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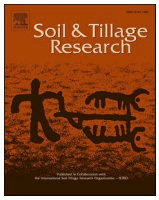

Impact of tillage practices and arbuscular mycorrhizal fungi inoculation on organic sweet corn yield and nutritional quality

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ABSTRACT

The application of mycorrhizal biofertilizers in agriculture has demonstrated potential for improving crop yield and nutrition. However, their effectiveness across different tillage systems and under on-farm conditions remain underexplored. This two-year study evaluated the effects of tillage practices and supplemental arbuscular mycorrhizal fungi (AMF) inoculation on the yield and nutrient composition of organically grown sweet corn (*Zea mays*). The experiment followed a split-plot design with two tillage practices—full tillage (FT) and reduced tillage (RT)—and four AMF treatments: mock (control), native AMF community (NAT), *Rhizophagus irregularis*, and *Funneliformis mosseae*. Results showed that FT significantly increased fresh and dry ear yields compared to RT. AMF inoculation, particularly with *R. irregularis*, enhanced kernel phosphorus (P) and potassium (K) concentrations. Inoculation with *R. irregularis* and *F. mosseae* also increased kernel vitamin B6 and C levels. Tillage influenced amino acid composition, with leucine and phenylalanine concentrations being higher in FT, while tryptophan was greater in RT. Additionally, *R. irregularis* and *F. mosseae* inoculation increased aspartic acid and glycine concentrations, which play a role in scavenging reactive oxygen species (ROS), suggesting a potential role for AMF in enhancing crop stress resilience and nutritional quality. Despite these benefits, natural AMF colonization across treatments may have masked the full effects of supplemental inoculation, highlighting the complexity of evaluating AMF biofertilizers in field conditions. Overall, this study suggests that while the presence of native AMF complicates the assessment of exogenous inoculation, AMF biofertilizers have positive implications for enhancing nutrient density of sweet corn across tillage practices.

1. Introduction

Annually, the United States, produces 1.4 billion kilograms (kg) of sweet corn on about 97,970 ha for fresh consumption, generating total sales of $1 billion (USDA, 2024a). In Pennsylvania, sweet corn is the leading vegetable crop, with about 5260 ha cultivated for fresh consumption annually of which less than 1 % is grown organically (USDA, 2024a). Tillage is commonly used in organic systems for weed management (Bilalis et al., 2001) and crop residue incorporation (Sidiras et al., 2001). However, studies have shown that frequent and intensive tillage can increase soil erosion, reduce soil health properties (Blevins et al., 1998; Singh et al., 2016; Zuber et al., 2015), and reduce microbial abundance, (Kabiri et al., 2016; Xiao et al., 2019; Zhang et al., 2019), particularly of arbuscular mycorrhizal fungi (AMF) (Balota et al., 2016; Bowles et al., 2017; Carrara et al., 2024; Oehl and Koch, 2018; Sale et al., 2015), by disrupting mycelial networks and limiting mycorrhizal root colonization in agricultural systems (Kabir, 2005a).

Arbuscular mycorrhizal fungi are obligate symbionts that form mutualistic relationships with most plant roots in natural and agricultural systems (Smith and Read, 2010). Plants allocate carbon (C) to AMF, which in turn extend mycelial networks in the soil to enhance water and nutrient acquisition, including phosphorus (P), nitrogen (N), potassium (K), calcium (Ca), sulfur (S), zinc (Zn), and copper (Cu). This symbiosis boosts plant productivity (Bowles et al., 2016; Hill et al., 2010; van der Heijden et al., 1998) and crop quality (Noceto et al., 2021), while AMF hyphal turnover contributes to soil aggregation and soil organic matter (SOM) formation (Wilson et al., 2009). These functions enhance agricultural productivity and plant resilience to

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environmental stresses. However, AMF effectiveness can vary among different AMF groups and depending on host species (Powell et al., 2009; Carrara and Heller, 2022; Carrara et al., 2023; Carrara et al., 2024).

Soil conservation practices such as reduced and no-tillage, is increasingly adopted for its positive impact on soil health (Kassam et al., 2019). Studies show that such tillage helps preserve AMF populations by minimizing soil disturbances (Sale et al., 2015; Sosa-Hernández et al., 2019; Ferreira et al., 2020). In organic reduced tillage systems, mechanical termination of cover crops using methods like cutting or roller crimping (Kornecki et al., 2012) - help maintain soil structure, promotes diverse microbial communities, including AMF, and enhances microbial biomass (Wang et al., 2020; Zheng et al., 2023). Additionally, organic amendments promotes AMF diversity and colonization, whereas synthetic fertilizers often reduce it (Chen et al., 2014; Liu et al., 2015; van der Gast et al., 2011).

Land use history and cultivation intensity significantly affect the availability of native mycorrhizal fungi for root colonization. In degraded or intensively tilled soil, AMF biofertilizer can supplement the natural AMF communities and restore land. Vegetable growers can either purchase commercial AMF products or produce their own inoculant on-farm (Douds Jr.. et al., 2012; Wertheim et al., 2014). AMF inoculation has been shown to enhance productivity and nutrient content in vegetable crops, particularly in disturbed farming systems. For example, Carrara and Heller (2022) reported a positive correlation between root mycorrhizal colonization and P concentration in young sweet corn seedlings, with *Rhizophagus* species showing the strongest effect. The increasing demand for organic vegetables and the shifts towards minimal tillage to conserve soil health, has increased interest in using AMF as a strategy to improve plant growth, yield, and nutrient quality. However, estimating the benefits of AMF in the field remains challenging, especially in evaluating the effects on vegetable yield, root colonization intensity, and nutrient uptake and with respect to different tillage practices.

This study aims to evaluate the effects of tillage practices and AMF inoculation on sweet corn yield, horticultural traits (e.g., plant dry weight, harvest index), nutrient composition, and root colonization in an organic system. We hypothesized that sweet corn yield would differ between tillage practices and AMF species, and that AMF inoculation will enhance nutrient quality.

2. Materials and methods

2.1. Study site, experimental design, and cultivation practice

The experiment was carried out at Rodale Institute, Kutztown, Berks County, Pennsylvania, USA (40° 55' 36" N, 75° 59' 90" W) during 2021 and 2022 growing seasons. Soils at the site are characterized as Clarksburg silt loam soil (super active, mesic Oxyaquic Fragiudalfs in the USDA Taxonomy), which predominantly feature a flat terrain with slopes ranging from 3 % to 8 %. The area has a subhumid temperate climate, with a hardiness zone classified as 6b (USDA, 2024b). The long-term (1990–2022) average annual precipitation is 1196.3 mm, with a mean annual temperature (MAT) of 11.3 °C (Fig. S1). During the study period, the mean annual precipitation (MAP) was 1228.0 mm in 2021 and 1286.0 mm in 2022, and the MAT was 11.5 °C and 11.0 for 2021 and 2022, respectively. Long term weather data (1990–2023) were taken from the National Weather Service (NOAA, 2024), while the weather data for the period under study were taken from the weather station located at the Rodale Institute Research Farm (HOBO RX3000 Station – CELL - 4 G) (Supplementary figure: Fig. S1).

The experimental design was a randomized split plot design with tillage treatments, i.e., full tillage (FT) and reduced tillage (RT)] as main factor and AMF inoculation as subplot, with four replications. The plots measured 26.0 m x 3.0 m, and they were separated by 6.1 m x 9.1 m wide grass buffer strips.

2.2. Field preparation and seeding of cover crops

Prior to the initiation of the research study, the fields were previously cropped to a cover crop mixture of winter triticale (*Triticosecale* Wittmack) 'Tulus' and Austrian winter pea (*Pisum sativum L.* variety unspecified, Albert Lee) at 1:1 ratio at 101 kg ha^{-1}. The cover crop was roll-crimped in spring and the plots were then prepared for the two-year project by chisel plowing, disking, and harrowing before seeding a cover crop mixture of hairy vetch (*Vicia villosa*) 'Purple Bounty' at a rate of 33.6 kg ha^{-1} and cereal rye (*Secale cereale* L., variety unspecified, Albert Lee) at a rate of 101 kg ha^{-1} (details in Supplementary Table S1) in fall of 2020 and 2021.

