

Synergistic Effects of Arbuscular Mycorrhizal Fungi Inoculation and Foliar Micronutrient Combinations on Yield, Biomass, and Grain Biofortification of Lowland Rice (*Oryza sativa* L.)

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Lowland rice (*Oryza sativa* L.) production in sub-Saharan Africa is constrained by micronutrient deficiencies and poor nutrient use efficiency in paddy soils. Arbuscular mycorrhizal fungi (AMF) inoculation and foliar micronutrient application are recognized as sustainable approaches to improve crop nutrition; however, their combined effects on yield and grain biofortification in West African lowland rice remain insufficiently studied. This study evaluated the independent and interactive effects of AMF inoculation and foliar micronutrient combinations on yield, biomass, and nutrient content of lowland rice (NERICA L-19). A screen-house pot experiment was conducted at the Federal University of Agriculture, Abeokuta, Nigeria, using a Completely Randomized Design in a 2 × 5 factorial arrangement: two AMF levels (inoculated with *Rhizophagus irregularis* and uninoculated) and five foliar treatments (Control, Zn + Fe, Fe + Mn, Zn + Mn, Zn + Fe + Mn at 0.5%), with three replications. Data were subjected to two-way ANOVA. AMF inoculation treatment was associated with significantly increased culm weight, root weight, total biomass, panicle number, and grain phosphorus uptake; root colonisation was not quantified, so these effects should be attributed to inoculation rather than confirmed AMF activity. The Zn + Fe + Mn treatment produced the highest values across most parameters. The AMF × Zn + Fe + Mn interaction resulted in maximum grain weight (12.3 g), grains per panicle (181.5), and increased grain N, P, and Zn concentrations. Grain weight showed exploratory positive associations with grain Mn and grains per panicle across treatment means ($n = 10$); these patterns should be interpreted with caution. In conclusion, the combined application of AMF and Zn + Fe + Mn foliar treatment enhanced yield, biomass accumulation, and grain nutrient enrichment. This integrated nutrient management strategy shows promise for improving productivity and nutritional quality of lowland rice in micronutrient-deficient soils; field-level validation is required before broad production recommendations can be made.

Keywords: arbuscular mycorrhizal fungi, biofortification, foliar micronutrients, lowland rice, zinc

1 Introduction

Rice (*Oryza sativa* L.) is one of the most critically important staple cereal crops globally, providing dietary energy for more than half the world's population, particularly across Asia and sub-Saharan Africa (FAO, 2018). Nigeria is ranked the 13th largest rice producer globally and its national output reached approximately 4.4 million metric tons in 2022/2023, representing roughly 1% of total world production (FAOSTAT, 2024). Despite this production volume, Nigeria continues to face a rice supply deficit, driven in part by persistently low farm-level yields that

remain well below potential (Olatunbosun et al., 2026). Rice cultivation in Nigerian lowlands is constrained by a combination of biotic and abiotic stresses, including low soil organic matter, micronutrient depletion and poor nutrient use efficiency under flooded conditions.

Micronutrient deficiency in rice-growing soils represents both a crop productivity problem and a human nutrition crisis. Iron (Fe), zinc (Zn), and manganese (Mn) are essential for key physiological processes such as chlorophyll biosynthesis, enzyme activation, photosynthetic integrity, and hormone regulation, all of which underpin

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rice growth and grain development (Prom-u-thai et al., 2020). Deficiencies in these elements are widespread in paddy soils where alternating flood and drain cycles alter redox chemistry and element availability (Sangothari et al., 2023). The resultant poor grain quality contributes to hidden hunger, with micronutrient malnutrition affecting approximately 2–3 billion people in rice-consuming regions of the world (Sharma et al., 2020).

Arbuscular Mycorrhizal Fungi (AMF), belonging to the phylum Glomeromycota, form obligate symbiotic associations with approximately 70–90% of terrestrial plant species, including rice (Diagne et al., 2020). Through their extensive extraradical hyphal networks, AMF substantially expand the effective root absorption surface, enhancing uptake of phosphorus (P), a relatively immobile macronutrient and micronutrients including Zn, Fe, and Mn (Wang et al., 2023). Beyond nutrient acquisition, AMF improve soil structure, foster beneficial rhizosphere microbial communities, and confer tolerance to abiotic stresses including drought and salinity (Chen et al., 2025). Recent work has confirmed that AMF can upregulate Fe transporter genes and influence grain Zn distribution in rice (Zhang et al., 2025).

Foliar micronutrient application offers a complementary strategy that bypasses soil-based constraints on nutrient bioavailability, including precipitation, adsorption, and pH-mediated immobilisation by delivering nutrients directly to photosynthetically active leaf tissue (Asare et al., 2023). Yogi et al. (2023) demonstrated that foliar applications of Zn and Fe during critical rice growth stages can increase grain yields by 15–25%. Multi-country Harvest Zinc trials have further established that foliar micronutrient cocktails effectively enrich grain Zn, Fe, and Mn concentrations across diverse pedoclimatic conditions (Prom-u-thai et al., 2020).

The synergistic combination of AMF inoculation and foliar micronutrient application represents a particularly promising integrated approach. Qin et al. (2023) demonstrated that AMF-colonised rice plants treated with foliar micronutrients exhibited greater nutrient uptake than those receiving either treatment alone. Similarly, Wu et al. (2024) reported synergistic gains in grain phosphorus and zinc uptake under combined AMF and micronutrient treatment in lowland rice. Nevertheless, there is a conspicuous paucity of studies that systematically compare multiple ternary micronutrient combinations (Zn + Fe + Mn, Zn + Fe, Zn + Mn, Fe + Mn) under AMF inoculation in lowland rice under West African conditions, particularly for the high-yielding NERICA L-19 variety.

This study addressed two specific objectives:

1. to evaluate the independent and interactive effects of AMF inoculation on the yield, biomass, and nutrient content of lowland rice NERICA L-19;
2. to determine which foliar micronutrient combination, applied with and without AMF, most effectively enhances grain yield and agronomic biofortification of Fe, Zn, and Mn.

These results advance the evidence base for integrated biostimulant-nutrition management in smallholder rice systems.

Arbuscular mycorrhizal fungi (AMF) form mutualistic symbioses with the roots of most terrestrial plants, including rice (*Oryza sativa* L.). However, AMF colonisation in lowland flooded rice can be reduced relative to upland conditions, as anaerobic or waterlogged soils may limit hyphal viability and spore germination (Smith and Read, 2008). The present study was therefore conducted in a screen-house under controlled irrigation rather than permanent flooding, a condition more conducive to AMF establishment. Despite the challenges of flooded conditions, multiple studies have confirmed functional AMF colonisation in irrigated and alternately wet-and-dry rice systems (Shi et al., 2023; Moreno Jiménez et al., 2024), supporting the relevance of AMF inoculation in lowland rice improvement programmes.

2 Material and Methods

2.1 Experimental Site

The experiment was conducted at the screen house of the College of Plant Science and Crop Production, Federal University of Agriculture, Abeokuta (FUNAAB), Nigeria, situated at latitude 7° 14' N–7° 15' N and longitude 3° 26' E, at 76 m above sea level. The screen house is a permanent structure with a galvanised steel frame and 40-mesh nylon insect-screen walls, providing full air breathability and natural light while excluding insects and wind-driven rainfall. A transparent polycarbonate roof prevents direct rainfall contact with experimental pots. Daytime temperatures within the screen house during the experimental period ranged from 28 °C to 35 °C, consistent with ambient conditions at the site, with relative humidity of 55–75%. Pots were irrigated manually every two days to maintain adequate soil moisture, simulating irrigated lowland conditions without waterlogging.

