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Arbuscular Mycorrhizal Symbiosis Modulates the Expression of ZmSWEET Genes to Enhance Sugar Partitioning and Accumulation in Maize (Zea mays L.)

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Abstract: Background: Arbuscular mycorrhizal fungi (AMF) form a crucial symbiosis with most land plants, including maize (*Zea mays L.*), enhancing nutrient uptake in exchange for plant-derived carbon. The SWEET (Sugars Will Eventually be Exported Transporters) family of proteins are key mediators of sugar flux, but their specific roles in regulating carbon partitioning during maize-AMF symbiosis and the downstream effects on sugar accumulation in sink tissues are not well understood.

Methods: We conducted a greenhouse experiment to investigate the effects of inoculating maize with the AMF species *Funneliformis mosseae*. We compared inoculated (AM) and non-inoculated (NM) plants, measuring mycorrhizal colonization, plant growth parameters, photosynthetic efficiency, and soluble sugar (sucrose, glucose, fructose) concentrations in roots, leaves, and kernels. The expression levels of core *ZmSWEET* genes in root and leaf tissues were quantified using quantitative real-time PCR (qRT-PCR).

Results: AMF inoculation led to successful root

colonization (~55%) and significantly increased plant biomass, and net photosynthetic rates compared to NM controls. Sugar concentrations were significantly elevated in the leaves and kernels of AM plants. In mycorrhizal roots, the expression of putative symbiosis-related genes *ZmSWEET1b* and *ZmSWEET4c* was upregulated by 4.2- and 3.5-fold, respectively. Critically, in the leaves of AM plants, the expression of key phloem-loading and sink-related genes, *ZmSWEET11* and *ZmSWEET13a*, was also significantly enhanced by 2.8- and 3.1-fold, respectively.

Conclusion: Our findings demonstrate that AMF symbiosis orchestrates a sophisticated, dual regulation of the *ZmSWEET* gene family in maize. It localizes specific *ZmSWEETs* to the root-fungus interface to facilitate carbon delivery to the symbiont, while systemically upregulating different *ZmSWEETs* in source leaves. This systemic reprogramming enhances sugar transport efficiency throughout the plant, leading to increased sugar accumulation in kernels. This work elucidates a key molecular mechanism by which AMF can improve both the growth and nutritional quality of maize.

Keywords: Arbuscular mycorrhizal fungi (AMF); *Zea mays L.*; SWEET transporters; Sugar metabolism; Gene expression; Plant-microbe symbiosis.

1. Introduction

Maize (*Zea mays L.*) stands as one of the world's most vital cereal crops, underpinning global food security, animal feed production, and a burgeoning bio-industrial sector [2]. In 2024 alone, global production reached unprecedented levels, reflecting its indispensability to modern civilization [3]. However, the ever-increasing demand for maize is set against a backdrop of significant agricultural challenges, including soil degradation, water scarcity, and the need to reduce reliance on synthetic fertilizers and chemical inputs [1]. To meet the goals of sustainable intensification—producing more with less environmental impact—it is imperative to harness beneficial biological processes that occur naturally within agricultural ecosystems [16].

Among the most powerful and ubiquitous of these processes is the symbiosis between plants and arbuscular mycorrhizal fungi (AMF). These obligate biotrophs from the phylum Glomeromycota form mutualistic associations with the roots of over 80% of terrestrial plant species, including maize [4, 5]. The benefits conferred by AMF to their host plants are extensive and well-documented. The extraradical mycelium of the fungus acts as a vast extension of the plant's root system, vastly improving its capacity to explore the soil volume and acquire growth-limiting nutrients, particularly phosphorus (P) and, to a lesser extent, nitrogen (N) [9, 10]. This enhanced nutrient acquisition often translates into significant improvements in plant growth, biomass accumulation, and overall productivity, especially in low-fertility soils [15, 17, 18]. Numerous studies focusing on maize have demonstrated the efficacy of AMF inoculation in promoting seedling growth and enhancing nutrient uptake [19, 20, 41, 42].

Beyond nutrition, the AMF symbiosis bolsters plant resilience against a range of abiotic stresses. Mycorrhizal plants frequently exhibit enhanced tolerance to drought, a trait attributed to improved plant water status, modulation of stomatal conductance, and the mitigation of oxidative stress [7, 8, 47]. The fungal symbionts also contribute directly to soil health and structure. Through the production of a unique glycoprotein called glomalin, AMF hyphae bind soil particles together into stable aggregates, which improves water infiltration, reduces erosion, and enhances soil carbon sequestration [11, 13, 14, 51].

This multifaceted symbiotic relationship, however, is built upon a fundamental economic exchange: the plant provides the fungus with the carbon (C) it needs to survive and grow, while the fungus provides the plant with essential mineral nutrients [6, 21]. As obligate biotrophs, AMF are entirely dependent on their host for reduced carbon, which is supplied primarily in the form of sugars and, as more recently discovered, lipids [62, 64]. This transfer represents a substantial C investment from the plant, with estimates suggesting that up to 20% of the plant's total photosynthate can be allocated to its mycorrhizal partner [31]. The regulation of this carbon flow is therefore central to the establishment, maintenance, and functional success of the symbiosis [27, 38].

The movement of sugars within a plant, from the photosynthetic source tissues (leaves) to various sink tissues (roots, fruits, seeds, and microbial symbionts), is a tightly controlled process mediated by specialized membrane-bound sugar transporters [22, 23]. A

particularly important family of these transporters is the SWEETs (Sugars Will Eventually be Exported Transporters). SWEETs are a relatively recently discovered class of sugar facilitators, typically possessing seven transmembrane helices arranged in a signature 3-1-3 pattern, which mediate the diffusion-driven transport of sugars like sucrose, glucose, and fructose across cellular membranes [24, 25, 57]. They play diverse and critical roles in plant physiology, including phloem loading in leaves, nectar secretion, pollen nutrition, seed and fruit development, and pathogen nutrition [56, 59, 60].