In spring of 2021 and 2022, cover crop biomass and soil were sampled for chemical analysis. Soil samples were collected from a depth of 0 – 20 cm. Details on cover crop biomass collection and nutrient analysis are provided in Section 2.4.1. In FT plots, the cover crop was mowed with a flail mower and then moldboard plowed. A blood meal fertilizer (12–0–0 NPK) was applied after plowing at a rate of 1793 kg ha^{-1} using a Frontier spreader, disked with a Krause 8100 disk (Kuhn Manufacturing Facility, Hutchinson, KS), and then packed using an Unverferth Perfecta harrow (Unverferth Manufacturing Company, Inc., Kalida, OH). For the RT plots, the cover crop was roll-crimped at anthesis to form a mulch using a 3.0 m wide roller-crimper (I&J Manufacturing, Gordonville, PA) front-attached to a tractor. Bloodmeal was applied at the same rate but was not incorporated into the soil.

2.3. Preparation of mycorrhizal inoculum, seed inoculation, and field transplantation

The study included four AMF treatments: two single AMF species, one mixed species, and a mock (control) treatment. The single AMF species accessions are *Funneliformis mosseae* and *Rhizophagus irregularis,* which were acquired from the International Culture Collection of Vesicular-Arbuscular Mycorrhizal Fungi (INVAM) at West Virginia University, Morgantown, WV. The mixed species inoculum (hereafter NAT) was propagated in November 2019 from soil sample (composite) collected from the Vegetable Systems Trial (VST: https://rodaleinstitute.org/science/vegetable-systems-trial/) at Rodale Institute, Kutztown, PA.

The AMF inocula were propagated on-farm at Rodale Institute during the 2020 and 2021 growing seasons by transplanting pre-colonized Bahia grass (*Paspalum notatum)* into five-gallon grow bags (four plants per bag) filled with a 3:1 mixture of vermiculite to sterilized compost mixture, following the protocol of Douds et al. (2010). Inoculum for each treatment was prepared by removing the aboveground biomass of Bahia grass, cutting the root tissue into ~ 1 cm lengths and incorporating it into a growing media mix (Pro-Mix BX, Premier Tech, Riviere-du-Loup, Quebec, Canada) at 1:10 dilution to achieve a spore density of ~ 100 spores and the colonized root fragments are place in 128 square standard nursery plug cell trays (27 cm^3/cell). A mock inoculum was prepared using Bahia grass grown in autoclaved soil and the resulting substrate was used as a negative control. This ensured that any observed treatment effects were due to AMF rather than the addition of the inoculum substrate, which contained a small amount of compost. Molecular analysis using multiplex qPCR (Heller and Carrara, 2022) was used to confirm the monospecific inoculum were free from contamination by other AMF and to identify that the NAT community inoculum contained *C. etunicatum, C. claroideum, F. mosseae, R. intraradices,* and *R. irregularis.*

To promote AMF spore germination and root colonization, trays filled with inoculated media were prepared three weeks before seeding sweet corn (*Zea mays* var. Coastal), in 128-cell trays. Seeding was done in the greenhouse on June 2, 2021 and May 31, 2022, following Douds et al., (2016). This pre-inoculation period allowed AMF to colonize the roots of 7-day-old sweet corn seedlings. To prevent cross-contamination, seeding trays for each treatment were placed on separate greenhouse

benches during watering.

In the field, 14 sweet corn seedlings per AMF treatment were transplanted by hand into four rows within the FT and RT plots on June 10, 2021, and June 9, 2022, respectively. Plants were spaced 76 cm between rows and 45.7 cm within rows. At the time of transplanting, seedlings were watered with 1 % fish emulsion (3–4–3, Fertrell, Bainbridge, PA) and irrigated using drip irrigation.

2.4. Sample collection and analysis

2.4.1. Cover crop biomass

Aboveground cover crop biomass (hairy vetch: cereal rye) was randomly sampled immediately prior to cover crop termination on May 3, 2021, and 2022 for FT plots, and May 18, 2021, and 2022 for RT plots. Biomass was collected by cutting plants at ground level within a 0.50 m^2 quadrat. Samples were placed in light cotton bags, dried in forced-air oven at 45 °C for one week, and weighed to determine dry biomass. Dried samples were ground using a Wiley Mill (2 mm screen) before nutrient analysis. All nutrient analyses were conducted at the Pennsylvania State University Agriculture Analytical Services Laboratory (PSU AASL) (State College, PA). Concentration of phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), manganese (Mn), iron (Fe), copper (Cu), zinc (Zn), and boron (B) were determined by HNO_3 and H_2O_2 digestion followed by inductively coupled plasma-optical emission spectrometry (ICP-OES, Agilent 5900 ICP-OES, Agilent Technologies, Santa Clara, CA), following the protocol of Huang and Schulte, (1985). Total nitrogen (N) and carbon (C) were measured via combustion using a Vario Max N/C Cube Analyzer (Elementar Inc. Langenselbold, Germany) following Junglee et al., (2014). Results of cover crop biomass and nutrient analysis are presented in supplementary tables (Table S4).

2.4.2. Sweet corn leaf

Four leaf tissue samples were randomly collected per AMF treated sweet corn plant about 65 days after seeding. Leaves were taken from the 5th node from the top, where no ear was present on July 28, 2021, and August 2nd, 2022. Samples were dried in a forced-air oven at 60 °C for one week, ground, and analyzed for mineral nutrients at PSU AASL, following methods described in Section 2.4.1.

2.4.3. Soil

For bulk density analysis, undisturbed soil cores were collected per plot from 0 to 10 cm and 10–20 cm with a JMC soil bulk density probe (15.5 cm high and 5.1 cm internal diameter cylinder; JMC Soil Samplers, Newton, IA). The soil cores were dried at 105 °C in an oven to determine the dry mass and calculate the soil bulk density (BD). Total soil porosity (Φ) was calculated as [1 – (bulk density/particle density (assumed to be 2.65 g cm^{-3})]). For chemical analysis, composite of 10 cores of soil samples were collected using a 2.5 cm diameter soil probe from the top 20 cm soil depth in a 'W' pattern per plot, avoiding edges and tractor wheel tracks. The soil samples were spread on trays laid with wax paper and air-dried. The dry soil samples were sieved through a 2-mm sieve, subsampled, and analyzed for mineral nutrients using Mehlich-3 soil test extractant method, pH water extractant method (1:2), and total C and N using combustion method at PSU AASL. Soil pH was measured in water according to Eckert and Sims, 1995. Extractable P, K, Ca, and Mg were measured by Melich III (ICP) according to Wolf and Beegle (2011). Soil organic matter was measured via loss on ignition according to Schulte and Hoskins (1995). Total C was measured via combustion as stated in Nelson and Sommers, 1982). Total N was determined via combustion as stated in Bremner (1996). Finally, Zn, Cu, and S were measured using EPA Method 3050B/3051 + 6010 (EPA, 1986). Results of soil chemical and physical and analyses are included in supplementary tables (Tables S2, and S3).

2.4.4. Sweet corn ear and whole plant

Sweet corn ears from the centermost plot rows were hand-harvested for each mycorrhizal treatment to determine yield (unhusked fresh ear weight per hectare). At harvest, ten whole plants per treatment were collected, and stalks were separated from unhusked ears, weighed fresh, and dried in a forced-air oven. The harvest index (HI) was calculated as the ratio of dry unhusked ear weight to stalk weight. Fresh kernels were removed from the ears, frozen at −20 °C, then freeze-dried, ground, and subsampled. Subsamples were analyzed for mineral nutrients using the acid digestion hot block method at PSU AASL, and total C and N were determined via dry combustion (Elementar Vario Max N/C Analyzer, Elementar Inc.). Amino acid profiling was conducted at the University of Missouri Agricultural Experiment Station Chemical Laboratories (St. Louis, MO) following AOAC Official Method 982.30 (AOAC, 2024), while crude protein was analyzed using the Kjeldahl method, with values expressed as N × 6.25 (AOAC, 2024). Additionally, sweet corn kernels were analyzed for vitamins B6 and C at Eurofins Lancaster Laboratories (Lancaster, PA).