2.2 Experimental Design and Treatments

A two-factor Completely Randomized Design (CRD) was used, comprising 10 treatment combinations replicated three times (30 pots). Factor 1 was AMF inoculation

status at two levels: inoculated (with *Rhizophagus irregularis*) and uninoculated (control). Factor 2 was foliar micronutrient combination at five levels:

- control (no foliar spray),
- Zn + Fe (0.5% each),
- Fe + Mn (0.5% each),
- Zn + Mn (0.5% each),
- Zn + Fe + Mn (0.5% each).

The experimental layout is illustrated in Figure 1.

2.3 Plant Material and Establishment

The rice variety NERICA L-19 (New Rice for Africa Lowland) was sourced from the International Institute for Tropical Agriculture (IITA), Ibadan, Nigeria. Seeds were soaked for 24 hours and pre-germinated for 48 hours before sowing on nursery beds (1 m × 4 m). At 21 days after sowing (DAS), two seedlings per pot were transplanted into pots (30 cm diameter × 35 cm depth, approximately 5-litre capacity) filled with a 3 : 1 (v/v) mixture of field-collected sandy loam soil and washed river sand (approximately 4 kg dry weight per pot). The soil-sand substrate was air-dried but not sterilised, retaining native soil microbial communities. Two seedlings per pot were maintained throughout the growing period. AMF inoculation was applied at transplanting by placing *R. irregularis* inoculum (commercial isolate DAOM 197198, Symbiom s.r.o., Czech Republic; ≥80 viable spores g⁻¹ carrier substrate; containing spores, hyphae, and colonised root fragments) at a dose of 10 g per pot, placed in a 2–5 cm layer directly

beneath the transplanted seedling roots. Note: root colonization percentage at harvest was not quantified in this study, which represents a methodological limitation; all treatment differences attributed to AMF should therefore be interpreted as effects associated with AMF inoculation rather than confirmed AMF-mediated mechanisms. Future studies should verify colonization using root clearing and staining protocols.

2.4 Nutrient Solution Preparation and Foliar Application

Zinc sulphate (ZnSO₄·7H₂O) and ferrous sulphate (FeSO₄·7H₂O) and manganese sulphate (MnSO₄·H₂O) solutions were prepared at 0.5% concentration (w/v). For zinc: $0.5/100 \times 287.54 \text{ g} \cdot \text{mol}^{-1} = 1.44 \text{ g}$ per litre; for iron: $0.5/100 \times 278.02 = 1.39 \text{ g}$ per litre. Foliar sprays were applied at 20 and 40 days after transplanting (DAT) to cover both vegetative and early reproductive stages. Adequate water was supplied every two days; weeds were controlled by hand pulling.

2.5 Data Collection

Yield and biomass parameters collected at harvest included: culm weight (g), root dry weight (g), leaf weight (g), total fresh weight (g), chlorophyll reading (SPAD units), number of days to flowering, 1000-grain weight (g), number of grains per panicle, number of panicles per plant, panicle length (cm), panicle weight (g), and grain weight (g). Nutrient analysis was conducted on grain

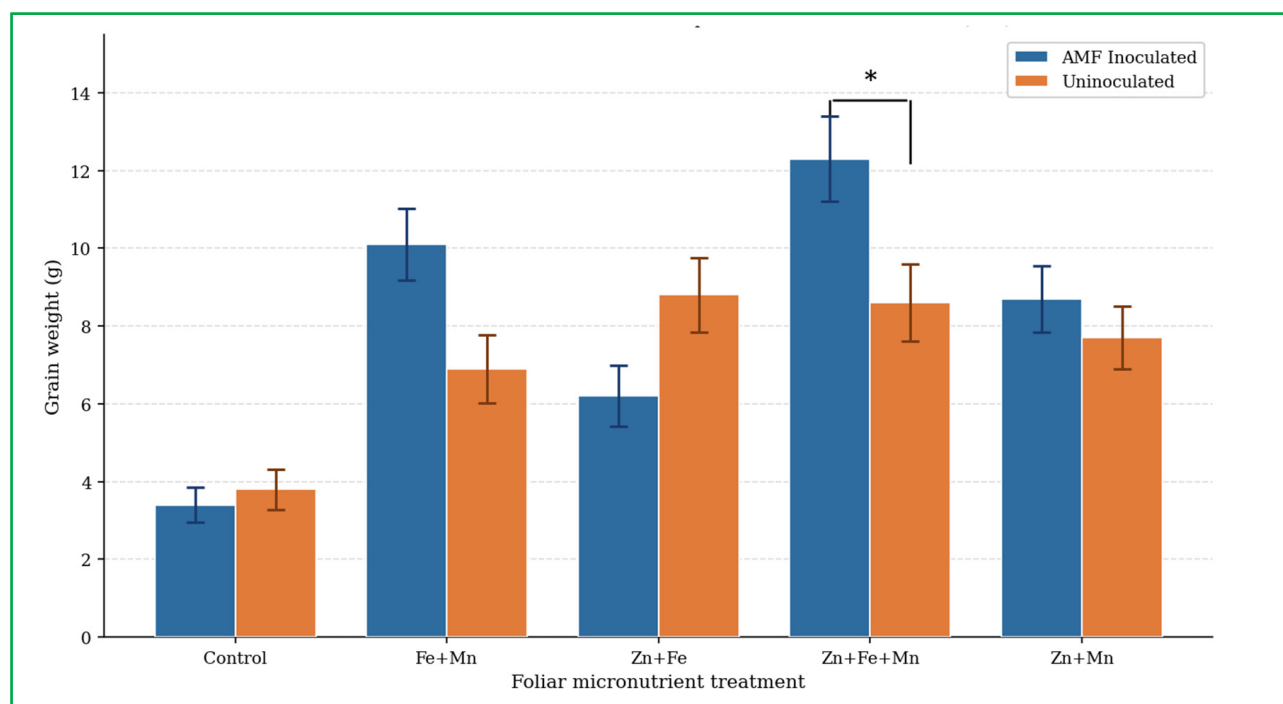


Figure 1 Grain weight (g) of lowland rice (NERICA L-19) under AMF inoculation and foliar micronutrient combinations. Bars represent treatment means ($n = 3$); * denotes significant AMF × Zn + Fe + Mn interaction

and shoot samples dried at 70 °C for 48 hours and ground to pass a 1-mm sieve. All nutrient concentrations are expressed on a dry matter basis. Total nitrogen (N) was determined by the macro-Kjeldahl digestion and steam distillation method. Phosphorus (P) was determined colorimetrically using the vanadomolybdate yellow colour method. Potassium (K), zinc (Zn), iron (Fe), and manganese (Mn) were determined by Atomic Absorption Spectrophotometry (AAS; Shimadzu AA-7000, Japan) following wet acid digestion with aqua regia (3 : 1 HCl : HNO₃). Secondary indices such as Biofortification Index (BI), Mycorrhizal Responsiveness (MR), and approximate Harvest Index (HI) were computed as follows:

$$BI (\%) = \frac{[(\text{treatment value} - \text{control value}) / \text{control value}] \times 100}{}$$

$$MR (\%) = \frac{[(AMF \text{ treatment} - \text{no-AMF treatment}) / \text{no-AMF treatment}] \times 100}{}$$

$$HI (\%) = \frac{[\text{grain weight} / (\text{grain weight} + 0.4 \times \text{culm weight} + 0.4 \times \text{leaf weight})] \times 100}{}$$

2.6 Statistical Analysis

All data were subjected to two-way analysis of variance (ANOVA) using GenStat 12th edition. Treatment means were separated by Least Significant Difference (LSD) at the 5% probability level ($p \leq 0.05$). Pearson correlation coefficients between yield and nutrient variables were computed across all 10 treatment combinations ($n = 10$). Statistical significance was accepted at $p \leq 0.05$. All secondary indices were computed in Python 3.12 using NumPy and SciPy libraries.

