRMZM2G143389 highlighted as key QTLs and candidate genes, potentially regulating pericarp thickness through mechanisms involving transcription factors and fatty acid transport.

Genetic Modification (GM)

CRISPR/Cas9 technology and the HI (Haploid Induction) Edit method represent transformative advancements in agricultural biotechnology that extremely impact specialty maize breeding. By targeting mutations in the *SH2* and *WX* genes, CRISPR/Cas9 has facilitated the development of super sweet corns with enhanced sugar content and waxy corns with increased amylopectin levels leading to unique textures (107). This technology has enabled the creation of sweet and waxy compound corns (SWCs) which have gained popularity in Southeast Asia and China, sgRNAs (single guide RNAs) enable precise mutations that alter the starch synthesis pathway. Simultaneously, the HI-Edit method, introduced by (108) influences CRISPR/Cas9 for one-step genome editing during haploid induction (HI), breaking out the need for traditional plant genetic engineering techniques. This approach not only simplifies the modification process but also produces transgene-free plants, crucial for regulatory acceptance and public perception, as these plants are not considered GMOs in the traditional sense. Together, these innovations offer a faster and more efficient pathway for enhancing crop traits such as disease resistance, yield and quality, predicting a new era in the breeding of commercial crop varieties with customized nutritional profiles and textures, potentially revolutionizing the agricultural industry.

High-Throughput Phenotyping

The study by (109) demonstrates the application of high-throughput phenotyping (HTP) using RGB (red, green, blue) and multispectral imaging to enhance the selection process in sweet corn breeding programs. By evaluating seven S3 populations and two commercial hybrids for ten different traits, the study aimed to assess the competence of HTP methodologies in differentiating sweet corn genotypes and to explore the correlation between conventional phenotyping methods and HTP-derived data. The findings revealed that traits related to vegetative canopy area, normalized difference vegetation index (NDVI) and visible atmospherically resistant index (VARI) extracted from digital images were strongly associated with grain yield, showcasing HTP's capability to efficiently identify genotypes with higher yield potential. This study highlights the efficiency and utility of HTP, offering a less labor-intensive and rapid alternative to traditional phenotyping methods by using digital imaging to assess traits linked to agronomic performance and chlorophyll content. The high degree of correlation between traits evaluated by conventional methods and those obtained from HTP underscores its potential to complement and enhance traditional breeding practices.

Omics technology for crop improvement

Global agriculture faces rising pressure due to increased food demands and climate changes. (110) highlight how omics technologies have simplified the identification of genes responsible for essential agronomic traits, including enhanced yield and resistance to biotic and abiotic stresses. Omics technologies have gained immense importance in agriculture, providing diverse applications like genomics which is based on genome sequences, transcriptomic which is based on gene expression and profiling, proteomics which is based on protein content and metabolomics which involves the study of the metabolism of an organism. Omics technologies allow the recognition of genes and genomic sequences associated with crop growth, senescence, increased yield, resistance against biotic and abiotic stresses and other desirable plant traits (92). By using omics technology, they have genome sequenced more than 700 plant species for a better understanding of plant response to environmental conditions (111). Integrating omics data provides comprehensive insights into biological processes underlying plant traits and their interactions (112). From wheat and soybeans to maize and rice, the impact of multi-omics is undeniable (113). Presented a review on the advances in omics and bioinformatics tools for plant systems analyses, addressing the integration of knowledge from omics-based research for a better understanding of plant biology (114).

Genomics

Conducted GWAS and genomic prediction analysis on sweet and waxy corn lines, identifying significant SNPs associated with plant architecture traits plant height (PH), ear height (EH) and tassel branch number (TBN), SNPs accounting for 3.50% to 7.0% of the phenotypic variance which is crucial for applying genomic selection in maize breeding to improve quantitative traits and provided a high-quality reference genome for sweet corn, revealing genetic variations key to traits like sweetness and kernel texture, facilitating comparative genomics and supporting breeding for taste, yield, disease resistance and nutritional quality (115,116) identified 12 SNPs related to sweetness in sweet corn through Genome-Wide Association Studies (GWAS) confirming the significant role of the *sh2* gene in sugar accumulation, aiding breeders in developing sweeter corn varieties via marker-assisted selection (MAS). (117) discovered 46 sweet corn inbred lines resistant to Sugarcane Mosaic Virus (SCMV) using SNP markers, highlighting the *Scm*1 locus's role in resistance, essential for breeding SCMV-resistant varieties and enhancing disease management in maize. Enhanced sweet corn's nutritional qualities by increasing β-carotene content using marker-aided breeding focusing on the *crtRB1* gene. This approach improved vitamin A precursor levels, demonstrating molecular breeding's effectiveness in enhancing crop nutritional traits and performed GWAS on sweet corn to analyze the genetic architecture of vitamin E content, identifying 119 loci associated with vitamin E compounds and developing elite cultivars with significantly increased α- and γ-tocopherols through marker-assisted selection and focused on increasing tocopherols in sweet corn via marker-assisted backcrossing of the *ZmVTE4* gene, demonstrating increased α-tocopherol content in backcross progenies and highlighting the gene's potential in enhancing sweet corn's nutritional value (118,119).