2.5. Determination of AMF colonization

At harvest, fresh sweet corn roots were gently collected, washed with water, and 0.5 g of fresh roots were soaked in 10 % potassium hydroxide (KOH) solution at room temperature for four days to remove root cell contents. The cleared roots were rinsed in tap water (2 times), acidified in 1 % hydrochloric acid (HCl) for 3 min, and then stained with 0.5 % trypan blue solution (Phillips and Hayman, 1970). The AMF root colonization was measured using the gridline intercept method (Giovannetti and Mosse, 1980) under a compound microscope (20–50 X magnification). The root colonization percentage was determined as follows:

$$\textit{Percentage of Root Colonization} = \frac{\textit{Number of colonized roots}}{\textit{Total number of roots } (\textit{colonized} + \textit{uncolonized})} \; x \quad 100$$

2.6. Statistical analysis

All data were analyzed using SAS (Version 9.4, 2013), except for Pearson correlation analysis, which was performed in R (ggcorrplot package, Version 4.4.2, 2024). Analysis of variance (ANOVA) was conducted for all response variables using the PROC GLIMMIX procedure, with block and year treated as random factors and all other factors as fixed. Data were checked for normality and homoscedasticity using Bartlett's test and the univariate procedure. Variables such as cover crop biomass, leaf mineral nutrients, kernel mineral nutrients, amino acids, and vitamins were log-transformed to satisfy ANOVA assumptions, and means were back-transformed for presentation in tables and figures. Post-hoc analyses were conducted using Fisher's LSD ($p < 0.05$), and multiple comparisons between treatments were evaluated using Tukey-Kramer adjusted P-values ($p < 0.05$).

3. Results

3.1. Leaf tissue nutrient concentration

Sweet corn leaf mineral concentrations of N, Ca, Mg, S, Mn, Fe, Cu, and B were significantly affected by tillage, with higher concentrations observed in FT compared to RT (Table 1). In contrast, P concentration was significantly greater in RT than in FT, while K and Zn concentrations in leaf tissue were not influenced by tillage. Among the AMF treatments, inoculation with the NAT mixed species significantly increased Fe concentrations in sweet corn leaves (Table 1). However, no significant interactions between tillage and AMF inoculation were detected for any of the assessed leaf mineral concentrations.

Macro-nutrient concentrations in sweet corn leaf tissue, assessed at the ear leaf stage, were within the critical sufficiency ranges for N, P, K,

Table 1
Mean leaf mineral concentrations of sweet corn as affected by tillage and AMF inoculation.

Source of variation	N	P	K	Ca	Mg	S	Mn	Fe	Cu	Zn	B
	g kg^{-1}					g	mg kg^{-1}				
Tillage (T)											
RT[†]	24.64 ± 0.64[b!]	4.85 ± 0.09[a]	20.99 ± 0.68	5.41 ± 0.11[b]	2.20 ± 0.10[b]	1.86 ± 0.05[b]	22.80 ± 1.09[b]	89.51 ± 4.61[b]	7.83 ± 0.33[b]	10.36 ± 0.34	4.19 ± 0.15[b]
FT[§]	30.63 ± 0.76[a]	4.32 ± 0.08[b]	19.61 ± 0.64	6.49 ± 0.13[a]	2.88 ± 0.13[a]	2.23 ± 0.06[a]	26.98 ± 1.26[a]	117.91 ± 5.84[a]	11.61 ± 0.47[a]	11.11 ± 0.36	4.85 ± 0.16[a]
AMF Inoculation											
Mock	27.91 ± 0.61	4.57 ± 0.09	19.88 ± 0.55	5.91 ± 0.12	2.52 ± 0.09	2.02 ± 0.04	24.55 ± 0.97	101 ± 4.31[b]	9.54 ± 0.33	10.68 ± 0.30	4.65 ± 0.19
NAT (mixed *spp.*)[‡]	28.05 ± 0.61	4.44 ± 0.09	20.32 ± 0.55	5.99 ± 0.12	2.51 ± 0.09	2.03 ± 0.05	25.62 ± 1.00	110 ± 4.54[a]	9.57 ± 0.33	10.83 ± 0.30	4.41 ± 0.18
F. mosseae	26.71 ± 0.60	4.72 ± 0.09	20.23 ± 0.55	5.86 ± 0.12	2.57 ± 0.09	2.04 ± 0.05	24.04 ± 0.96	99 ± 4.27[b]	9.40 ± 0.33	10.59 ± 0.30	4.72 ± 0.19
R. irregularis	27.26 ± 0.61	4.59 ± 0.09	20.73 ± 0.56	5.93 ± 0.12	2.49 ± 0.09	2.06 ± 0.05	25.02 ± 0.99	101 ± 4.36[b]	9.62 ± 0.34	10.80 ± 0.31	4.26 ± 0.18
Significance											
T	< 0.0001	0.0012	ns	< 0.0001	0.0008	0.0002	0.025	0.002	< 0.0001	ns	0.011
AMF	ns	ns	ns	ns	ns	ns	ns	0.034	ns	ns	ns
T x AMF	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[†]RT: reduced tillage where soil was chisel plowed and prepared for seeding the cover crop mixture hairy vetch (34 kg ha^{-1}) and cereal rye (101 kg ha^{-1}) in the fall and then roll-crimped at anthesis prior to transplanting sweet corn seedlings in spring.
[§]FT: soil was plowed with moldboard plow and prepared for seeding the cover crop mixture in the fall and similarly prior to transplanting sweet corn seedlings in the spring.
[‡]NAT: natural source of mycorrhizal fungi sourced from organic soils in the Vegetable Systems Trial at Rodale Institute.
[!]Analysis was performed on transformed data and untransformed data are reported. Means ± SE within column per tillage and mycorrhizal species followed by the same letter are not significantly different ($p < 0.05$) by Tukey-Kramer adjusted LSD. ns: nonsignificant at $p \leq 0.05$, based on F test. N = 32 when sample was grouped based on tillage, and N = 16 when sample was grouped based on AMF treatment.

Ca, Mg, and S (28, 2.5, 18.0, 3.0, 2.5, and 2.0 g kg^{-1}, respectively). Mn levels (25 mg kg^{-1}) were also within the sufficiency range, while Zn and B were below the critical thresholds (20 mg kg^{-1} and 6 mg kg^{-1}, respectively). Fe concentrations were approximately twice the sufficiency level (60 mg kg^{-1}), while Cu levels were 1.3 times higher than the critical value (6 mg kg^{-1}).

3.2. Sweet corn yield, ear dry weight, stalk dry weight, harvest index, crude protein, vitamin B6 and Vitamin C

Fresh sweet corn yield was significantly influenced by tillage, with higher yields observed in FT compared to RT ($p = 0.0004$; Table 2). Similarly, unhusked ear dry weight was significantly greater in FT than in RT ($p = 0.004$). In contrast, vitamin C concentration in sweet corn

Table 2
Sweet corn fresh yield, stalk dry weight, and harvest index (HI) as affected by tillage practices and AMF inoculation treatments.

