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Evaluating Nutrient Removal and Use Efficiency in Pearl Millet (*Pennisetum glaucum* L.) through Arbuscular Mycorrhizal Fungi Inoculation and Fertilizer Microdosing in Sahelian Sandy Soils

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Abstract

Pearl millet (*Pennisetum glaucum*), a staple cereal in the Sahel, faces severe yield limitations due to sandy, nutrient-poor soils and erratic rainfall. Sustainable fertilization strategies that enhance nutrient use efficiency are urgently needed. This study evaluated the combined effects of arbuscular mycorrhizal fungi (AMF) inoculation and fertilizer microdosing on nutrient removal and agronomic efficiency in pearl millet grown in Sahelian sandy soil. A greenhouse experiment with nine treatments combining NPK, urea, cow manure, and AMF was conducted using soil pots arranged in a completely randomized design with five replicates. Nutrient removal (N, P, K, Ca, Mg, Cu, Mn, Fe, Ni) and shoot dry biomass were measured after 12 weeks, and agronomic efficiency (AE) was calculated for N, P, and K. Treatments significantly affected nutrient removal ($p < 0.001$). AMF alone enhanced micronutrient removal, particularly Mn (296 mg/kg) and Fe (550 mg/kg), while manure + AMF increased macronutrient removal (N ≈ 17 mg/kg, K ≈ 81 mg/kg). Moderate NPK microdosing with AMF achieved the highest AE values (AEN = 6.7 g/g; AEP = 15.8 g/g; AEK = 15.8 g/g). High-input treatments increased nutrient removal but reduced efficiency. This controlled environment study demonstrates that AMF-based microdosing is a promising strategy to improve nutrient efficiency in pearl millet grown on

Sahelian sandy soils.

Keywords

Sustainable Fertilization, Nutrient Use Efficiency, Arbuscular Mycorrhizal Symbiosis, Organic Amendment, Microdosing Strategy, Sahelian Agroecosystems

1. Introduction

Pearl millet (*Pennisetum glaucum*) plays a crucial role in food security and rural livelihoods in Senegal and across West Africa, where it remains one of the few crops capable of thriving under extreme climatic conditions. Its remarkable adaptability to low annual rainfall (300 - 500 mm) and nutrient-poor sandy soils has led to its establishment as a staple food for smallholder farmers in the Sahel [1]-[5]. Beyond its agronomic resilience, pearl millet is a multi-purpose crop. It serves as a vital source of calories, fodder, and biomass for soil fertility improvement [6]-[10]. However, despite these advantages, yields remain consistently less than 1000 kg/ha, largely due to erratic rainfall, high temperatures, and severe soil nutrient depletion [11].

One of the key constraints limiting pearl millet productivity is nutrient depletion caused by continuous nutrient mining and low replenishment rates [12]-[15]. In traditional rain-fed systems, where mineral fertilizers are applied infrequently due to high costs and logistical challenges [16]-[18], nutrient removal through biomass removal progressively exhausts soil reserves. This issue is particularly problematic for essential macronutrients (N, P, K, Ca, Mg) and micronutrients (Mn, Ni, Zn, Fe, Cu), which are absorbed by the plant but removed from the field upon harvest. Without proper nutrient cycling, soil fertility declines over time, leading to reduced nutrient use efficiency (NUE) and the exacerbation of the already fragile balance of Sahelian agroecosystems [13] [19].

In order to address these challenges, the practice of microdosing fertilizer has emerged as a cost-effective approach to optimize nutrient availability. This technique, which was pioneered by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), involves the direct application of small, targeted doses (≤3 g per planting hole) of fertilizers to the root zone. This approach has been shown to significantly improve nutrient uptake efficiency while minimizing losses [20]. Studies have demonstrated the effectiveness of this practice in boosting short-term crop productivity [21]. However, its success is often constrained by the low organic matter content and poor microbial activity of Sahelian soils [17] [22].

To enhance the sustainability of microdosing, its integration with arbuscular mycorrhizal fungi (AMF) is increasingly being explored. AMF colonization can improve root absorption of nutrients, particularly phosphorus (P), and facilitate better soil-plant nutrient dynamics [2]. Research by Ndiaye *et al.* showed that AMF inoculation significantly enhanced biomass accumulation and root colonization in pearl millet [23]. Diagne *et al.* and Founoune-Mboup *et al.* have reported positive interactions between AMF inoculation and NPK fertilization in improving the growth and nutrient content of pearl millet, particularly iron and zinc [24] [25]. These studies indicated that the combined approach resulted in higher nutrient uptake and biomass production compared to treatments with only fertilizers or AMF alone. However, the extent to which AMF influence nutrient removal and the partitioning of absorbed nutrients into harvestable biomass remains insufficiently explored. Although previous studies have investigated the effect of AMF and NPK interactions, this study brings a unique perspective by focusing on the nutrient export aspect, which hasn't been as extensively explored. Most studies focus on nutrient uptake, but understanding how much of those nutrients are translocated to the harvested biomass (*i.e.*, removal from the soil) provides additional insights into the efficiency of the system. This study investigates the combined effect of AMF inoculation and fertilizer microdosing on pearl millet nutrient acquisition, focusing on how this synergy influences macronutrient and micronutrient removal. By quantifying nutrient removal, this study aims to offer insights into sustainable soil fertility management strategies, contributing to improved crop productivity and long-term ecological resilience in the Sahel.