Growing evidence indicates that SWEET transporters are key players in the plant-AMF dialogue [61]. To deliver sugars from the root cortical cells to the intricately branched fungal arbuscules—the primary site of nutrient exchange—plants must employ specific transporters at the periarbuscular membrane. Seminal studies in other model plant systems have identified specific *SWEET* genes that are strongly induced upon AMF colonization and are essential for a functional symbiosis. For instance, in potato (*Solanum tuberosum*), several *StSWEET* genes were found to be transcriptionally reprogrammed in mycorrhizal roots [28]. In soybean (*Glycine max*), *GmSWEET6* was shown to participate in sucrose transport towards the fungus [29], while in *Medicago truncatula*, *MtSWEET1b* is critically implicated in the maintenance of arbuscules [30]. These findings highlight a conserved strategy whereby plants recruit members of the SWEET family to control carbon allocation to their fungal partners.

In maize, a comprehensive genome-wide analysis has identified and characterized the *ZmSWEET* gene family, revealing its complexity and potential involvement in responses to hormones and abiotic stress [36]. However, a significant knowledge gap persists regarding the specific roles of these *ZmSWEET* genes in the context of the arbuscular mycorrhizal symbiosis. It remains unknown which *ZmSWEETs* are recruited to the symbiotic interface in maize roots to mediate carbon flow. Furthermore, the systemic consequences of this localized carbon sink on whole-plant sugar partitioning and accumulation have not been explored. The establishment of a strong symbiotic sink in the roots could potentially trigger systemic changes in source-sink dynamics, altering sugar transport and leading to changes in sugar content in distal tissues like leaves and kernels [53, 54].

Therefore, this study was designed to investigate the role of AMF in regulating *ZmSWEET* genes and its subsequent impact on sugar accumulation in maize. We hypothesized that AMF colonization of maize roots specifically induces the expression of a subset of *ZmSWEET* genes at the symbiotic interface to facilitate carbon flow to the fungus. Concurrently, we posited that this symbiotic relationship systemically remodels the expression of other *ZmSWEET* genes in source leaves, thereby enhancing overall sugar partitioning and leading to increased sugar accumulation in aerial plant tissues, including developing kernels. By elucidating this dual regulatory mechanism, our work aims to provide novel insights into the molecular basis of carbon allocation in mycorrhizal maize and highlight the potential of AMF to enhance not only plant growth but also its qualitative traits.

2. Materials and Methods

2.1. Biological Materials and Inoculum

The plant material used in this study was maize (*Zea mays L.*) cv. 'Zhengdan 958', a widely cultivated hybrid in China known for its high yield potential. Seeds were surface-sterilized by immersion in 75% (v/v) ethanol for 1 minute, followed by 10% (v/v) sodium hypochlorite solution for 10 minutes, and then rinsed thoroughly with sterile deionized water.

The arbuscular mycorrhizal fungus used was *Funneliformis mosseae* (BGC GD01A), obtained from the Bank of Glomeromycota in China (BGC). The inoculum consisted of a mixture of spores, infected root fragments, and mycelium propagated in pot cultures with clover (*Trifolium repens* L.) as the host plant.

2.2. Experimental Design and Growth Conditions

The experiment was conducted in a controlled environment greenhouse at Hebei Agricultural University, Baoding, China. The growth substrate was a mixture of autoclaved (121°C for 2 hours) field soil and sand (2:1, v/v) to eliminate native microbial populations. The soil had a pH of 7.2, organic matter content of 1.2%, available N of 55.4 mg kg^{-1}, available P of 11.8 mg kg^{-1}, and available K of 121.5 mg kg^{-1}.

Plastic pots (25 cm diameter, 30 cm height) were filled with 5 kg of the sterile substrate. Two treatments were established: (1) AMF-inoculated (AM) and (2) non-mycorrhizal control (NM). For the AM treatment, 100 g of the *F. mosseae* inoculum was thoroughly mixed into the top 10 cm of the substrate in each pot. For the NM treatment, an equal amount of autoclaved inoculum was added, along with a 20 mL aliquot of a microbial filtrate (prepared by passing a suspension of the live inoculum through a 10 µm filter) to provide a similar microbial background minus the AMF propagules.

Three surface-sterilized maize seeds were sown in each pot and thinned to one seedling per pot after one week of germination. The experiment was arranged in a completely randomized design with 15 replicates per treatment. Plants were grown for 90 days under a 16 h light (28°C) / 8 h dark (22°C) cycle, with a relative humidity of 60-70% and a light intensity of approximately 800 µmol m^{-2} s^{-1}. All pots were watered with tap water as needed to maintain soil moisture at ~75% of field capacity and were fertilized weekly with 100 mL of a modified Long Ashton nutrient solution containing half-strength phosphorus (0.25 mM KH_2PO_4).

2.3. Assessment of Mycorrhizal Colonization

At harvest (90 days after sowing), fine roots (<2 mm diameter) were carefully sampled from each plant. A representative subsample of fresh roots (~1 g) was washed, cleared in 10% (w/v) potassium hydroxide (KOH) at 90°C for 60 minutes, and then rinsed with water. The cleared roots were acidified with 2% (v/v) HCl for 5 minutes and subsequently stained with 0.05% (w/v) trypan blue in a lactoglycerol solution overnight [33]. Stained roots were destained in a fresh lactoglycerol solution and cut into 1 cm segments. Mycorrhizal colonization was quantified on 100 randomly selected root segments per sample under a compound microscope (Olympus BX53, Tokyo, Japan) using the magnified gridline-intersect method. The percentage of root length colonized by hyphae, arbuscules, and vesicles was determined.