Source of variation	Yield (Mg ha^{-1})	Unhusked ear dry weight (Mg ha^{-1})	Stalk dry weight (Mg ha^{-1})	HI (%)	Crude protein (%)	Vitamin B6 (mg 100 g^{-1})	Vitamin C (mg 100 g^{-1})
Tillage (T)							
RT[†]	15.00 ± 0.47[b!]	2.44 ± 0.13[b]	5.10 ± 0.78	47.45 ± 6.52	13.73 ± 0.41	0.59 ± 0.016	24.55 ± 2.48[a]
FT[§]	18.27 ± 0.53[a]	3.15 ± 0.16[a]	7.52 ± 1.12	43.11 ± 6.00	13.88 ± 0.42	0.62 ± 0.016	17.69 ± 1.84[b]
AMF Inoculation							
Mock	16.57 ± 0.51	2.82 ± 0.14[a]	6.06 ± 0.68	47.97 ± 4.92	13.79 ± 0.33	0.60 ± 0.013[ab]	21.66 ± 1.77[ab]
NAT (mixed *spp.*)[‡]	16.93 ± 0.51	2.95 ± 0.14[a]	7.00 ± 0.77	42.42 ± 4.43	13.58 ± 0.32	0.58 ± 0.012[b]	18.92 ± 1.61[b]
F. mosseae	16.30 ± 0.51	2.54 ± 0.13[b]	5.78 ± 0.65	44.17 ± 4.57	13.97 ± 0.33	0.61 ± 0.012[a]	20.21 ± 1.69[ab]
R. irregularis	16.34 ± 0.51	2.82 ± 0.14[a]	6.02 ± 0.67	46.53 ± 4.79	13.87 ± 0.33	0.61 ± 0.012[a]	22.83 ± 1.89[a]
Significance							
T	0.0004	0.004	ns	ns	ns	ns	0.040
AMF	ns	0.050	ns	ns	ns	0.013	0.049
T x AMF	ns	ns	ns	ns	ns	0.024	0.006

[†]RT: reduced tillage where soil was chisel plowed and prepared for seeding the cover crop mixture hairy vetch (34 kg ha^{-1});and cereal rye (101 kg ha^{-1}) in the fall and then roll-crimped at anthesis prior to transplanting sweet corn seedlings in spring.
[§]FT: soil was plowed with moldboard plow and prepared for seeding the cover crop mixture in the fall and similarly. prior to transplanting sweet corn seedlings in the spring.
[‡]NAT: natural source of mycorrhizal fungi sourced from organic soils in the Vegetable Systems Trial at Rodale Institute.
[!]Analysis was performed on transformed data and untransformed data are reported. Means ± SE within column per tillage and mycorrhizal species followed by the same letter are not significantly different ($p < 0.05$) by Tukey-Kramer adjusted LSD. ns: nonsignificant at $p \leq 0.05$, based on F test. N = 32 when sample was grouped based on tillage, and N = 16 when sample was grouped based on AMF treatment.

kernels was significantly affected by tillage, with higher levels in RT than in FT ($p = 0.040$). Stalk dry weight, harvest index (HI), and crude protein content were not significantly impacted by tillage ($p < 0.05$). Among the AMF treatments, *R. irregularis* inoculation enhanced unhusked ear dry weight compared to *F. mosseae*. Additionally, both single AMF inoculants (*R. irregularis* and *F. mosseae*) significantly increased vitamin B6 and C concentrations compared to NAT ($p = 0.013$ and $p = 0.049$, respectively; Table 2). A significant interaction between tillage and AMF inoculation was observed for vitamin B6 and C concentrations (Fig 1A and B). Specifically, sweet corn plants inoculated with *R. irregularis* and grown in FT plots exhibited higher vitamin B6 levels than those in RT plots. Conversely, for the same AMF species, vitamin C concentrations were greater in RT-grown sweet corn kernels than in FT.

3.3. Kernel mineral nutrient concentration

The concentrations of K, Ca, Mg, Mn, Zn, and B in sweet corn kernels were influenced by tillage, with higher levels observed in RT compared to FT (Table 3). Inoculation with *R. irregularis* significantly increased P, K, and Zn concentrations in the kernels ($p = 0.0117$, $p = 0.0170$, and $p = 0.0109$, respectively) compared to the mock, NAT, and *F. mosseae* treatments but led to a reduction in B concentration ($p = 0.0001$; Table 3). No significant interactions between tillage and mycorrhizal inoculation were detected for most mineral nutrients in sweet corn kernels, except for B. Specifically, B levels were significantly higher in kernels from *R. irregularis*-inoculated plants grown in RT plots compared to those in FT ($p = 0.0308$; Table 3, Fig. 2).

3.4. Essential amino acids

Leucine was the most abundant essential amino acid in sweet corn kernels, followed in descending order by valine, lysine, phenylalanine, isoleucine, threonine, methionine, histidine, and tryptophan (Table 4). Tillage significantly influenced leucine and phenylalanine concentrations ($p = 0.0036$ and $p = 0.0481$, respectively), with higher levels observed in FT plots. Additionally, tillage led to a significant reduction in tryptophan concentration ($p = 0.0053$; Table 4). However, AMF inoculation and its interaction with tillage had no significant effects on essential amino acid concentrations in sweet corn kernels.

3.5. Non-essential amino acids

Glutamic acid was the most abundant non-essential amino acid in sweet corn kernels, followed by alanine, aspartic acid, proline, serine, arginine, glycine, tyrosine, taurine, and hydroxylamine (Table 5). Among these, only proline concentration was influenced by tillage, with higher levels observed in FT compared to RT. Inoculation with *R. irregularis* and *F. mosseae* significantly increased aspartic acid and glycine concentrations compared to the mock and NAT treatments ($p = 0.0022$ and $p = 0.0251$, respectively; Table 5). No significant interactions between tillage and AMF inoculation were detected for non-essential amino acids in sweet corn kernels.

3.6. Root colonization

AMF root colonization was slightly higher in RT plots (58.94 % ± 4.95 %) compared to FT plots (55.96 % ± 4.73 %), though the difference was not statistically significant (Table 6). Despite the lack of significant variation in overall AMF colonization, sweet corn plants inoculated with *R. irregularis* exhibited greater root colonization than those inoculated with *F. mosseae*, NAT, or the mock treatment. No significant interactions between tillage and AMF inoculation were observed for root colonization in sweet corn roots.

3.7. Relationship between root colonization and nutrients

There was no observed correlation between AMF root colonization and sweet corn yield, crude protein, Mg, Zn, P, N, and S levels (Fig. 3). However, AMF root colonization showed a strong positive correlation with vitamin B6 and K levels in sweet corn kernels, a moderate positive correlation with vitamin C, Mn, Fe, and Cu, and a negative correlation with B. Sweet corn yield was negatively associated with K, vitamin C, Cu, Ca, Mn, Mg, and Zn levels (Fig. 3). Crude protein content exhibited a positive correlation with N, P, S, Fe, Cu, vitamin C, vitamin B6, and Zn, along with a slight positive correlation with K, Ca, Mg, and Mn (Fig. 3). Vitamin B6 was positively correlated only with N but showed a negative correlation with B concentration in sweet corn kernels. In contrast, vitamin C demonstrated a positive correlation with all macro- and micronutrients.

4. Discussion

Soil microorganisms dynamically control the crop productivity by regulating nutrient mineralization and solubilization and cycling (Bender et al., 2016), particularly AMF, which can form a symbiotic relationships with plants to enhance plant growth and nutrient uptake (Herrmann and Lesueur, 2013). While many studies have investigated AMF effects on plant growth, most were conducted in controlled greenhouse environments, often neglecting species-specific AMF

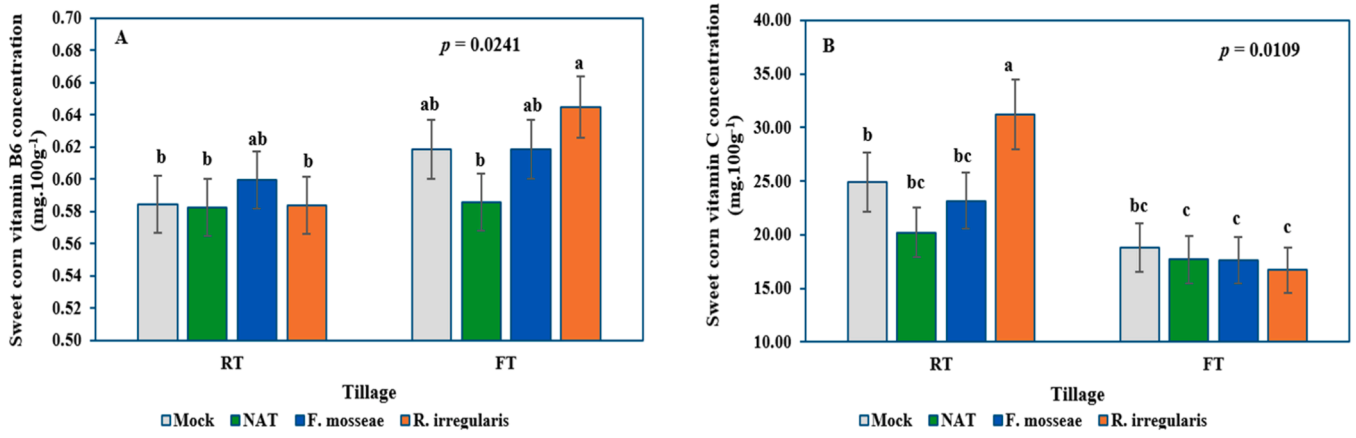

Fig. 1. Mean vitamin B6 concentration (A) and vitamin C concentration in sweet corn kernel (B) as affected by tillage and AMF inoculation. Data were transformed and untransformed means are reported ± standard errors (SE). Different letters above bars indicated significant differences between treatments ($p < 0.05$) by Tukey-Kramer adjusted LSD. N = 8.