3 Results and Discussion

3.1 Soil Physico-Chemical Properties before Planting

The baseline soil properties are summarised in table 1. The soil had a sandy loam texture (72.6% sand, 4.3% clay, 23.1% silt) and a slightly alkaline pH of 7.20, which is within the acceptable range for most rice cultivars. Organic matter (1.696%) and total nitrogen (0.228%) were at moderate levels. Available phosphorus was adequate (18.85 mg·kg⁻¹). Among micronutrients, iron was very high (201.682 mg·kg⁻¹), while zinc (2.664 mg·kg⁻¹), manganese (1.521 mg·kg⁻¹), and copper (1.122 mg·kg⁻¹) were present at comparatively low levels, suggesting a need for Zn and Mn supplementation consistent with the treatment design.

Table 1 Physico-chemical properties of soil before planting

Parameters	Values
Sand (%)	72.6
Clay (%)	4.3
Silt (%)	23.1
Textural class	sandy loam
Total N (%)	0.2
pH	7.2
Available P (mg·kg ⁻¹)	18.9
Organic matter (%)	1.7
Organic carbon (%)	0.2
Exchangeable acidity (cmol·kg ⁻¹)	0.8
Na (cmol·kg ⁻¹)	0.3
K (cmol·kg ⁻¹)	0.5
Ca (cmol·kg ⁻¹)	0.3
Mg (cmol·kg ⁻¹)	0.4
Zn (mg·kg ⁻¹)	2.66
Fe (mg·kg ⁻¹)	201.7
Cu (mg·kg ⁻¹)	1.1
Mn (mg·kg ⁻¹)	1.5

3.2 Effects of AMF and Foliar Micronutrients on Growth and Vegetative Biomass

AMF inoculation significantly increased culm weight (43.9 vs 36.8 g, root weight (15.9 vs 12.7 g and total fresh weight (68.2 vs 57.3 (Table 2). Leaf weight, days to flowering and chlorophyll content were not significantly affected by AMF alone. Among foliar micronutrient treatments, Zn + Fe + Mn produced the highest culm weight (55.0 g), root weight (21.2 g), leaf weight (10.2 g), total fresh weight (86.4 g), and SPAD chlorophyll reading (48.1), all significantly superior to the control (LSD. Delayed flowering was noted with Zn + Mn and Zn + Fe treatments (87.8 days each) compared to the control (84.5 days).

The AMF × micronutrient interaction significantly affected all growth parameters. The highest culm weight (65.6 g) was recorded for AMF-inoculated plants receiving Zn + Fe + Mn, representing a 152% increase over the uninoculated control (29.6 g). The interaction term for chlorophyll showed the highest SPAD value (49.4) under AMF + Zn + Fe + Mn, suggesting a possible enhancement of photosynthetic pigmentation under this treatment combination (Table 2).

Table 2 Effects of AMF inoculation and foliar micronutrient combinations on vegetative biomass and physiological parameters of lowland rice

Treatment	Culm weight (g)	Root weight (g)	Leaf weight (g)	Total fresh Weight (g)	Days to flowering	Chlorophyll (SPAD)
AMF (A)						
Inoculated	43.9a	15.9a	8.4	68.2a	86.8	45.8
Uninoculated	36.8b	12.7b	7.8	57.3b	87.3	44.8
LSD ($p \leq 0.05$)	6.85	2.89	3.50ns	8.18	4.42ns	3.10ns
Micronutrient (M)						
Control	27.8c	8.3c	4.0c	41.0c	84.5b	41.9c
Fe + Mn	40.0b	14.1b	8.1b	62.2b	86.3ab	45.7b
Zn + Fe	38.9b	11.3bc	8.8ab	59.0b	87.8a	46.0b
Zn + Mn	40.1b	16.6ab	8.6ab	64.2b	87.8a	44.8b
Zn + Fe + Mn	55.0a	21.2a	10.2a	86.4a	86.3ab	48.1a
LSD ($p \leq 0.05$)	8.67	4.36	1.763	13.23	1.60	1.96
A $\times$ M	11.38	6.89	2.99	17.11	3.413	2.97

Means followed by the same letter within a column are not significantly different at $p \leq 0.05$ (LSD test); ns – not significant

3.3 Effects of AMF Inoculation and Foliar Micronutrient Combinations on Yield Components

AMF inoculation had no significant effect on 1000-grain weight, grains per panicle, panicle length, panicle weight, or grain weight in the main-effect analysis (Table 3); however, it significantly increased the number of panicles per plant (4.3 vs 3.9). Foliar micronutrient treatments significantly influenced all yield components. Zn + Fe + Mn produced the highest values: 1000-grain weight (23.3 g), grains per panicle (160.8), panicles per plant (5.0), panicle length (27.1 cm), panicle weight (10.6 g), and grain weight (10.4 g) (Table 3). The control

treatment recorded the lowest values across all parameters. The AMF $\times$ micronutrient interaction was highly significant for yield components.

3.4 Effects of AMF Inoculation and Foliar Micronutrient Combinations on Grain Macro- and Micronutrient Content

AMF inoculation significantly enhanced grain phosphorus uptake (315.7 vs 291.6 mg·100 g⁻¹), grain Fe (6.3 vs 4.4 mg·100 g⁻¹) and grain Mn (5.6 vs 4.2 mg·100 g⁻¹), but not grain N or Zn (Table 4). Among micronutrient treatments, Zn + Fe + Mn consistently produced the highest grain concentrations of all

Table 3 Effects of AMF inoculation and foliar micronutrient combinations on yield and yield components of lowland rice

Treatment	1,000-grain weight (g)	Grains/panicle	Panicles/plant	Panicle length (cm)	Panicle weight (g)	Grain weight (g)
AMF (A)						
Inoculated	20.5	124.8	4.3a	24.4	8.0	8.2
Uninoculated	19.3	117.8	3.9b	24.5	7.9	7.1
LSD ($p \leq 0.05$)	5.93ns	10.27ns	0.29	1.51ns	3.07ns	3.94ns
Micronutrient (M)						
Control	14.3b	76.6c	3.7b	20.8c	4.2c	3.3c
Fe + Mn	21.7a	123.2b	3.8b	23.7b	7.3b	8.5b
Zn + Fe	18.5b	118.2b	3.8b	25.7ab	8.7ab	7.5b
Zn + Mn	20.7ab	127.6b	4.2b	24.1ab	8.9ab	8.2b
Zn + Fe + Mn	23.3a	160.8a	5.0a	27.1a	10.6a	10.4a
LSD ($p \leq 0.05$)	2.98	22.92	0.59	2.61	2.26	1.85
A $\times$ M	4.91	29.31	0.76	3.36	3.23	3.22

Means followed by the same letter within a column are not significantly different at $p \leq 0.05$ (LSD test); ns – not significant

Table 4 Effects of AMF inoculation and foliar micronutrient combinations on grain macro- and micronutrient content of lowland rice