2.4. Plant Growth and Physiological Measurements

At 75 days after sowing, leaf gas exchange parameters were measured on the youngest fully expanded leaf of each plant between 09:00 and 11:00 using a portable photosynthesis system (LI-6800, LI-COR, Lincoln, NE, USA). The measurements were conducted under a photosynthetic photon flux density (PPFD) of 1200 µmol m^{-2} s^{-1}, a CO_2 concentration of 400 µmol mol^{-1}, and a leaf temperature of 28°C. The net photosynthetic rate (Pn), stomatal conductance (Gs), and transpiration rate (E) were recorded.

At harvest (90 days), plant height was measured. Plants were then separated into shoots, roots, and kernels. The roots were carefully washed free of soil. All plant parts were oven-dried at 75°C for 72 hours to a constant weight to determine the dry biomass.

2.5. Analysis of Glomalin-Related Soil Protein (GRSP)

Rhizosphere soil was collected from each pot by gently shaking the roots. Easily extractable glomalin-related soil protein (EE-GRSP) was extracted as described previously [34]. Briefly, 1 g of air-dried soil was mixed with 8 mL of 20 mM citrate solution (pH 7.0) and autoclaved at 121°C for 30 minutes. After centrifugation at 10,000× *g* for 10 minutes, the supernatant containing EE-GRSP was collected. The protein concentration in the supernatant was determined using the Bradford assay with bovine serum albumin (BSA) as the standard [11, 51].

2.6. Quantification of Soluble Sugars

Samples of fresh roots, the youngest fully expanded leaves, and developing kernels (at the milk stage) were collected at harvest, immediately frozen in liquid nitrogen, and stored at -80°C until analysis. The frozen samples were lyophilized and ground into a fine powder. Soluble sugars were extracted from 100 mg of powder with 5 mL of 80% (v/v) ethanol in a water bath at 80°C for 30 minutes. The extraction was repeated twice, and the supernatants were combined and evaporated to dryness. The residue was redissolved in 2 mL of sterile deionized water and filtered through a 0.22 µm membrane filter [55, 63].

The concentrations of sucrose, glucose, and fructose were determined using a high-performance liquid chromatography (HPLC) system (Agilent 1260, Santa Clara, CA, USA) equipped with a refractive index detector (RID). Separation was achieved on a

carbohydrate analysis column (ZORBAX NH_2 column, 4.6 × 250 mm, 5 µm) with a mobile phase of acetonitrile:water (80:20, v/v) at a flow rate of 1.0 mL min^{-1}. Sugar concentrations were quantified by comparison with external standards and expressed as mg g^{-1} dry weight (DW).

2.7. RNA Extraction and Quantitative Real-Time PCR (qRT-PCR) Analysis

Total RNA was extracted from flash-frozen root and leaf samples (~100 mg) using the TRIzol reagent (Invitrogen, Carlsbad, CA, USA) according to the manufacturer's protocol. RNA quality and concentration were assessed using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) and by 1.2% agarose gel electrophoresis. First-strand cDNA was synthesized from 1 µg of total RNA using the PrimeScript™ RT Reagent Kit with gDNA Eraser (Takara, Dalian, China).

Based on the maize genome annotation and previous studies on *ZmSWEET* genes [36], primers for selected *ZmSWEET* genes implicated in symbiotic transport or phloem loading were designed using Primer Premier 5.0. The maize *Actin1* gene (*Zm00001d010159*) was used as the internal reference gene for normalization. The primer sequences are listed in Supplementary Table S1.

qRT-PCR was performed on a CFX96 Real-Time PCR Detection System (Bio-Rad, Hercules, CA, USA) using SYBR® Premix Ex Taq™ II (Takara, Dalian, China). The reaction volume was 20 µL, containing 10 µL of SYBR Premix, 0.4 µL of each primer (10 µM), 2 µL of diluted cDNA (1:10), and 7.2 µL of nuclease-free water. The thermal cycling program was: 95°C for 30 s, followed by 40 cycles of 95°C for 5 s and 60°C for 30 s. A melting curve analysis was performed to verify primer specificity. The relative expression levels of the target genes were calculated using the 2^{-ΔΔCt} method [37]. Three biological replicates with three technical replicates each were analyzed for each treatment.

2.8. Statistical Analysis

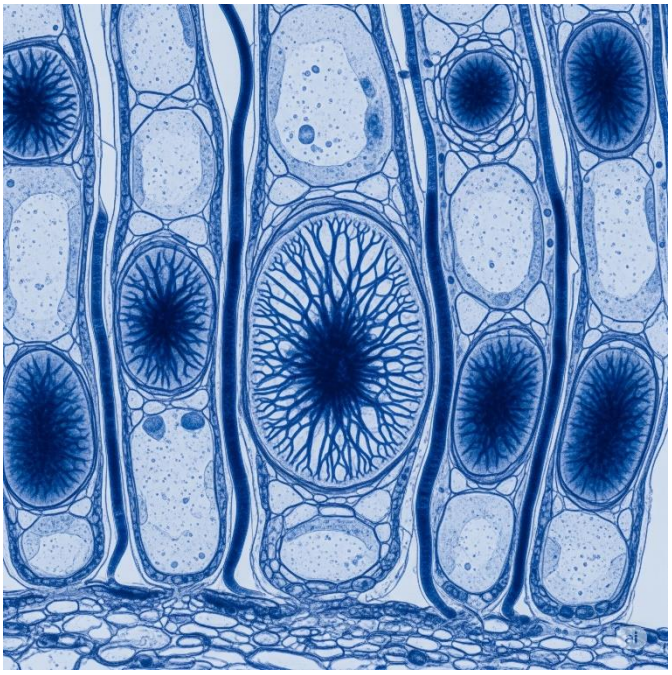
All data were analyzed using SPSS software (version 22.0, IBM Corp., Armonk, NY, USA). An independent samples t-test was used to determine the significance of differences between the AM and NM treatments for all measured parameters. Data are presented as the mean ± standard error (SE). Differences were considered statistically significant at $p < 0.05$.