Table 3
Sweet corn kernel mineral concentrations as affected by tillage, and AMF inoculation treatments.

Source of variation	N	P	K	Ca	Mg	S	Mn	Fe	Cu	Zn	B
	g kg^{-1}						mg kg^{-1}				
Tillage (T)											
RT†	21.07 ± 0.67	4.29 ± 0.07	11.80 ± 0.30$^{a!}$	0.14 ± 0.0^{a}	1.30 ± 0.03^{a}	1.73 ± 0.04	9.05 ± 0.54^{a}	14.20 ± 0.71	3.28 ± 0.27	24.46 ± 0.73^{a}	5.66 ± 0.21^{a}
FT§	21.23 ± 0.68	4.20 ± 0.07	10.81 ± 0.28^{b}	0.09 ± 0.00^{b}	1.17 ± 0.03^{b}	1.67 ± 0.04	6.96 ± 0.43^{b}	13.96 ± 0.70	2.60 0.21	20.87 ± 0.64^{b}	4.85 ± 0.20^{b}
Mycorrhizal Inoculation (AMF)											
Mock	21.10 ± 0.52	4.23 ± 0.06^{b}	11.32 ± 0.26^{b}	0.11 ± 0.01	1.24 ± 0.03	1.69 ± 0.03	7.74 ± 040	14.21 ± 0.60	2.89 ± 0.20	22.27 ± 0.56^{b}	6.20 ± 0.25^{a}
NAT (mixed *spp.*)‡	20.68 ± 0.51	4.17 ± 0.06^{b}	11.03 ± 0.26^{b}	0.11 ± 0.01	1.20 ± 0.03	1.67 ± 0.03	7.87 ± 0.40	13.59 ± 0.59	2.85 ± 0.20	22.04 ± 0.59^{b}	5.23 ± 0.24^{b}
F. mosseae	21.30 ± 0.53	4.21 ± 0.06^{b}	11.03 ± 0.26^{b}	0.12 ± 0.01	1.22 ± 0.03	1.70 ± 0.03	7.87 ± 0.40	13.85 ± 0.59	2.89 ± 0.20	22.51 ± 0.56^{b}	5.13 ± 0.24^{bc}
R. irregularis	21.43 ± 0.53	4.36 ± 0.06^{a}	11.81 ± 0.27^{a}	0.13 ± 0.01	1.28 ± 0.04	1.73 ± 0.03	8.29 ± 0.41	14.68 ± 0.61	2.98 ± 0.20	23.61 ± 0.58^{a}	4.54 ± 0.25^{c}
Significance											
T	ns	ns	0.0307	0.0028	0.0132	ns	0.0088	ns	ns	0.0023	0.0133
AMF	ns	0.0117	0.0170	ns	ns	ns	ns	ns	ns	0.0109	0.0001
T x AMF	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.0308

†RT: reduced tillage where soil was chisel plowed and prepared for seeding the cover crop mixture hairy vetch (34 kg ha^{-1}) and cereal rye (101 kg ha^{-1}) in the fall and then roll-crimped at anthesis prior to transplanting sweet corn seedlings in spring.
§FT: soil was plowed with moldboard plow and prepared for seeding the cover crop mixture in the fall and similarly prior to transplanting sweet corn seedlings in the spring.
‡NAT: natural source of mycorrhizal fungi sourced from organic soils in the Vegetable Systems Trial at Rodale Institute.
!Analysis was performed on transformed data and untransformed data are reported. Means ± SE within column per tillage and mycorrhizal species followed by the same letter are not significantly different ($p < 0.05$) by Tukey-Kramer adjusted LSD. ns: nonsignificant at $p \leq 0.05$, based on F test. N = 32 when sample was grouped based on tillage, and N = 16 when sample was grouped based on AMF treatment.

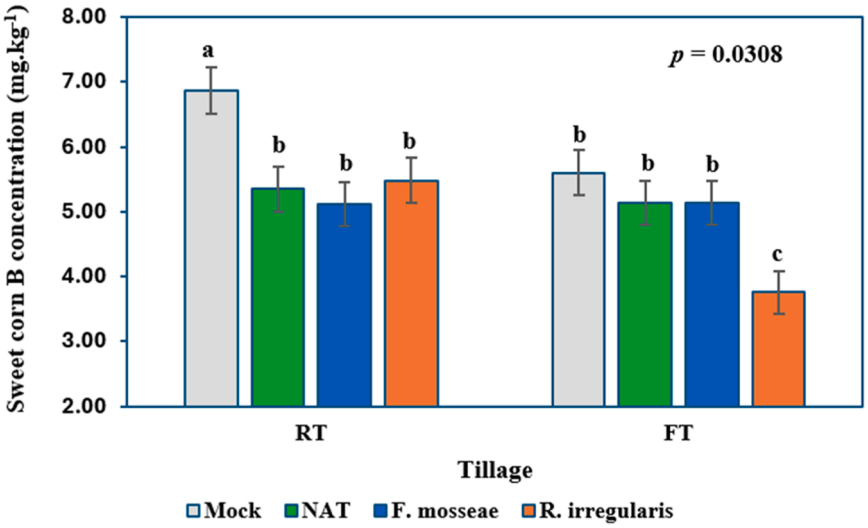

Fig. 2. Mean B concentration in sweet corn kernel as affected by tillage and AMF inoculation. Data were transformed and untransformed means are reported ± standard errors (SE). Different letters above bars indicated significant differences between treatments ($p < 0.05$) by Tukey-Kramer adjusted LSD. N = 8.

interactions and competition with native soil microbiota (Berruti et al., 2016).

In this study, sweet corn plants were pre-inoculated in the greenhouse with AMF treatments, including NAT, *F. mosseae*, and *R. irregularis*, before being transplanted into the field to assess their nutrient uptake efficiency. Despite the presence of indigenous AMF, as indicated by root colonization in the mock treatment (Table 6), these plants continued to absorb nutrients effectively (Tables 3-5) but differentially. These aligns with the findings of Dias et al., (2018), who demonstrated that maize could be successfully inoculated with *F. mosseae* and *R. irregularis* even in the presence of a native AMF community.

Arbuscular mycorrhizal fungi extends the functional root zone via hyphal networks, facilitating the uptake of essential nutrients such as P, Zn, Cu, which are typically immobile in soil (Huey et al., 2020). This study observed that *F. mosseae* and *R. irregularis* positively influenced nutrient uptake in sweet corn, even under high P conditions. These findings align with previous studies indicating AMF can enhance P efficiency and recruit phosphate-solubilizing bacteria to improve P availability in P-rich soils (Bravo et al., 2006). However, elevated soil P

Table 4
Sweet corn kernel essential amino acids concentrations as affected by interactions of year by tillage and year by mycorrhizal fungi inoculum.