Treatment	N grain (%)	P grain (mg·100 g ⁻¹)	K grain (mg·100 g ⁻¹)	Zn grain (mg·100 g ⁻¹)	Fe grain (mg·100 g ⁻¹)	Mn grain (mg·100 g ⁻¹)
AMF (A)						
Inoculated	2.5	315.7a	501.9	4.8	6.3a	5.6a
Uninoculated	2.3	291.6b	453.5	3.6	4.4b	4.2b
LSD ($p \leq 0.05$)	0.15ns	12.58	263.63ns	3.58ns	0.77	4.13
Micronutrient (M)						
Control	2.1d	290.8d	359.4c	2.5b	2.7d	2.0c
Fe + Mn	2.4bc	299.9c	527.5a	2.6b	7.1a	6.9a
Zn + Fe	2.3c	300.3c	434.2b	4.9ab	6.5bc	4.7b
Zn + Mn	2.5b	309.2b	524.1a	5.6a	6.1c	6.3ab
Zn + Fe + Mn	2.7a	318.1a	541.1a	4.4a	6.9ab	7.1a
LSD ($p \leq 0.05$)	0.10	6.40	60.30	0.74	0.50	1.73
A × M	0.13	8.27	92.49	1.20	0.64	2.34

Means followed by the same letter within a column are not significantly different at $p \leq 0.05$ (LSD test); ns – not significant

six nutrients: N (2.7%), P (318.1 mg·100 g⁻¹), K (541.1 mg·100 g⁻¹), Zn (5.4 mg·100 g⁻¹), Fe (6.9 mg·100 g⁻¹), and Mn (7.1 mg·100 g⁻¹). The control treatment recorded the lowest values in all cases. Interaction effects were significant for all grain nutrients.

3.5 Effects of AMF Inoculation and Foliar Micronutrient Combinations on Shoot Macro- and Micronutrient Content

AMF inoculation significantly enhanced all shoot nutrient parameters: N (1.9 vs 1.7%), P (261.0 vs 252.3 mg·100 g⁻¹), K (453.6 vs 420.1 mg·100 g⁻¹), Zn (7.8 vs 7.2 mg·100 g⁻¹), Fe (8.6 vs 7.8 mg·100 g⁻¹) and Mn (10.2 vs 9.1 mg·100 g⁻¹)

(Table 5). The consistent improvement in shoot nutrient status associated with AMF inoculation across all six nutrients is noteworthy, though the absence of colonisation data means these differences cannot be mechanistically attributed to AMF activity. Zn + Fe + Mn produced the highest shoot values for most nutrients, while the control produced the lowest. The AMF × Zn + Fe + Mn combination achieved maximum shoot Mn of 14.1 mg·100 g⁻¹ (AMF-inoculated) compared to 14.0 mg·100 g⁻¹ (uninoculated), a small difference that should be interpreted cautiously given the marginal gap between values.

Table 5 Effects of AMF inoculation and foliar micronutrient combinations on shoot macro- and micronutrient content of lowland rice

Treatment	N shoot (%)	P shoot (mg·100 g ⁻¹)	K shoot (mg·100 g ⁻¹)	Zn shoot (mg·100 g ⁻¹)	Fe shoot (mg·100 g ⁻¹)	Mn shoot (mg·100 g ⁻¹)
AMF (A)						
Inoculated	1.9a	261.0a	453.6a	7.8a	8.6a	10.2a
Uninoculated	1.7b	252.3b	420.1b	7.2b	7.8b	9.1b
LSD ($p \leq 0.05$)	0.02	0.05	13.98	0.44	0.42	4.21
Micronutrient (M)						
Control	1.5e	192.0e	315.6e	4.6e	5.7e	3.6d
Fe + Mn	1.8b	274.2b	461.3c	4.1d	10.0a	12.4b
Zn + Fe	1.7d	266.3d	448.4d	9.0a	8.8c	5.7c
Zn + Mn	1.8c	268.0c	469.7b	8.9c	7.1d	11.8b
Zn + Fe + Mn	1.9a	279.8a	489.1a	9.3b	9.5b	14.6a
LSD ($p \leq 0.05$)	0.001	0.01	8.08	0.07	0.05	0.69
A × M	0.01	0.02	10.37	0.14	0.14	1.73

Means followed by the same letter within a column are not significantly different at $p \leq 0.05$ (LSD test); ns – not significant

Table 6 Secondary nutrient and productivity indices for AMF-inoculated treatments (calculated from experimental data)

Micronutrient	HI (%)	MR-Grain weight (%)	BI-Grain weight (%)	BI-Grain Zn (%)	BI-Grain Mn (%)	AMF Responsea
Control	21.7	–	0.0	0.0	0.0	-10.5
Fe + Mn	32.5	46.4	+197	-22	+204	46.4
Zn + Fe	24.2	-29.5	+82	+112	+8	-29.5
Zn + Fe + Mn	28.2	+43.0	+262	+104	+200	43.0
Zn + Mn	28.6	+13.0	+156	+115	+216	13.0

HI – Harvest index; MR – mycorrhizal responsiveness; BI – Biofortification index relative to AMF + control; a grain weight MR

3.6 Secondary Indices and Correlation Analysis

Biofortification Index, Mycorrhizal Responsiveness, and approximate Harvest Index values for AMF-inoculated treatments are presented in Table 6. Grain weight BI was highest under Zn + Fe + Mn (+262%), followed by Fe + Mn (+197%) and Zn + Mn (+156%). Mycorrhizal Responsiveness for grain weight was highest under Fe + Mn (+46.4%) and Zn + Fe + Mn (+43.0%), and was negative for the control (-10.5%) and Zn + Fe (-29.5%), suggesting that AMF benefit is nutrient-mediated rather than constitutive.

3.7 Grain Weight Response to AMF and Foliar Micronutrient Combinations

The figure reveals a pronounced synergistic effect when AMF inoculation is combined with Zn + Fe + Mn foliar application, achieving the maximum grain weight of 12.3 g (Figure 1). This represents a remarkable +262% increase over the AMF-inoculated control (3.4 g) and +43% above the uninoculated Zn + Fe + Mn treatment (8.6 g). The significant AMF × Zn + Fe + Mn interaction ($p \leq 0.05$) underscores that the combined application of biological (AMF) and chemical (foliar micronutrients) inputs creates a mutually reinforcing system that substantially outperforms either treatment applied individually.

3.8 Radar Plot of Grain Nutrient Profiles

Figure 2 presents a radar plot visualizing normalized grain nutrient profiles (N, P, K, Zn, Fe, Mn) across six key treatment combinations. The polygon area serves as a comprehensive indicator of overall grain nutritional quality, with larger areas reflecting superior multi-nutrient enrichment. The AMF + Zn + Fe + Mn treatment exhibits the most expansive polygon,

indicating the highest cumulative grain nutritional quality among all treatments. The radar plot effectively demonstrates that micronutrient combinations containing all three elements (Zn + Fe + Mn) consistently outperform binary combinations across multiple nutrient dimensions. This multi-nutrient superiority is particularly evident in the enhanced Zn, Fe, and Mn concentrations, which are of potential relevance for addressing micronutrient