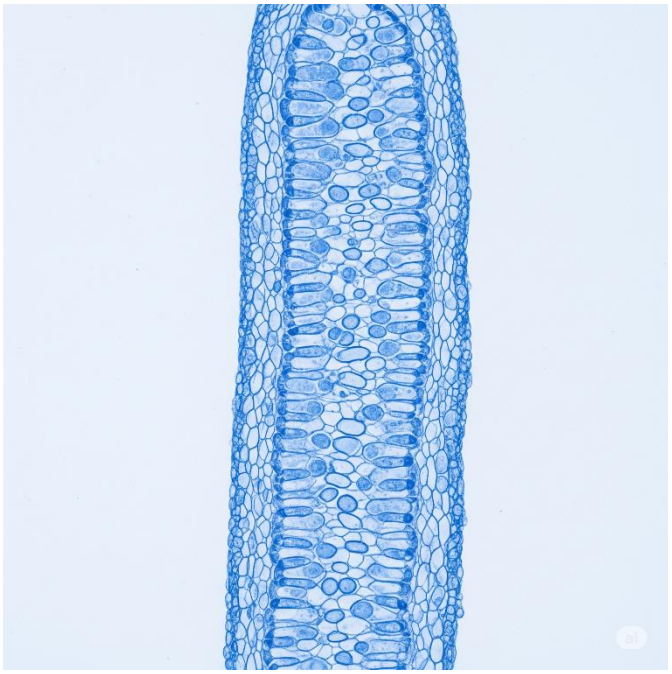
3. Results

3.1. AMF Colonization and Promotion of Maize Growth

At 90 days after sowing, microscopic examination confirmed the successful establishment of AMF symbiosis in the roots of inoculated maize plants. The roots of AM plants showed extensive colonization, with characteristic fungal structures including hyphae, arbuscules, and vesicles being readily observed (Figure 1A). The mean percentage of root length colonized by *F. mosseae* was 58.3 ± 4.1%. In contrast, no signs of mycorrhizal colonization were detected in the roots of the non-mycorrhizal (NM) control plants (Figure 1B).

Inoculation with *F. mosseae* had a significant positive effect on the growth and biomass accumulation of maize plants. As shown in Figure 1C, the plant height of AM plants (185.4 ± 7.2 cm) was significantly greater than that of NM plants (152.1 ± 6.5 cm). More notably, the dry biomass of both shoots and roots was substantially enhanced by AMF symbiosis. The shoot dry weight of AM plants (121.6 ± 5.8 g) was 42.7% higher than that of NM plants (85.2 ± 4.9 g), and the root dry weight (45.3 ± 3.1 g) showed an even greater increase of 55.1% over the control (29.2 ± 2.5 g) ($p < 0.05$).





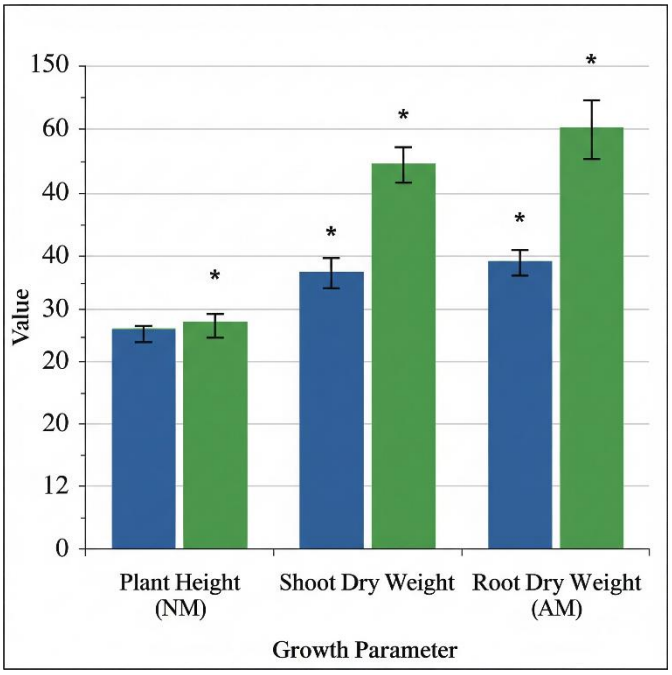


Figure 1. Effects of AMF inoculation on maize root colonization and plant growth. **(A)** Micrograph of a trypan blue-stained maize root showing successful colonization by *F. mosseae*, with visible arbuscules and hyphae. **(B)** Micrograph of a non-mycorrhizal (NM) control root showing the absence of fungal structures. **(C)** Bar chart comparing plant height, shoot dry weight, and root dry weight between NM and AMF-inoculated (AM) plants. Asterisks (*) denote significant differences ($p < 0.05$).

3.2. Enhancement of Photosynthetic Capacity by AMF

To determine if the observed growth promotion was associated with improved carbon fixation, leaf gas exchange parameters were measured. The results, summarized in Table 1, indicate that AMF inoculation significantly enhanced the photosynthetic capacity of maize leaves. The net photosynthetic rate (Pn) in AM plants was 24.8 ± 1.3 µmol CO_2 m^{-2} s^{-1}, which was 28.9% higher than the rate of 19.2 ± 1.1 µmol CO_2 m^{-2} s^{-1} recorded for NM plants ($p < 0.05$). Concomitantly, stomatal conductance (Gs) and transpiration rate (E) were also significantly higher in AM plants compared to their NM counterparts, suggesting a more active gas exchange status in the mycorrhizal plants.