Source of variation	His[++]	Ile	Leu	Lys	Met	Phe	Thr	Trp	Val
	%								
Tillage (T)									
RT[†]	0.28 ± 0.01	0.45 ± 0.01	1.04 ± 0.30[b]	0.61 ± 0.02	0.30 ± 0.01	0.50 ± 0.01[b]	0.46 ± 0.01	0.13 ± 0.00[a]	0.61 ± 0.01
FT[§]	0.29 ± 0.01	0.46 ± 0.01	1.20 ± 0.03[a]	0.59 ± 0.02	0.31 ± 0.01	0.54 ± 0.01[a]	0.46 ± 0.01	0.11 ± 0.00[b]	0.63 ± 0.01
Mycorrhizal Inoculation (AMF)[!]									
Mock	0.28 ± 0.01	0.45 ± 0.01	1.10 ± 0.03	0.60 ± 0.01	0.30 ± 0.01	0.51 ± 0.01	0.46 ± 0.01	0.12 ± 0.00	0.61 ± 0.01
NAT (mixed *spp.*)[‡]	0.28 ± 0.01	0.45 ± 0.01	1.12 ± 0.03	0.59 ± 0.01	0.30 ± 0.01	0.52 ± 0.01	0.45 ± 0.01	0.12 ± 0.00	0.62 ± 0.01
F. mosseae	0.29 ± 0.01	0.46 ± 0.01	1.14 ± 0.03	0.60 ± 0.01	0.31 ± 0.01	0.53 ± 0.01	0.46 ± 0.01	0.12 ± 0.00	0.63 ± 0.01
R. irregularis	0.28 ± 0.01	0.46 ± 0.01	1.12 ± 0.03	0.61 ± 0.01	0.31 ± 0.01	0.52 ± 0.01	0.46 ± 0.01	0.12 ± 0.00	0.63 ± 0.01
Significance									
T	ns	ns	0.0036	ns	ns	0.0481	ns	0.0053	ns
AMF	ns	ns	ns	ns	ns	ns	ns	ns	ns
T x AMF	ns	ns	ns	ns	ns	ns	ns	ns	ns

†RT: reduced tillage where soil was chisel plowed and prepared for seeding the cover crop mixture hairy vetch (34 kg ha^{-1}) and cereal rye (101 kg ha^{-1}) in the fall and then roll-crimped at anthesis prior to transplanting sweet corn seedlings in spring.
§FT: soil was plowed with moldboard plow and prepared for seeding the cover crop mixture in the fall and similarly prior to transplanting sweet corn seedlings in the spring.
‡NAT: natural source of mycorrhizal fungi sourced from organic soils in the Vegetable Systems Trial at Rodale Institute.
[++]His = histidine, Ille= isoleucine, Leu= leucine, Lys =lysine, Met =methionine, Phe =phenylalanine, Thr =threonine, Trp =tryptophan, and Val = valine.
[!]Analysis was performed on transformed data and untransformed data are reported. Means ± SE within column per tillage and mycorrhizal species followed by the same letter are not significantly different ($p < 0.05$) by Tukey-Kramer adjusted LSD. ns: nonsignificant at $p \leq 0.05$, based on F test. N = 32 when sample was grouped based on tillage, and N = 16 when sample was grouped based on AMF treatment.

levels (Table S2) likely masked AMF's additional contribution to P uptake.

Tillage practices also influenced nutrient translocation. The full tillage (FT) treatment led to higher leaf nutrient concentrations, except for P, which was higher under reduced tillage (RT). This suggests that FT enhances nutrient availability by modifying soil structure and microbial interactions, whereas AMF in RT facilitated P availability and accumulation in kernel tissues. Notably, *R. irregularis* inoculation significantly increased kernel P ($p = 0.0117$) and K ($p = 0.0170$) concentrations (Table 3), corroborating previous studies demonstrating AMF's role in improving K transport in various crops (Khalediyan et al., 2021). The relationship between AMF inoculation and increased K suggests an active role of AMF in improving K transportation to the plant, which is critical for crop quality and yield. AMF can mobilize nutrients from decaying organic matter to living plants (Newman and Eason, 1989), promoting crop-resilience and improving yield, particularly under suboptimal soil conditions. The observed enhancements in P and K uptake align with past research (Carrara and Heller, 2022) and underscores the importance of AMF as a biofertilization strategy which can be adapted to varying tillage regimes.

Nutrient uptake in sweet corn was likely influenced by soil pH, which decreased from 6.8 to 6.6 during the growing season, improving the availability of mineral nutrients (Anderson and Rubin, 1982). Lower pH increased the uptake of N, Ca, Mg, S, Mn, Fe, Cu and B in leaf tissue under FT (Table 1), while RT led to higher kernel concentrations of K, Ca, Mg, Mn, Zn, and B (Table 3). This aligns with (Eriksson, 1989) and (Zhang et al., 2012), who documented improved Zn and Mn availability under lower pH.

Potassium (K), an essential element for crop quality, showed a negative correlation with both sweet corn yield and vitamin C concentration, consistent with previous studies in corn, soybean, and cotton (Jones et al., 1977; Pettigrew, 2008; Qiu et al., 2014). However, AMF colonization in this study was positively associated with kernel vitamin C, likely due to enhanced K uptake through AMF-mediated pathways (Table 3). This observation parallels findings by Collins et al. (2022) in tomatoes, where higher K availability raised vitamin C, protein, and sugar levels. Similar increases in vitamin C due to improved K availability have been documented in garlic, apples, and peppers (Liu et al., 2021), reinforcing the potential of AMF inoculation to enhance crop nutritional value by facilitating K uptake.

Zinc (Zn) is an essential micronutrient required for plant growth, playing a crucial role in gene regulation and abiotic stress mitigation, enzyme activation, protein and auxin synthesis, carbohydrate metabolism, and membrane integrity (Marschner, 1995). In this study, Zn concentrations in sweet corn kernels were higher in plants grown in RT plots. Similarly, tryptophan levels—where Zn is integral to metabolism—were also elevated in RT-grown plants compared to FT-grown plants. The significant correlations between P, K, and Zn in sweet corn kernels (Fig. 3) along with the increased P, K, and Zn levels in *R. irregularis*-inoculated sweet corn kernels (Table 3), suggest that AMF-mediated nutrient acquisition contributed to these increases. Extraradical fungal hyphae likely facilitated the uptake of these nutrients, particularly immobile ones such as P and Zn, by extending beyond the rhizosphere and improving nutrient scavenging efficiency (Ortas, 2012).

Boron (B) play a critical role in plant cell wall strength and development. In this study, B concentration in sweet corn kernels were lower FT plots, particularly in *R. irregularis* inoculated plants compared to RT (Fig. 2). Boron uptake decreased significantly in plants inoculated with *F. mossease* and *R. irregularis* compared with mock inoculated plants (Table 3). Results align with the findings from Liu et al., (2018) and Clark and Zeto, (2000), where AMF-inoculated plants showed reduced B uptake and accumulation. The mechanism of mycorrhizal B uptake remains unclear. In vascular plants, sucrose plays a primary role in B mobilization due to its low affinity for B. In contrast, fungal carbohydrates like mannitol exhibit a high affinity for forming complexes with

Table 5
Sweet corn kernel non-essential amino acids concentrations as affected by interactions of year by tillage and year by mycorrhizal fungi inoculum.

Source of variation	Ala[++]	Arg	Asp	Cys	Glu	Gly	Hydr	Pro	Ser	Tau	Tyr
								%			
Tillage (T)											
RT[†]	1.39 ± 0.05	0.51 ± 0.01	1.10 ± 0.05	0.23 ± 0.01	2.31 ± 0.10	0.52 ± 0.01	0.13 ± 0.02	0.82 ± 0.02[b]	0.62 ± 0.02	0.24 ± 0.02	0.34 ± 0.01
FT[§]	1.34 ± 0.05	0.51 ± 0.01	1.00 ± 0.04	0.24 ± 0.01	2.51 ± 0.11	0.51 ± 0.01	0.09 ± 0.01	0.90 ± 0.02[a]	0.60 ± 0.02	0.25 ± 0.02	0.35 ± 0.01
Mycorrhizal Inoculation (AMF)											
Mock	1.36 ± 0.04	0.50 ± 0.01	1.02 ± 0.03[bc!]	0.24 ± 0.01	2.40 ± 0.08	0.51 ± 0.01[bc]	0.11 ± 0.01	0.85 ± 0.02	0.61 ± 0.02	0.24 ± 0.02	0.34 ± 0.01
NAT (mixed *spp*)[‡]	1.32 ± 0.04	0.51 ± 0.01	1.01 ± 0.03[c]	0.23 ± 0.01	2.36 ± 0.08	0.50 ± 0.01[c]	0.10 ± 0.01	0.86 ± 0.02	0.60 ± 0.02	0.25 ± 0.02	0.34 ± 0.01
F. mosseae	1.38 ± 0.04	0.52 ± 0.01	1.07 ± 0.03[ab]	0.24 ± 0.01	2.44 ± 0.09	0.53 ± 0.01[a]	0.11 ± 0.01	0.87 ± 0.02	0.61 ± 0.02	0.24 ± 0.02	0.34 ± 0.01
R. irregularis	1.39 ± 0.04	0.52 ± 0.01	1.09 ± 0.03[a]	0.23 ± 0.01	2.45 ± 0.09	0.53 ± 0.01[ab]	0.11 ± 0.01	0.86 ± 0.02	0.62 ± 0.02	0.24 ± 0.02	0.35 ± 0.01
Significance											
T	ns	ns	ns	ns	ns	ns	ns	0.0217	ns	ns	ns
AMF	ns	ns	0.0022	ns	ns	0.0251	ns	ns	ns	ns	ns
T x AMF	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