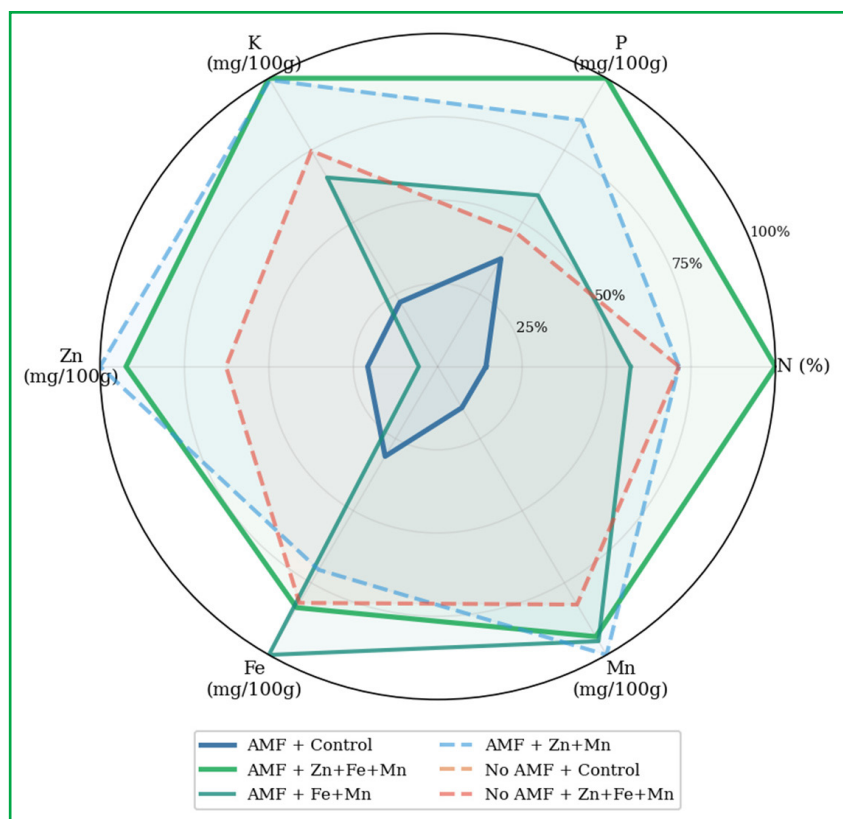


Figure 2 Radar plot of normalized grain nutrient profiles (N, P, K, Zn, Fe, Mn) for six key treatment combinations. Values are normalized to the treatment range (0–1); larger polygon area indicates higher overall grain nutritional quality

inadequacy in rice-dependent populations. It should be noted, however, that grain mineral concentration as measured here does not equate to mineral bioavailability, since antinutritional factors such as phytate were not assessed in this study

3.9 Heat Map of Normalized Yield and Nutrient Responses

In Figure 3, a comprehensive heat map visualization of normalized yield and grain nutrient responses across all 10 AMF × micronutrient treatment combinations. The blue-highlighted cell column (AMF + Zn + Fe + Mn) shows the highest or near-highest values across most parameters, including grain weight (12.3 g), grains per panicle (181.5), panicles per plant (5.7), panicle weight (12.0 g), grain N (2.8%), grain P (331.5 mg·100 g⁻¹), and competitive Zn (6.0 mg·100 g⁻¹), Fe (6.9 mg·100 g⁻¹), and Mn (7.5 mg·100 g⁻¹) concentrations. The heat map's gradient visualization (from pale yellow = minimum to dark red = maximum) facilitates rapid identification of treatment performance patterns. Notably, treatments combining AMF inoculation with micronutrient sprays generally exhibited darker coloration than uninoculated counterparts, a pattern consistent with a possible additive effect of AMF inoculation on the response to foliar nutrient applications. The 1000-grain weight parameter shows particularly high values (23.3 g) under both AMF + Zn + Fe + Mn and NoAMF + Zn + Fe + Mn treatments, suggesting that foliar nutrition alone can substantially improve grain filling, though the synergistic effect with AMF yields the absolute maximum.

3.10 Biofortification Index for Grain Micronutrients

The Biofortification Index (%) for grain Zn, Fe, and Mn under AMF-inoculated conditions, expressed as percentage increases relative to the AMF + Control baseline. The results reveal notable

Grain Zn Biofortification: The Zn + Fe treatment achieved +112% increase, while Zn + Mn reached +115%, and Zn + Fe + Mn attained +104%. The marginal reduction in the triple combination compared to binary Zn-containing treatments may reflect competitive interactions during nutrient translocation or dilution effects from enhanced overall grain mass.

Grain Fe Biofortification: The Fe + Mn treatment exhibited the highest Fe enrichment at +114%, followed by Zn + Fe at +89%, and Zn + Fe + Mn at +86%. This pattern suggests that Fe biofortification efficacy is maximized when Fe is applied without competing Zn, though all Fe-containing treatments substantially exceeded the control.

Grain Mn Biofortification: Mn biofortification showed the largest responses, with Fe + Mn at +204%, Zn + Fe + Mn at +200%, and Zn + Mn at +216%. These increases (+200% to +216%) substantially exceed typical biofortification targets, suggesting that Mn accumulation in rice grain under these screen-house conditions was highly responsive to foliar Mn application; however, these values should be interpreted in the context of the low Mn baseline in the control treatment rather than as evidence of an AMF-specific effect, given that root colonisation was not confirmed.

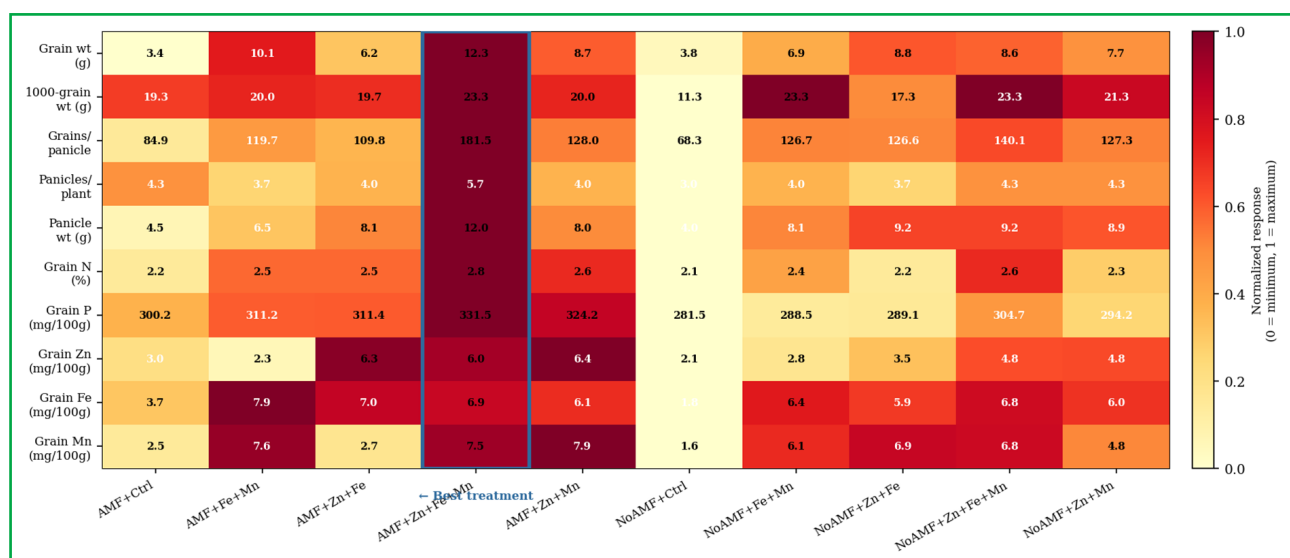


Figure 3 Heat map of normalized yield and grain nutrient responses across all AMF × micronutrient treatment combinations. Raw values shown in each cell; blue box highlights the AMF + Zn + Fe + Mn treatment. Scale: 0 (minimum) to 1 (maximum).