Table 1. Photosynthetic gas exchange parameters of non-mycorrhizal (NM) and AMF-inoculated (AM) maize plants.

Parameter	Non-mycorrhizal (NM)	AMF-inoculated (AM)
Net Photosynthetic Rate (Pn) (µmol CO_2 m^{-2} s^{-1})	19.2 ± 1.1	24.8 ± 1.3*
Stomatal Conductance (Gs) (mol H_2O m^{-2} s^{-1})	0.26 ± 0.02	0.37 ± 0.03*
Transpiration Rate (E) (mmol H_2O m^{-2} s^{-1})	4.5 ± 0.3	6.2 ± 0.4*

Values are presented as mean ± standard error (n = 15). An asterisk () indicates a significant difference between NM and AM treatments at p < 0.05 according to a Student's t-test.*

3.3. AMF Inoculation Increased Soil GRSP Content

The contribution of AMF to soil conditioning was assessed by measuring the concentration of easily extractable glomalin-related soil protein (EE-GRSP) in the rhizosphere. The EE-GRSP content in the rhizosphere of AM plants was 3.45 ± 0.21 mg g^{-1} soil. This value was significantly higher, by approximately 74%, than the EE-GRSP content of 1.98 ± 0.15 mg g^{-1} soil found in the rhizosphere of NM plants ($p < 0.05$) (Figure 2). This result confirms the active proliferation and metabolic activity of *F. mosseae* in the soil surrounding the roots of AM plants.

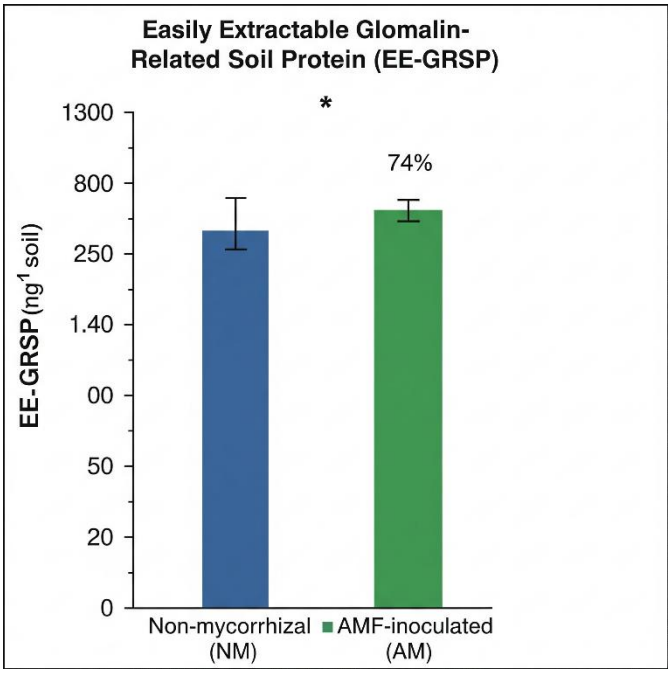
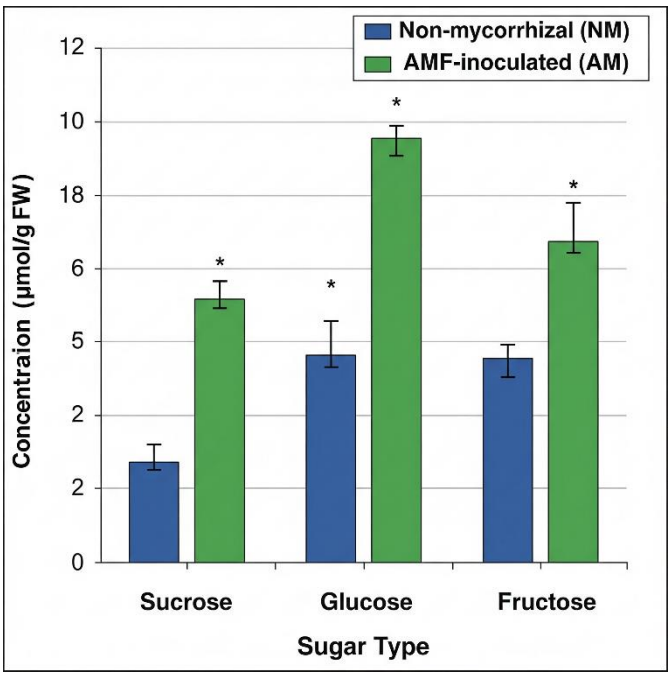


Figure 2. Concentration of easily extractable glomalin-related soil protein (EE-GRSP) in the rhizosphere of non-mycorrhizal (NM) and AMF-inoculated (AM) maize plants. The asterisk (*) indicates a significant difference between treatments ($p < 0.05$).

3.4. AMF Symbiosis Alters Sugar Partitioning and Accumulation

To investigate the impact of AMF symbiosis on the host plant's carbon economy, we analyzed the concentrations of soluble sugars (sucrose, glucose, and fructose) in different tissues (Figure 3). In the roots, there was no significant difference in the concentrations of sucrose, glucose, or fructose between AM and NM plants. However, a striking difference was observed in the aerial parts of the plants. In the leaves, the concentrations of sucrose, glucose, and fructose in AM plants were 28.5 ± 2.1, 15.8 ± 1.3, and 12.4 ± 0.9 mg g^{-1} DW, respectively. These values were significantly higher by 1.6-fold, 1.8-fold, and 1.5-fold, respectively, compared to the levels in NM plants ($p < 0.05$) (Figure 3A).