†RT: reduced tillage where soil was chisel plowed and prepared for seeding the cover crop mixture hairy vetch (34 kg ha^{-1}) and cereal rye (101 kg ha^{-1}) in the fall and then roll-crimped at anthesis prior to transplanting sweet corn seedlings in spring.
§FT: soil was plowed with moldboard plow and prepared for seeding the cover crop mixture in the fall and similarly prior to transplanting sweet corn seedlings in the spring.
‡NAT: natural source of mycorrhizal fungi sourced from organic soils in the Vegetable Systems Trial at Rodale Institute.
[++]Ala =alanine, Arg =arginine, Asp = aspartic acid, Cys =cysteine, Glu =glutamic acid, Gly =glycine, Hydr =hydrxyoalanine, Pro =proline, Ser =serine, Tau =taurine, and Tyr =tyrosine.
[!]Analysis was performed on transformed data and untransformed data are reported. Means ± SE within column per tillage and mycorrhizal species followed by the same letter are not significantly different ($p < 0.05$) by Tukey-Kramer adjusted LSD. ns: nonsignificant at $p \leq 0.05$, based on F test. N = 32 when sample was grouped based on tillage, and N = 16 when sample was grouped based on AMF treatment.

B, which restricts its mobility to the host plant. (Pommerrenig et al., 2019).

The increased concentration of aspartic acid and glycine in sweet corn inoculated with *F. mosseae* and *R. irregularis* (Table 5) align with the findings of Whiteside et al. (2012), who reported that AMF enhance the uptake of amino acids, particularly highly hydrophilic and neutrally charged amino acids like glycine. Aspartic acid and glycine contribute to various physiological functions, including energy production, neurotransmission, muscle function, and immune system support (Raiteri, 2024). Similar increases in amino acid concentrations following AMF inoculation have been observed in other studies, such as Rivero et al. (2015) and Salvioli et al. (2012), which reported elevated glutamic acid and asparagine levels in crops like tomatoes and common bugloss inoculated with *R. irregularis*.

Plants have developed various mechanisms to accumulate proteins and metabolites in response to abiotic stress. A stress response is the increased production of reactive oxygen species (ROS). To counteract these stresses, plants also accumulate low molecular weight solutes - highly soluble non-toxic organic compounds that provide cellular protection. These solutes include proline, sucrose, and glycine betaine. Proline, in particular, is known to accumulate under abiotic stress conditions such as heat, drought, and prolonged sunlight exposure (Furlan et al., 2020). As a proteinogenic amino acid, proline functions as a ROS scavenger under a variety of stress conditions (Hayat et al., 2012). In this study, sweet corn kernels from plants grown in FT plots exhibited higher proline levels than those from RT plots (Table 5). Shinde and Singh, (2017) similarly reported increased proline concentrations in sweet corn under water deficit stress. The elevated proline levels in FT-grown sweet corn kernels may be attributed to drier conditions in these plots during July and August 2022 (Supplementary Figure S1), which resulted from faster water evaporation and plant growth. These dry conditions likely induced stress, particularly during the tasseling, ear formation, and maturation stages. In contrast, residue retention in RT plots helped mitigate soil moisture loss and reduced stress (Wagger and Mengel, 1988).

Aspartic acid plays a critical role in the biosynthesis of various essential metabolites, including arginine, glutamate, and aromatic amino acids such as tyrosine and phenylalanine, which are vital for plant defense against abiotic stress (Ji et al., 2023). Consequently, the observed increase in phenylalanine levels in sweet corn kernels may be attributed to plant defense mechanisms activated by intensive tillage (FT plots) combined with drought stress (Supplementary Figure S1). The positive correlation between N, S, and crude protein could further explain the greater accumulation of S-containing amino acids such as phenylalanine (Fig. 3). In this study, glycine, and aspartic acid, two soluble amino acids known for their role in ROS scavenging (Ji et al., 2023) - increased in sweet corn kernels inoculated with AMF species *F. mosseae and R. irregularis*.

AMF are typically concentrated in the upper root zone, where their hyphal networks can be disrupted by plowing (Kabir, 2005b; Helgason et al., 1998; Schnoor et al., 2011). However, despite potential tillage-induced disruptions, AMF colonization in sweet corn roots remained similar between treatments, averaging 59 % and 56 % in FT and RT, respectively (Table 6). Given this, the increased accumulation of glycine and aspartic acid in FT plots may be influenced by stress responses triggered by intensive tillage, which can alter root exudation patterns, nutrient availability, and microbial interactions. Tillage-induced soil disturbances often increase oxidative stress, potentially leading to the upregulation of amino acids involved in ROS scavenging. Additionally, changes in AMF community composition—rather than overall colonization rates—could have played a role in influencing plant amino acid metabolism. Our findings align with those of Metwally et al., (2021) who noted increased levels of glycine and arginine in AMF-inoculated onion and Rivero et al. (2015) with tomato. Further studies evaluating AMF community shifts and amino acid metabolism under different tillage regimes would provide deeper

Table 6
Sweet corn percent root colonization by arbuscular mycorrhizal fungi (AMF) as affected by year, tillage, and interactions of year, tillage, and AMF inoculation.

Source of variation	Arbuscular mycorrhizal fungi (AMF) root colonization
	%
Tillage (T)	
RT[†]	56 ± 5[!]
FT[§]	59 ± 5
Mycorrhizal Inoculation (AMF)[!]	
Mock	59 ± 4
NAT (mixed *spp.*)[‡]	57 ± 4
F. mosseae	54 ± 4
R. irregularis	60 ± 4
Significance	
T	ns
M	ns
T x M	ns

NS, * , * *, * ** nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively, based on F test.
[†]RT: reduced tillage where soil was chisel plowed and prepared for seeding the cover crop mixture Hairy vetch (34 kg ha^{-1}) and cereal rye (101 kg ha^{-1}) in the fall and then roll-crimped at anthesis prior to transplanting sweet corn seedlings in spring.
[§]FT: soil was plowed with moldboard plow and prepared for seeding the cover crop mixture in the fall and similarly prior to transplanting sweet corn seedlings in the spring.
[‡]NAT: natural source of mycorrhizal fungi sourced from organic soils in the Vegetable Systems Trial at Rodale Institute.
[!]Analysis was performed on transformed data and untransformed Means ± SE are reported.
ns: nonsignificant at $p \leq 0.05$, based on F test. N = 32 when sample was grouped based on tillage, and N = 16 when sample was grouped based on AMF treatment. N = 32 when sample was grouped based on tillage, and N = 16 when sample was grouped based on AMF treatment.

insights into these interactions.

Overall, this study demonstrates that reduced tillage enhances the accumulation of K, Ca, Mg, Mn, Zn, and B in sweet corn kernels, supporting the hypothesis that AMF can improve the nutritional quality of sweet corn, with potential benefits for human health. These findings reinforce the role of beneficial soil microbes, such as AMF, in enhancing crop nutrient content—a critical consideration given global soil nutrient depletion and declining crop nutrient density (Bamji et al., 2021; Vance, 2001). By fostering AMF associations, regenerative organic practices, including reduced tillage, can increase the nutritional value of crops, helping to address "hidden hunger" in nutrient-deficient diets (Drewnowski, 2020). This effect was also observed in greenhouse studies in microgreens by Kathi et al. (2022), who linked K increases to improved vitamin C levels, which is essential for human health (Linster and Van Schaftingen, 2007).