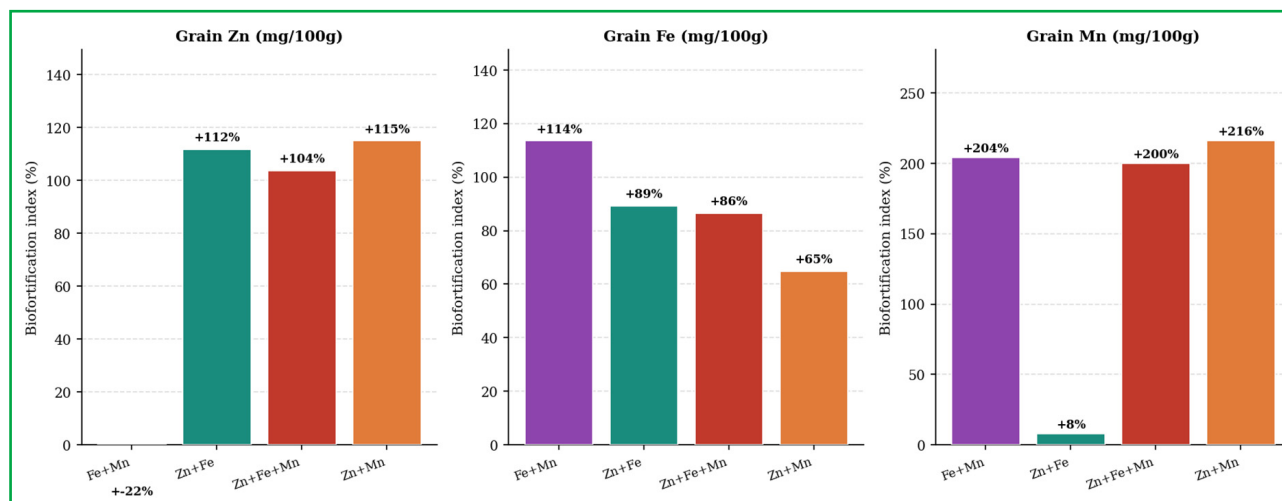


Figure 4 Biofortification Index (%) for grain Zn, Fe, and Mn under AMF-inoculated conditions
Values represent percentage increase relative to the AMF + control baseline

3.11 Mycorrhizal Responsiveness for Yield Parameters

Figure 5 presents Mycorrhizal Responsiveness (MR, %) for grain weight and grains per panicle across foliar micronutrient treatments. MR is calculated as $[(AMF - No\ AMF) / No\ AMF] \times 100$ per micronutrient treatment, providing a standardized metric of AMF benefit magnitude.

Grain Weight MR: The Fe + Mn treatment exhibited the highest MR at +46.4%, followed by Zn + Fe + Mn at +43.0%, and Zn + Mn at +13.0%. Crucially, the Control and Zn + Fe treatments showed negative MR values (-10.5% and -29.5%, respectively), indicating that AMF inoculation alone, without adequate micronutrient supplementation, may not confer yield benefits

and could even impose a carbon cost on the host plant that outweighs nutritional gains.

Grains per Panicle MR: A similar pattern emerges for grains per panicle, with Zn + Fe + Mn achieving +29.6% MR and Control at +24.3%, while Fe + Mn (-4.5%) and Zn + Fe (-13.3%) showed negative responses. The Zn + Mn treatment exhibited marginal positive MR (+0.5%).

The nutrient-dependent nature of mycorrhizal responsiveness is a critical finding. It demonstrates that AMF benefit is contingent upon adequate micronutrient availability in the growing environment. When micronutrients are deficient (Control) or imbalanced (Zn + Fe without Mn), the symbiotic relationship may become parasitic or neutral, as the plant expends photosynthates

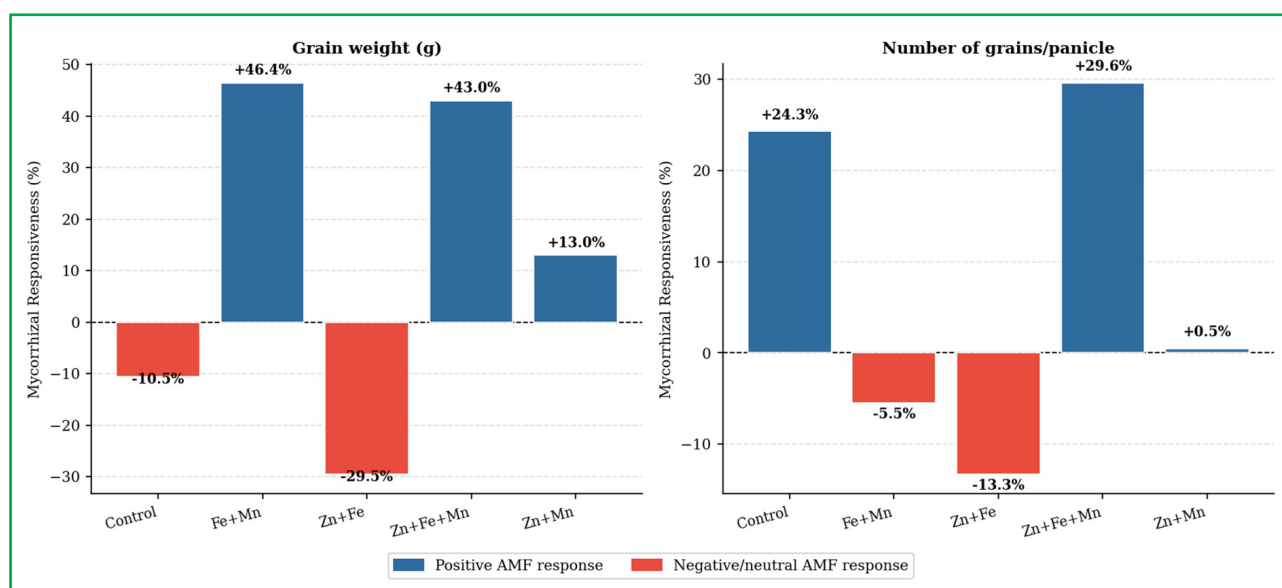


Figure 5 Mycorrhizal Responsiveness (MR, %) for grain weight and grains per panicle across foliar micronutrient treatments
Blue bars indicate positive AMF benefit; red bars indicate neutral or negative response

to sustain the fungal partner without receiving proportional nutritional returns. Conversely, when foliar micronutrient supply is optimized (particularly Zn + Fe + Mn or Fe + Mn), AMF inoculation yields substantial positive returns, indicating a true mutualistic synergy.

3.12 Pearson Correlation Matrix for Yield and Grain Nutrients

Pearson correlation analysis (Figure 6) revealed exploratory positive associations based on treatment means ($n = 10$): grain weight $\times$ grains per panicle ($r = 0.909$, $p = 0.0003$), grain weight $\times$ grain Mn ($r = 0.881$, $p = 0.0008$), grain weight $\times$ grain N ($r = 0.767$, $p = 0.0096$), grain weight $\times$ grain Fe ($r = 0.770$, $p = 0.0092$), and grain weight $\times$ grain P ($r = 0.641$, $p = 0.0457$). Given the low statistical power of correlation analysis based on $n = 10$ treatment means, these relationships should be interpreted with caution as exploratory patterns rather than as evidence of causal mechanisms.