This pattern of increased sugar accumulation in mycorrhizal plants was even more pronounced in the developing kernels. The total soluble sugar content in the kernels of AM plants was 135.7 ± 8.2 mg g^{-1} DW, which was 35% higher than the 100.5 ± 6.9 mg g^{-1} DW measured in NM plants ($p < 0.05$) (Figure 3B). This indicates that the AMF symbiosis not only enhanced photosynthesis but also promoted the allocation and accumulation of sugars in key sink tissues.



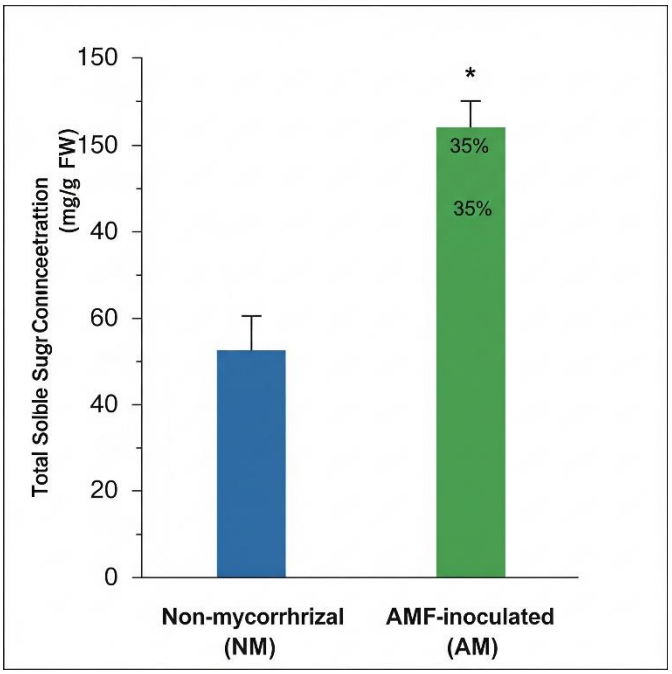


Figure 3. Soluble sugar concentrations in maize tissues. **(A)** Concentrations of sucrose, glucose, and fructose in the leaves of non-mycorrhizal (NM) and AMF-inoculated (AM) plants. **(B)** Total soluble sugar concentration in the kernels. Asterisks (*) denote significant differences between treatments for each sugar type ($p < 0.05$).

3.5. Expression of ZmSWEET *Genes is Upregulated in Mycorrhizal Roots*

To explore the molecular basis for carbon transfer to the fungal symbiont, we analyzed the expression of several *ZmSWEET* genes in the roots using qRT-PCR (Figure 4A). The results revealed a distinct upregulation of two specific *ZmSWEET* genes in response to AMF colonization. The relative expression of *ZmSWEET1b*, a close homolog of the symbiosis-associated *MtSWEET1b* in *Medicago*, was 4.2-fold higher in AM roots compared to NM roots. Similarly, the transcript level of *ZmSWEET4c* was significantly upregulated by 3.5-fold in mycorrhizal roots. In contrast, the expression of *ZmSWEET13a* was not significantly different between the two treatments, suggesting a specialized role for *ZmSWEET1b* and *ZmSWEET4c* at the plant-fungus

interface.

3.6. Systemic Upregulation of ZmSWEET *Genes in Leaves of Mycorrhizal Plants*

To test our hypothesis that AMF symbiosis systemically remodels sugar transport from source tissues, we also profiled the expression of key *ZmSWEET* genes in the leaves (Figure 4B). Remarkably, we found that AMF colonization in the roots led to a significant increase in the transcript abundance of *ZmSWEET* genes known to be involved in phloem loading and sugar export. The relative expression of *ZmSWEET11*, an ortholog of the rice seed-filling transporter *OsSWEET11*, was 2.8-fold higher in the leaves of AM plants than in NM plants. Furthermore, the expression of *ZmSWEET13a*, a major sucrose transporter involved in phloem loading, was significantly enhanced by 3.1-fold in AM plants. The expression of *ZmSWEET1b*, which was strongly induced in roots, was not significantly altered in the leaves, highlighting a tissue-specific regulation of the *ZmSWEET* family members.

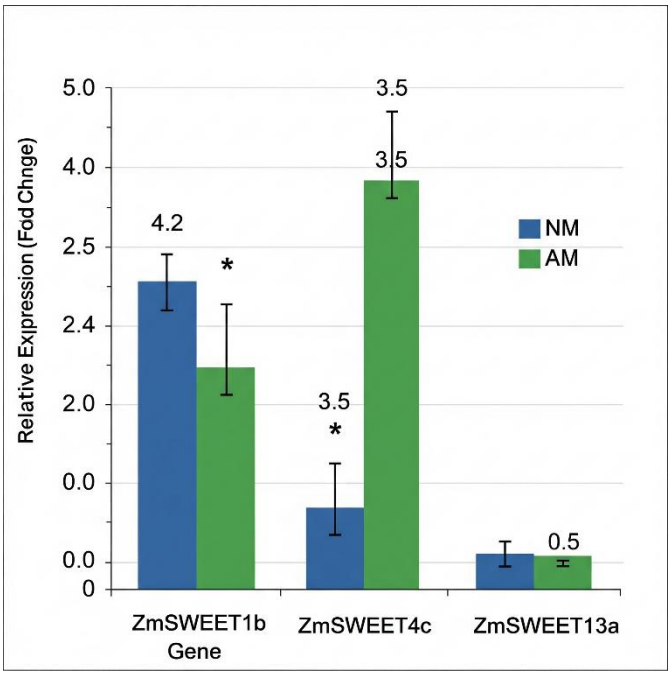


Figure 4. Relative expression of *ZmSWEET* genes in non-mycorrhizal (NM) and AMF-inoculated (AM) maize plants. (A) Expression levels of *ZmSWEET1b*, *ZmSWEET4c*, and *ZmSWEET13a* in root tissues. (B) Expression levels of *ZmSWEET11*, *ZmSWEET13a*, and *ZmSWEET1b* in leaf tissues. Expression is normalized to the NM control. Asterisks (*) denote significant differences ($p < 0.05$).