Transcriptomics

In sweet corn, they identified key loci for carotenoid biosynthesis, underlining the importance of these genes in kernel carotenoid composition and making it a primary target for biofortification strategies (120). Later highlighted the genetic variability in traits related to nutrient profiles, especially through genes like *crtRB1* and *vte4*, associated with carotenoids and tocopherols. These findings highlight the genetic basis for improving the nutritional value of sweet corn, including provitamin A, lutein, zeaxanthin and α-tocopherol levels. Later used transcriptomic data for TWAS and transcriptome prediction on 39 nutrients, that validated four causal genes (*crtRB1, lcyE, vte4, hggt1*) for vitamin accumulation and discovered new gene associations (*dxs2, dmes2, cmk1, ggh1*) which are new to the context of sweet corn biofortification, suggesting novel pathway for enhancing nutrient profiles through genetic means. This work shows that models incorporating both genomic and transcriptomic data offer superior predictive capabilities over those based on genomic data alone or derivable candidate genes (121-123). And identified 45,748 DEGs (differentially expressed genes) in kernels and 596 in leaves, pinpointing crucial genes like *PsbS* (*photosynthetic system II subunit S*) and those in glycolysis, starch and sucrose metabolism as essential for sugar accumulation in super sweet corn, underscoring the complexity of breeding for enhanced kernel sweetness (124).

Proteomics

Proteomic technologies like 2D gel electrophoresis, mass spectrometry and shotgun proteomics are advancing our understanding of plant genomes, proteome mapping, comparative analysis and protein interactions (125,126). It has been instrumental in identifying proteins responsible for the formation and regulation of this three-dimensional architecture across different developmental stages, as highlighted. Studies on maize roots, including shoot-borne, lateral and seminal roots show specific protein modifications related to their structure and function. Proteomics has demonstrated the protein composition in different root zones and the molecular basis for hybrid seedling root vigor over parental lines (127). The study on sweet corn cob explores the hypoglycemic effects of Polysaccharide (SCP-80-I) on diabetic rats, revealing its role in reducing blood glucose levels and improving insulin resistance, thereby showcasing its potential as a natural hypoglycemic agent. Employing tandem mass tag (TMT)-labeled quantitative proteomics, the research identifies significant alterations in the expression of key proteins Pik3r5, Ndufb3, Pygl, Cbl, Prkcd and Stat1 involved in crucial metabolic pathways, such as PI3K-Akt and JAK-STAT signaling, which are essential for insulin sensitivity and glucose homeostasis. These findings underscore SCP-80-I's ability to modulate insulin secretion and action and its protective role in pancreatic tissue highlighting its therapeutic potential in diabetes treatment (128). Phytase-transgenic maize shows 148 differentially expressed proteins with 106 down-regulated and 42 up-regulated indicating genetic modification affects protein regulation not the introduction of new proteins. These proteins are mainly involved in post-transcriptional modifications suggesting an adaptive response to gene insertion and also highlighted complex protein-protein interactions mainly involving ribosomal and heat-shock proteins underscoring the profound impact of genetic modification on various plant growth and stress response aspects (50).

Metabolomics

Metabolomics, a modern "omics" technology, involves the identification, characterization and measurement of small biomolecules (known as the metabolome) within a biological system (129).

Utilized high-performance liquid chromatography-mass spectrometry (HPLC-MS/MS) to analyze the metabolite profiles of different sweet corn cultivars and identified 568 metabolites, with 262 showing significant variations among cultivars, underscoring the biochemical diversity that influences sweet corn's flavour, texture and nutritional value. Notably, primary metabolites such as carbohydrates and essential amino acids, along with secondary metabolites including phenylpropanoids and flavonoids, were highlighted for their roles in plant metabolism and health benefits (113). Later another one explored the adaptive mechanisms of sweet corn seedlings to temperature stress, employing transcriptomics and metabolomics. Their research revealed distinct volatile and hormonal profiles under low and high temperature stresses highlighting the crucial role of specific hormones and genes in the plant's stress response. This collective approach provides a deeper understanding of sweet corn's physiological and molecular responses to temperature stresses, suggesting pathways for enhancing its resilience (130). Further, they demonstrated the impact of *Bacillus subtilis* R31 on enhancing sweet corn's quality and yield. The application of *B. subtilis* R31 was associated with improvements in physical attributes and an upregulation of 110 differential metabolites, enriching flavonoid biosynthesis. This suggests *B. subtilis* R31's potential in boosting plant secondary metabolite production, linked to improved plant health and stress resistance (131).

Future Perspectives

The future of sweet corn breeding and improvement is promising, driven by advancements in agriculture, biotechnology and genetic practices. The integration of traditional and modern breeding techniques, along with omics technologies, present numerous opportunities for enhancing the nutritional, agronomic and economic value of sweet corn.