Grain Weight $\times$ Grains per Panicle ($r = 0.91$, $p < 0.05$): This strong positive association (the highest in the matrix) is consistent with sink capacity (more grains per panicle) playing a role in driving higher total grain yield across the treatments examined.

Grain Weight $\times$ Grain Mn ($r = 0.88$, $p < 0.05$): The second-strongest correlation reveals that treatments enhancing grain Mn concentration simultaneously produce heavier grains. This suggests that Mn-sufficient plants exhibit superior grain filling, likely due to Mn's role in photosynthesis and carbohydrate metabolism.

Grain Weight $\times$ Grain N ($r = 0.77$, $p < 0.05$) and Grain Fe ($r = 0.77$, $p < 0.05$): These strong correlations indicate that improved nitrogen nutrition and iron accumulation are closely linked to enhanced grain yield. Nitrogen is fundamental to protein synthesis and photosynthetic capacity, while iron is essential for chlorophyll biosynthesis and electron transport.

Grain N $\times$ Grains per Panicle ($r = 0.82$, $p < 0.05$) and Grain N $\times$ Grain P ($r = 0.88$, $p < 0.05$): These relationships underscore the interconnectedness of macronutrient status and yield component development. Adequate N nutrition supports both grain number formation and P accumulation, reflecting synergistic nutrient interactions.

Grain P $\times$ Grain N ($r = 0.88$, $p < 0.05$): The strong P-N correlation reflects the biochemical interdependence of these nutrients in energy metabolism (ATP synthesis requires both N-containing adenine and P-containing phosphate groups) and nucleic acid synthesis.

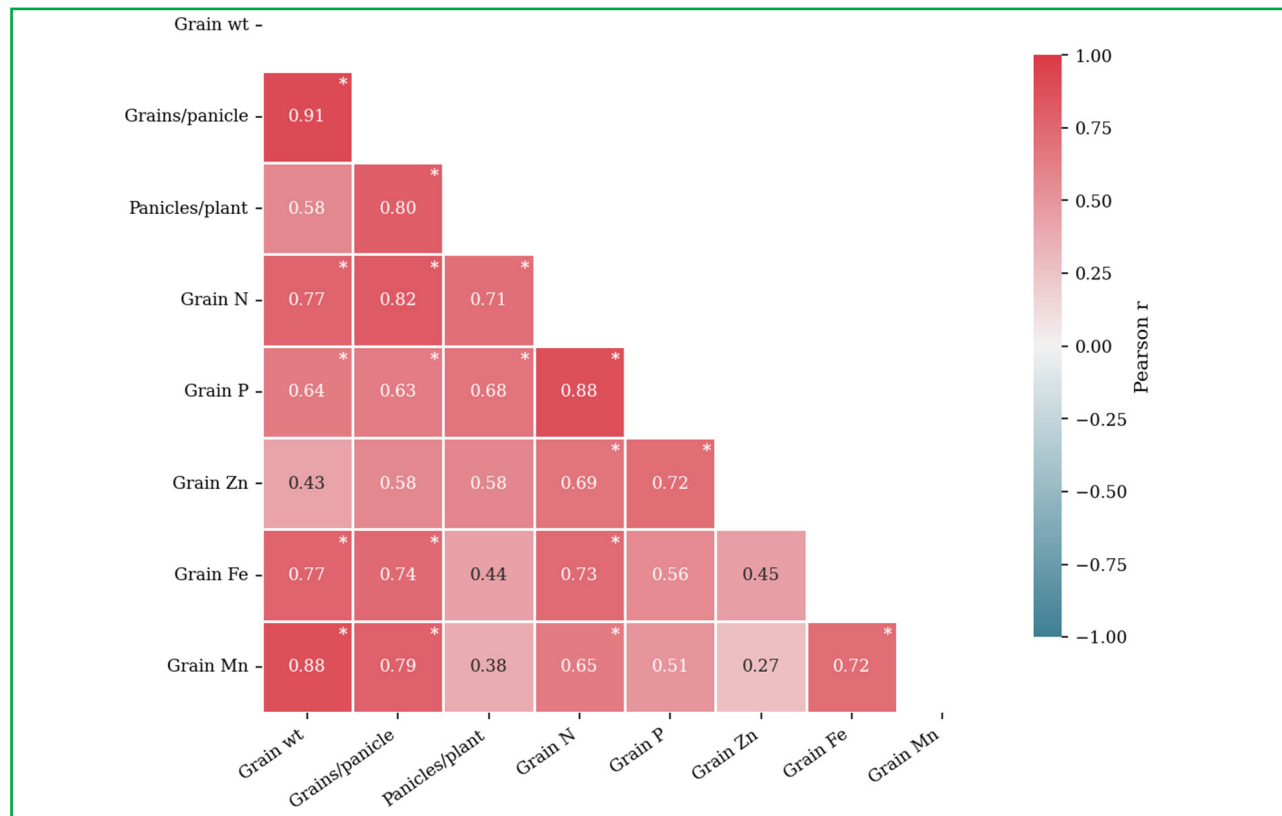


Figure 6 Pearson correlation matrix (lower triangle) for yield and grain nutrient variables across all 10 treatment combinations ($n = 10$)
* $p < 0.05$; diverging colour scale: blue = positive correlation, red = negative correlation

3.13 AMF Inoculation and Vegetative Biomass

The significant enhancement of culm weight, root weight, and total fresh weight under AMF inoculation corroborates a substantial body of evidence demonstrating that AMF symbiosis improves the structural and functional architecture of rice root systems (Madhushan et al., 2023). The estimated 19% increase in culm weight and 25% increase in root biomass are consistent with values reported by Wu et al. (2024), who observed 43–50% improvements in phosphorus uptake and associated biomass in AMF-inoculated lowland rice. The absence of a significant AMF effect on leaf weight and chlorophyll content as main effects likely reflects preferential carbon partitioning toward root and culm elongation during early vegetative stages, a well-documented ontogenetic priority in AMF-colonised graminaceous species (Begum et al., 2019). The significant AMF $\times$ micronutrient interaction for chlorophyll (Table 2) nevertheless suggests that AMF inoculation combined with Zn + Fe + Mn supply may enhance the photosynthetic apparatus, a pattern consistent with the known roles of Fe in chlorophyll biosynthesis and Mn in photosystem II integrity (Gao et al., 2023).

3.14 Foliar Micronutrient Combinations and Their Effects

The consistent superiority of Zn + Fe + Mn across nearly all growth, yield, and nutrient parameters constitutes the central agronomic finding of this study. This pattern aligns with Alloway (2008) and Broadley et al. (2012), who established that the three micronutrients function through distinct but complementary biochemical pathways: zinc regulates auxin synthesis and enzyme activity; iron drives chlorophyll production and redox reactions; and manganese is essential for photosynthetic oxygen evolution and superoxide dismutase activity. Their simultaneous supply thus produces additive or synergistic effects on multiple physiological processes, which manifested in this study as higher culm growth (+98% over control), root development (+156%), grain weight (+215%), and grains per panicle (+110%).