4. Discussion

The intricate relationship between plants and arbuscular mycorrhizal fungi is a cornerstone of terrestrial ecosystems, fundamentally shaping plant growth, nutrition, and resilience. This study sought to unravel the molecular mechanisms governing the carbon-for-nutrient exchange in the maize-AMF symbiosis, focusing on the regulatory role of the *ZmSWEET* sugar transporter family and its systemic consequences for whole-plant sugar economy. Our findings demonstrate that AMF symbiosis orchestrates a sophisticated, dual regulation of *ZmSWEET* gene expression, locally at the root-fungus interface and systemically in source leaves, which ultimately leads to enhanced sugar accumulation in maize kernels.

4.1. AMF Inoculation as an Effective Strategy for Promoting Maize Growth and Photosynthesis

Our results clearly show that inoculation with *Funneliformis mosseae* significantly promoted the growth and biomass of maize plants (Figure 1). This is in strong agreement with a large body of literature demonstrating the growth-promoting effects of AMF on maize and other crops [9, 17, 18, 41]. This 'benefit' to the plant is classically attributed to improved nutrient acquisition, particularly phosphorus, which is often a limiting factor for growth [15, 42]. The extensive extraradical mycelium of the AMF effectively expands the volume of soil accessible to the plant, leading to enhanced nutrient uptake and, consequently, greater biomass production [10].

A key finding of our study is the significant enhancement of the net photosynthetic rate in mycorrhizal maize (Table 1). This phenomenon, often termed the "mycorrhizal effect" on photosynthesis, has been observed in various plant species, including maize under stress conditions [5, 44, 47]. There are two primary, non-mutually exclusive explanations for this observation. First, the improved nutritional status, especially of phosphorus, in AM plants can lead to higher concentrations of phosphorus-containing compounds like ATP and RuBP in the chloroplasts, thereby boosting the efficiency of the Calvin cycle and carbon fixation [49]. Second, the establishment of a strong carbon sink in the roots by the fungal symbiont can systemically stimulate photosynthesis in the source leaves to meet the increased carbon demand [6, 53]. Our data, which show both enhanced growth (indicating higher nutrient demand) and a powerful symbiotic sink, suggest that both mechanisms are likely at play. The increased stomatal conductance in AM plants further supports the idea of a more active photosynthetic apparatus, although this can also be linked to improved plant water status mediated by AMF [48].

4.2. Localized Upregulation of ZmSWEET *Genes Facilitates Carbon Flow to the Intraradical Fungus*

The transfer of sugars from the host plant to the fungal symbiont is the energetic engine of the mycorrhizal symbiosis. Our qRT-PCR analysis revealed that the expression of *ZmSWEET1b* and *ZmSWEET4c* was specifically and significantly upregulated in the colonized roots of maize (Figure 4A). This provides strong molecular evidence for their involvement in mediating sugar transport at the symbiotic interface. The upregulation of *ZmSWEET1b* is particularly noteworthy, as its homolog in *Medicago truncatula*, *MtSWEET1b*, is essential for the formation and maintenance of functional arbuscules [30]. It is highly probable that ZmSWEET1b is localized to the periarbuscular membrane, where it facilitates the efflux of hexoses from the plant cytoplasm into the peri-arbuscular space, making them available for uptake by the fungus.

The induction of *ZmSWEET4c*, a hexose transporter homolog [60], further supports this model. The coordinated upregulation of these transporters is a clear indication of the plant's active role in nourishing its fungal partner, a process central to the plant-fungi dialogue [21, 27]. This finding aligns with studies in other mycorrhizal systems, such as soybean and potato, where specific members of the SWEET family are recruited to sustain the symbiosis [28, 29]. Our results thus identify *ZmSWEET1b* and *ZmSWEET4c* as key candidate genes for facilitating carbon allocation to AMF in maize, a crucial step in understanding the molecular genetics of this important interaction.

4.3. Systemic Reprogramming of Sugar Transport Is a Key Outcome of Mycorrhization

Perhaps the most novel finding of this study is the systemic effect of root colonization on gene expression and sugar metabolism in the leaves. We demonstrated that the transcript levels of *ZmSWEET11* and *ZmSWEET13a* were significantly increased in the leaves of mycorrhizal plants (Figure 4B). These genes are homologs of well-characterized SWEETs involved in phloem loading and sugar export from source leaves [25, 59]. *ZmSWEET13a*, in particular, is a sucrose transporter likely responsible for exporting sucrose from mesophyll cells into the apoplast for subsequent loading into the phloem. Its upregulation suggests a more efficient and higher-capacity sugar export system in the leaves of AM plants.

This systemic reprogramming of gene expression is likely a plant-wide response to the creation of a new and powerful carbon sink in the roots [53]. The continuous demand for carbon by the fungus acts as a signal that stimulates both the rate of photosynthesis (source activity) and the efficiency of sugar transport from the source [49]. This prevents feedback inhibition of photosynthesis that can occur when sugars accumulate in leaves, thus maintaining a high rate of carbon fixation. This distal regulation of source leaf metabolism highlights the profound integration of the AM fungus into the host plant's overall physiology. The fungus is not merely a passive recipient of carbon; its presence actively remodels the plant's entire carbon transport network to ensure a sufficient supply, a process that ultimately leads to a larger pool of available photosynthates for all plant sinks.