Additionally, this study's findings of elevated essential amino acids under AMF inoculation align with the established role of AMF in promoting nitrogen-rich root exudates, which enhance protein and amino acid synthesis (Prem Kumari and Srimeena, 2019). The influence of AMF on crop quality extends beyond basic nutrient content, as amino acids such as glutamic and aspartic acid, which contribute to the sweet flavor of corn, were also affected by AMF associations (Li et al., 2022).

Despite these positive effects, no significant differences in yield or nutrient concentrations (except for P, K, Zn, and B) were observed between AMF treatments. This could be due to several factors inherent to field conditions and existing soil nutrient levels. AMF typically exhibit the most pronounced effects under phosphorus-limited conditions, where their symbiotic relationship enhances nutrient acquisition. However, in P-rich soils, plants may rely less on AMF, reducing their observable impact on yield and nutrient uptake. Additionally, in field conditions, natural colonization by indigenous AMF communities may have resulted in a baseline level of colonization across all treatments, minimizing differences between inoculated and mock treatments. This widespread colonization likely contributed to a uniform effect on nutrient uptake and yield, as native AMF present in the soil may have provided similar functional benefits. Unlike controlled greenhouse or laboratory settings, field environments introduce variability that can obscure differences between AMF-inoculated and mock treatments in terms of their influence on yield, protein content, and amino acid concentrations. These findings highlight the complexity of AMF interactions in real-world agricultural settings, emphasizing the need to consider environmental factors and existing soil microbial communities when evaluating the benefits of AMF inoculation on crop performance.

5. Conclusion

This two-year study examined the effects of tillage practices and AMF inoculation on crop yield and nutrient uptake in sweet corn. While the presence of native AMF complicated the assessment of supplemental inoculation, the results suggest that AMF biofertilizers can contribute to enhancing specific nutrient density in sweet corn across different tillage systems, which may have implications for nutritional quality. Specific AMF inoculations with *F. mosseae* and *R. irregularis* were associated with increased levels of K and vitamins B6 and C in sweet corn kernels. However, their overall impact on yield and other nutrient concentrations was less pronounced, likely due to high baseline phosphorus levels and natural AMF colonization across treatments. The findings suggest that native AMF populations contributed to baseline colonization even in mock treatments, potentially reducing differences between AMF-inoculated and non-inoculated plants under field conditions. Additionally, the interaction between tillage practices and AMF inoculation emphasized the potential of reduced tillage systems to support AMF-driven nutrient enhancements in phosphorus-rich soils, aligning with agricultural practices that prioritize soil health. This study provides evidence that AMF inoculation can influence crop nutritional quality, though its effectiveness may depend on field conditions, existing soil nutrient levels, and native microbial communities. Future research should further investigate AMF applications in nutrient-deficient soils and assess their long-term impacts on soil and crop health. Additionally, further research on developing large-scale AMF inoculants that can establish effectively alongside native AMF populations may improve the efficacy of AMF-based biofertilization in sustainable crop production.

6. Funding

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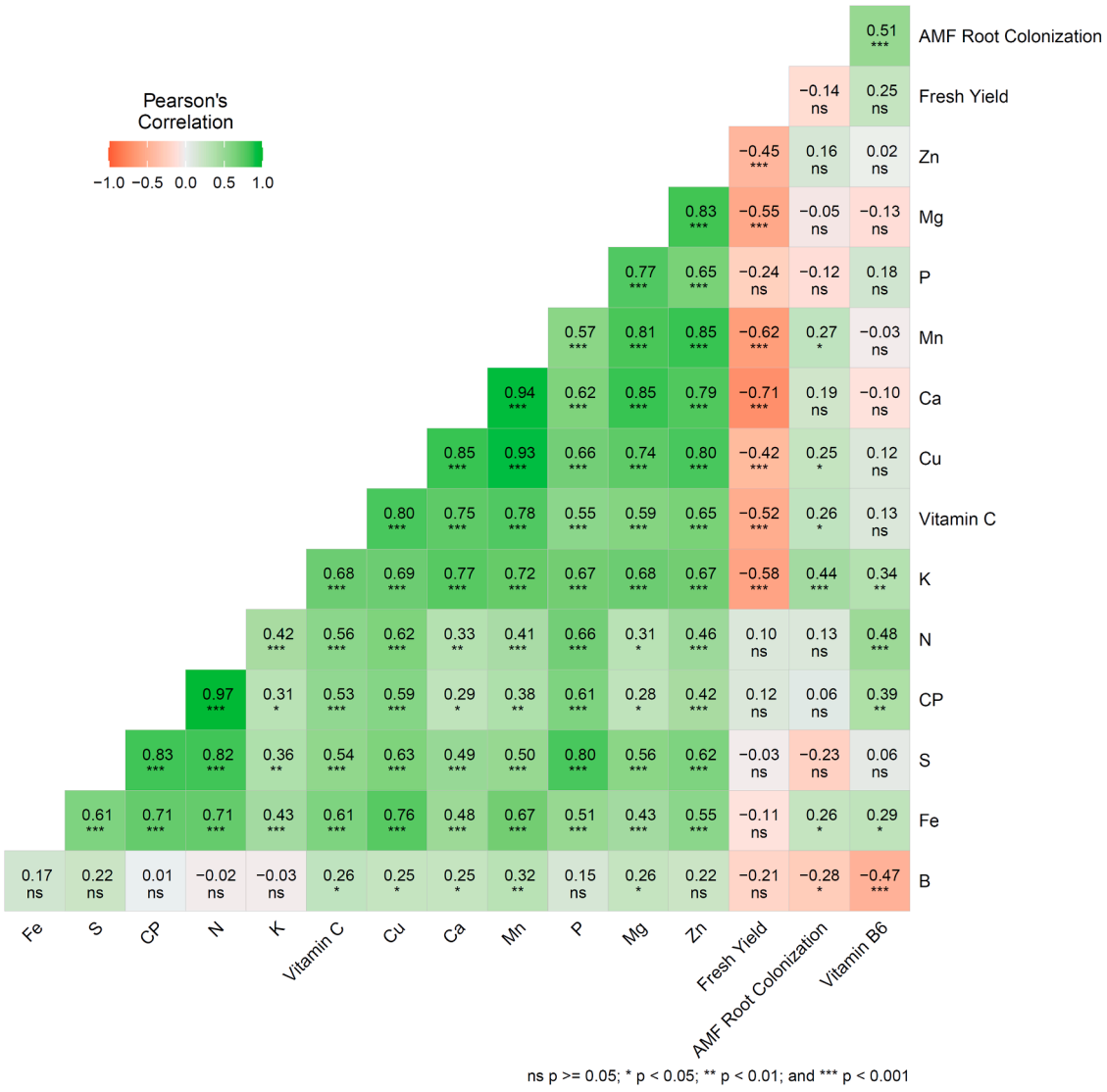

Fig. 3. Pearson correlation between the sweet corn yield, nutrients, and arbuscular mycorrhizal colonization.

agreement dated December 17, 2020, and USDA-ARS in-house project 8072–12000–014–000-D. Its contents are solely the responsibility of the authors and do not necessarily represent the official views of the USDA or the Grantham Foundation. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the United States Department of Agriculture. USDA is an equal opportunity provider and employer.

CRediT authorship contribution statement

Zinati Gladis: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Carrara Joseph E.:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Das Saurav:** Writing – review & editing, Visualization. **Caetani Romans:** Writing – review & editing, Visualization, Data curation. **Kalra Amiya:** Writing – review & editing, Data curation. **Carr Eric A.:** Writing – review & editing, Resources. **Heller Wade P.:** Writing – review & editing, Methodology, Investigation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Gladis Zinati reports financial support was provided by United States Department of Agriculture. Gladis Zinati reports financial support was provided by Grantham Foundation for the Protection of the Environment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.still.2025.106545.

Data availability

Data will be made available on request.

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