Marker-assisted selection (MAS) has revolutionized plant breeding by allowing accurate identification and selection of desirable traits. Recent studies have identified key genes such as *ZmVTE4* for vitamin E content and *crtRB1* for provitamin-A biosynthesis, enabling the development of biofortified sweet corn hybrids. QTL mapping has pinpointed critical loci for traits like kernel soluble sugar content, zeaxanthin and pericarp thickness, enhancing our understanding of the genetic basis of these important attributes. CRISPR/Cas9 technology has facilitated targeted mutations in genes such as *sh2 (shrunken2)* and *wx1 (waxy)*, leading to the development of super-sweet and waxy corn varieties with improved textures and sweetness. The HI (Haploid Induction)-Edit method offers a streamlined approach for genome editing during haploid induction, producing transgene-free plants and accelerating the breeding process. HTP using RGB and multispectral imaging has proven effective in assessing traits related to yield potential, vegetative canopy area and chlorophyll content. This technology complements traditional phenotyping methods, offering a rapid and less labour-intensive alternative for evaluating agronomic performance.

Genomic studies have identified SNP markers associated with traits like sweetness, disease resistance and plant architecture. Transcriptomic analyses have revealed the genetic variability in nutrient profiles, highlighting genes such as *vte4* for tocopherol biosynthesis and *crtRB1* for carotenoid accumulation. These insights are crucial for developing sweet corn varieties with enhanced nutritional qualities. Proteomic analyses have explained the protein composition and modifications in sweet corn, contributing to our understanding of plant growth, stress response and metabolic pathways. Metabolomics studies have identified significant variations in metabolites among sweet corn cultivars, underscoring the biochemical diversity that influences flavor, texture and nutritional value. Key metabolites such as phenylpropanoids and flavonoids play essential roles in plant health and stress resistance. Biofortification efforts focus on enhancing the nutritional content of sweet corn through breeding and biotechnological interventions. The incorporation of genes like *ZmVTE4* and *crtRB1* has led to the development of sweet corn hybrids enriched with essential nutrients such as vitamin E and provitamin A, addressing global nutritional challenges and improving public health. Integrating beneficial microbes such as *B. subtilis* R31 into sweet corn cultivation has shown the potential to enhance plant health, yield and stress resistance. This sustainable approach reduces the reliance on synthetic fertilizers and pesticides, promoting environmentally friendly agricultural practices.

By exploiting genetic insights and innovative approaches, breeders can develop sweet corn varieties that meet consumer preferences, enhance nutritional value and withstand environmental challenges. The continued exploration of genetic diversity, advanced breeding techniques and sustainable practices will secure sweet corn's position as a nutritionally rich and globally significant crop.

Conclusion

Sweet corn domesticated between 5000-8000 BC in Central America, is famous for its sweetness, slender pericarp and high nutritional value. It displays higher sugar content but lower total carbohydrates and calories compared to standard corn making it a valuable global crop. The distinctive sweetness of sweet corn is due to genetic mutations such as *sugary-1* (*su1*) and *shrunken-2 (sh2)*, which reduce normal carbohydrate biosynthesis in the endosperm, preventing the conversion of sugars into starch. These mutations, along with other critical genes like *ae1, bt1, bt2, du1, se1* and *wx1*, contribute to the sweetness, texture and overall quality of the kernels. Despite challenges like lower germination rates and reduced strength against pests and diseases, advancements in genetic research and breeding techniques have addressed these issues. Modern breeding methods, including marker-assisted selection (MAS) and genomic selection, have developed biofortified sweet corn hybrids enriched with essential nutrients such as lysine, tryptophan and provitamin-A. Traditional breeding methods like recurrent selection, participatory plant breeding (PPB), pure line selection, pedigree breeding and hybrid breeding have also been instrumental in improving sweet corn traits.

For instance, hybrids like Godangok 1 and Baekgeumok in Korea exhibit high sugar content and excellent flavor. Marker-assisted pyramiding and selection have enabled the development of biofortified hybrids with enhanced vitamin E and folic acid content. Quantitative Trait Loci (QTL) mapping has identified key loci associated with traits like kernel soluble sugar content, pericarp thickness and zeaxanthin concentration. Genetic modification techniques, including CRISPR/Cas9, have facilitated the development of super-sweet and waxy corn varieties with customised nutritional profiles. Omics technologies, broad genomics, transcriptomics, proteomics and metabolomics, have significantly advanced sweet corn research. Genomics has revealed significant SNPs and loci associated with essential traits, while transcriptomics has identified genes crucial for nutrient biosynthesis and stress response. Proteomics has elucidated protein interactions and modifications related to sweet corn's growth and stress responses and metabolomics has highlighted the biochemical diversity among sweet corn cultivars.

The integration of traditional and modern breeding methods, combined with advanced omics technologies, has significantly enhanced sweet corn's nutritional profile, yield potential and resilience to environmental challenges. These advancements ensure that sweet corn remains a nutritionally rich and globally significant crop capable of meeting the growing demands for healthier and more sustainable food sources. As research continues to evolve, sweet corn's genetic diversity and breeding potential will play a crucial role in addressing future agricultural and nutritional needs.

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Authors' contributions

BTK was responsible for conceptualization and writing. KVN contributed to review and editing. SS, VK and MP did the validation.

Compliance with ethical standards

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