4.4. A Proposed Model for AMF-Mediated Sugar Accumulation in Maize

Based on our collective results, we propose a comprehensive model for how AMF symbiosis governs sugar accumulation in maize (Figure 5). First, the establishment of a functional AM symbiosis creates a strong and persistent carbon sink in the root system. To satisfy the carbon demand of the fungus, the plant upregulates specific sugar transporters, namely *ZmSWEET1b* and *ZmSWEET4c*, at the periarbuscular membrane, facilitating sugar efflux to the fungal partner. Second, this high sink strength in the roots sends a systemic signal to the shoots, which leads to an increase in the net photosynthetic rate to boost overall carbon fixation. Third, to efficiently transport this increased supply of photosynthate from the source leaves, the expression of key phloem-loading transporters, such as *ZmSWEET11* and *ZmSWEET13a*, is upregulated. This "supercharges" the plant's sugar transport highway. Finally, this enhanced flow of sugars through the phloem results in greater allocation not only to the mycorrhizal roots but also to the plant's own primary sinks, such as the developing kernels. The consequence is a significant increase in the concentration of soluble sugars in these economically important organs, as observed in our results (Figure 3B). This model explains how a localized symbiotic interaction in the roots can translate into an improved qualitative trait in the harvested product.

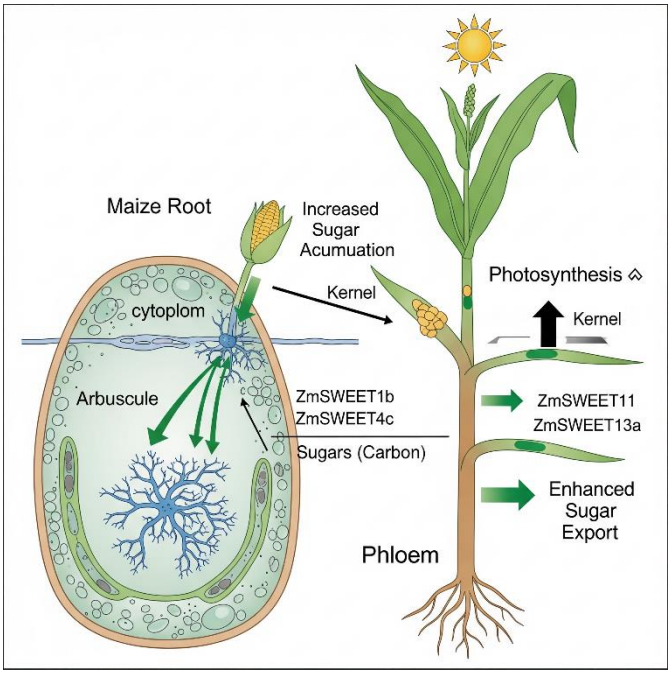


Figure 5. Conceptual model illustrating the dual regulation of *ZmSWEET* genes by AMF symbiosis in maize. In the root, *ZmSWEET1b* and *ZmSWEET4c* are upregulated to transport sugars to the fungus. This creates a strong sink, which systemically signals the leaf to increase photosynthesis and upregulate *ZmSWEET11* and *ZmSWEET13a* for enhanced sugar export, leading to increased sugar accumulation in the kernels.

4.5. Implications for Crop Improvement and Future Research

Our findings have significant implications for sustainable agriculture. They reposition AMF not just as biofertilizers that enhance nutrient uptake and stress tolerance [7, 46], but as potent modulators of plant carbon metabolism that can be used to improve crop quality [12, 63]. For crops like sweet corn, where sugar content is a primary quality trait, or for maize destined for biofuel production, where carbohydrate content is critical, leveraging AMF symbiosis could be a valuable agronomic strategy [2, 16]. This research provides a molecular roadmap for how this enhancement occurs.

While this study provides compelling evidence for the role of *ZmSWEET*s in mycorrhizal maize, further research is needed. Future work should focus on the functional validation of the identified candidate genes using reverse genetics approaches, such as CRISPR/Cas9-mediated knockout mutants, to confirm their necessity for the symbiotic interaction and for the systemic effects on

sugar partitioning. In situ hybridization or promoter-GUS fusion studies would also be invaluable for precisely localizing the expression of these *ZmSWEETs* within mycorrhizal roots and leaves. Finally, while our study was conducted under controlled greenhouse conditions, it is crucial to extend these investigations to field trials to assess the performance of this plant-microbe system under real-world agricultural conditions [17, 18, 20]. Investigating how the lipid transfer pathway [62, 64] interacts with sugar-based carbon transport in maize would also be a fascinating avenue for future exploration.

5. Conclusion

In conclusion, this study elucidates a sophisticated, dual-level regulatory mechanism by which arbuscular mycorrhizal symbiosis governs sugar metabolism and accumulation in maize. We have shown that the colonization by *Funneliformis mosseae* locally induces the expression of specific root-expressed genes, *ZmSWEET1b* and *ZmSWEET4c*, to facilitate carbon delivery to the fungal partner. More importantly, this interaction triggers a systemic response in the plant, upregulating the expression of key phloem-loading transporters, *ZmSWEET11* and *ZmSWEET13a*, in source leaves. This systemic reprogramming enhances the plant's overall capacity for sugar transport, leading to increased photosynthetic rates and greater accumulation of soluble sugars in the kernels. These findings provide novel insights into the molecular control of carbon partitioning in one of the world's most important crops and highlight the transformative potential of harnessing the AMF symbiosis to sustainably improve both the yield and quality of maize.

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