The positive effect of foliar Zn + Fe on grain Zn ($6.27 \text{ mg} \cdot 100 \text{ g}^{-1}$ AMF-inoculated vs $2.96 \text{ mg} \cdot 100 \text{ g}^{-1}$ for control) is consistent with multi-country biofortification trials reporting that foliar Zn application reliably increases grain Zn by 30–80% in cereals (Cakmak et al., 2020). The Fe + Mn combination achieved the highest grain Fe ($7.9 \text{ mg} \cdot 100 \text{ g}^{-1}$), demonstrating the effectiveness of Fe foliar spray in elevating grain Fe concentrations above the $7 \text{ mg} \cdot 100 \text{ g}^{-1}$ threshold recommended by Harvest Plus for rice biofortification targets (Pfeiffer and McClafferty, 2007). The Zn + Fe + Mn triple combination, while producing slightly lower grain Fe than Fe + Mn alone,

provided a balanced multi-nutrient biofortification outcome, simultaneously improving grain Zn (+104%), Fe (+87%), and Mn (+200%) above the inoculated control. This trade-off between single-nutrient maximisation and multi-nutrient balance is an important agronomic consideration for nutrition-sensitive rice improvement.

3.15 AMF and Foliar Micronutrient Interactions on Yield

The AMF $\times$ Zn + Fe + Mn interaction producing the highest grain weight (12.3 g), grains per panicle (181.5), and number of panicles per plant (5.7) suggests a multi-pathway synergy associated with AMF inoculation. The improved growth and yield observed in AMF-inoculated plants receiving Zn + Fe + Mn may reflect enhanced nutrient acquisition associated with AMF inoculation combined with the direct foliar supply of above-ground nutritional inputs. Since root colonisation was not quantified, specific mechanisms such as hyphal expansion cannot be confirmed; however, this dual-route nutrient supply likely creates a resource complementarity that reduces the plant's dependence on soil nutrient availability, a pattern consistent with observations by Wang et al. (2017), who showed that combined Zn and Fe application facilitates P mobilisation in soil particularly under mycorrhizal colonisation. The +43.0% Mycorrhizal Responsiveness for grain weight under Zn + Fe + Mn treatment compared to -10.5% under the control is particularly informative; it demonstrates that AMF benefit for yield is largely contingent on adequate micronutrient supply. This conditionality has important practical implications: AMF inoculation alone may be insufficient to improve yields in nutrient-poor lowland soils; however, when co-applied with foliar nutrition, substantial and consistent yield gains are achievable.

3.16 Grain Biofortification and Nutritional Significance

The grain Zn biofortification achieved in this study (+104%, reaching $6.03 \text{ mg} \cdot 100 \text{ g}^{-1}$) under AMF + Zn + Fe + Mn represents a meaningful improvement for human nutrition. In West African diets where rice contributes a substantial portion of daily micronutrient intake, such enrichment could partially offset the Zn deficiency affecting approximately 30% of the Nigerian population. Similarly, the grain Mn biofortification (+200%) is noteworthy given the role of Mn in antioxidant defence (superoxide dismutase), neurological function, and bone health. These biofortification levels are comparable to or exceed those reported in the multi-country Harvest Zinc foliar cocktail trials (Prom-u-Thai et al., 2020), which involved Zn + I + Fe + Se combinations, suggesting that Zn + Fe + Mn combinations without Se or I are already highly effective for enhancing rice grain mineral density.

The exploratory correlations of grain weight with grain Mn ($r = 0.881$), grain N ($r = 0.767$), and grain Fe ($r = 0.770$) suggest a pattern in which treatments improving grain micronutrient concentrations tend to produce heavier grains, possibly because well-nourished grains fill more completely; however, given the low n (10 treatment means), these associations cannot be interpreted as mechanistic evidence. Similarly, the strong association between grains per panicle and grain weight ($r = 0.909$) is consistent with sink capacity playing a role in yield under these treatments, though causal conclusions require further investigation.

3.17 Shoot Nutrient Enhancement and Agronomic Implications

under AMF + Zn + Fe + Mn represents a +320% increase over the uninoculated control ($3.1 \text{ mg} \cdot 100 \text{ g}^{-1}$). Elevated shoot micronutrient concentrations enhance the nutritional value of rice straw as fodder, an important consideration in integrated crop-livestock systems. The consistent increase associated with AMF inoculation in all six shoot nutrients (N, P, K, Zn, Fe, Mn) is particularly significant. Furthermore, improvements in shoot K and P concentration associated with AMF inoculation reflect enhanced osmotic regulation and energy metabolism, contributing to the improved plant vigour observed in inoculated treatments (Mohammad et al., 2004). Shoot Mn content of $14.1 \text{ mg} \cdot 100 \text{ g}^{-1}$ et al., 2004). The comprehensive shoot nutritional enhancement under AMF + Zn + Fe + Mn, but not under AMF alone, reaffirms that the full complement of mycorrhizal benefit requires an enabling nutritional environment (Senguttuvel et al., 2023).

4 Conclusions

Under the conditions of this screen-house pot experiment, the combined application of AMF (*Rhizophagus irregularis*) inoculation and Zn + Fe + Mn foliar micronutrient spray (0.5% each) was associated with improved rice growth, yield components, and grain mineral concentration. Field-level validation across multiple agro-ecological zones in West Africa is required before production-scale recommendations can be made. Key conclusions are:

1. AMF inoculation alone significantly improved culm weight (+19%), root weight (+25%), total fresh weight (+19%), panicles per plant, and grain phosphorus uptake, suggesting a potential agronomic benefit associated with AMF inoculation under these screen-house conditions; as root colonisation was not verified, these effects should be attributed to inoculation treatment rather than confirmed AMF activity.
2. The Zn + Fe + Mn foliar combination was the most effective of the five treatments tested, enhancing grain weight by +215% over the control, grains per panicle by +110%, and producing the highest concentrations of N, P, K, Zn, Fe, and Mn in both grain and shoot.
3. The AMF $\times$ Zn + Fe + Mn interaction yielded the maximum grain weight (12.3 g), the highest Biofortification Index for grain weight (+262%), and MR of +43.0%, demonstrating a strong positive synergy between biological and chemical nutrient management.
4. Mycorrhizal benefit for grain yield was nutrient-dependent: AMF responsiveness was positive and large when foliar micronutrients were supplied, but negligible or negative under the control and Zn + Fe-only treatments.
5. Grain weight showed exploratory positive associations with grain Mn ($r = 0.881$), grain N ($r = 0.767$), grain Fe ($r = 0.770$), and grains per panicle ($r = 0.909$) across treatment means ($n = 10$); these patterns are suggestive but should not be over-interpreted given the low sample size.
6. Based on these screen-house results, the co-application of *Rhizophagus irregularis* inoculation (10 g per pot at transplanting) with foliar Zn + Fe + Mn spray (0.5% each, applied at 20 and 40 days after transplanting) is a promising integrated nutrient management practice for lowland rice (NERICA L-19) grown in micronutrient-deficient sandy loam soils in South-West Nigeria. This combination is expected to improve grain yield, panicle number, grain filling, and simultaneously biofortify grain with Zn, Fe, and Mn. Large-scale adoption, however, requires field validation under diverse agro-ecological conditions and in farmer-managed systems.

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Conflict of Interest

The authors declare no known competing financial interests or personal relationships that could have influenced the work reported in this study.

Author Contributions

Oni Olanrewaju E.: Conceptualization, Methodology, Writing, Original Draft. Adeyemi Nurudeen: Data Curation. Falaiye O. O.: Supervision. Ajibola A. O.: Data collection

AI and AI-Assisted Technologies use Declaration

The authors declare that artificial intelligence (AI) tools were not used in the design of the study, data collection, analysis, or interpretation. AI-assisted technology (ChatGPT, OpenAI, based on the GPT-4.3 model) were used only for language refinement and readability improvement. The authors take full responsibility for the content and integrity of the manuscript.

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