2. Materials and Methods

2.1. Experimental Setup

The experiment was conducted in a controlled greenhouse at the Department of Plant Biology, Cheikh Anta Diop University of Dakar (Senegal), using a homogenized sandy soil from Touba Toul at 5 - 20 cm depth (70 km from Dakar, Senegal). The greenhouse conditions were controlled to maintain a 12-h day/night photoperiod with temperatures of 32˚C during the day and 25˚C at night, and a relative humidity level of 40% - 50%. Plastic pots of 4 L (0.004 m^3) capacity were filled with 3 kg of sandy soil, which was composed of 92% sand, 3.6% clay, and 1.6% silt of dry soil. The soil contained 1.24% organic matter, had a total nitrogen (N) content of 0.11% dry soil, and an available P concentration of 3.1 mg/kg. The pH of the soil was 4.5 - 4.6. The pots were irrigated with tap water at 80% of the soil water holding capacity to maintain adequate soil moisture.

2.2. Treatments and Arbuscular Mycorrhizal Fungi Inoculation

A completely randomized design was used with nine treatment combinations (**Table 1**), each replicated five times, totaling 45 pots. Treatments combined three types of inputs: mineral fertilizer (NPK, urea), organic manure, and AMF inoculation applied singly or in combination. The treatments were: T0 (control, no inputs), T1 (3 g NPK + 2 g urea), T2 (600 g organic manure), T3 (AMF only), T4 (3 g NPK + 2 g urea + AMF), T5 (600 g organic manure + AMF), T6 (5 g NPK + 4 g urea + 600 g organic manure), T7 (3 g NPK + 2 g urea + 600 g organic manure), and T8 (5 g NPK + 4 g urea + 600 g organic manure + AMF) (**Table 1**). NPK

(15/10/10; 150 g/kg N, 100 g/kg P_2O_5, 100 g/kg K_2O) was applied 10 days after emergence, and urea (460 g/kg N) was applied 30 days after emergence (**Table 2**). The organic manure used in this study consisted of well-decomposed cow manure collected from local smallholder farms in Touba Toul. It was air-dried and sieved (<2 mm) before mixing into the soil. Its average nutrient content at 12% moisture was 22.8 g/kg K, 186.4 g/kg C, 9.6 g/kg N, and 2.9 g/kg P (**Table 2**). Prior to inoculation, the soil used in this experiment was sterilized at 121˚C for 1 h to eliminate background microbial activity, including native AMF spores. Microscopic inspection confirmed the absence of viable AMF propagules in the control soil (T0), ensuring that only inoculated treatments contained active mycorrhizal fungi. AMF inoculants were prepared by mixing sandy soil with spores of *Rhizophagus irregularis* and *Rhizophagus aggregatum* (40,000 spores/kg soil each), together with extraradical mycelium from maize pot cultures. The final 1:1 inoculum mixture had a density of 80,000 spores/kg and achieved 85% root colonization. At sowing, 20 g of live inoculum was placed in the hole of each pot, corresponding to approximately 1600 spores per pot, or 0.8×10^6 spores/m^3 of soil, given that each pot contained 0.002 m^3 of soil. AMF inoculation was omitted in treatments T0, T1, and T2.

In this study, the fertilizer microdoses applied to each 4-L pot were designed to represent the per-hill microdosing practice commonly used by farmers in West Africa. Because microdosing in the field is applied directly to individual planting holes rather than per unit of land area, each pot corresponds to a single planting hill. Thus, the per-pot doses (e.g., 3 g NPK + 2 g urea) reflect realistic point-source applications at the plant level currently recommended (≤3 - 6 g of NPK-based fertilizer per hill) in the Sahel. Scaling these doses to per-hectare fertilizer rates depends on planting density (*i.e.*, hill spacing), as the same per-hill microdose may correspond to different area-based rates depending on inter-row and intra-row spacing. This clarification ensures that our greenhouse treatments accurately represent farmer-level microdosing practices while allowing for appropriate agronomic interpretation of the results.

Table 1. List of treatments. The indices for the treatment names indicate the amount of NPK fertilizer, urea, and cow manure (OM) added per pot (g).

Code	Treatments	Description
T0	Control	Without treatment
T1	$(NPK)_3U_2$	3 g NPK + 2 g urea/pot
T2	OM_{600}	600 g OM/pot
T3	AMF	AMF
T4	$(NPK)_3U_2$ + AMF	3 g NPK and 2 g urea/pot + AMF
T5	OM_{600} + AMF	600 g/pot OM + AMF
T6	$(NPK)_2U_1$ + OM_{200} + AMF	2 g NPK and 1 g urea + 200 g OM/pot + AMF
T7	$(NPK)_3U_2$ + OM_{400} + AMF	3 g NPK and 2 g urea/pot + 400 g OM/pot + AMF
T8	$(NPK)_5U_4$ + OM_{600} + AMF	5 g NPK and 4 g urea + 600 g OM/pot + AMF

Table 2. Nutrient inputs per treatment (g/kg dry soil) from different sources. Each pot contained 3 kg of dry sandy soil.

Code	N from NPK	N from Urea	N from OM	Total N	P from NPK	P from OM	Total P	K from NPK	K from OM	Total K
T0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T1	0.45	0.00	0.00	0.45	0.13	0.00	0.13	0.25	0.00	0.25
T2	0.00	0.00	5.76	5.76	0.00	1.74	1.74	0.00	13.68	13.68
T3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T4	0.45	0.92	0.00	1.37	0.13	0.00	0.13	0.25	0.00	0.25
T5	0.00	0.00	5.76	5.76	0.00	1.74	1.74	0.00	13.68	13.68
T6	0.30	0.46	1.92	2.68	0.08	0.58	0.67	0.16	4.56	4.73
T7	0.45	0.92	3.84	5.21	0.13	1.16	1.29	0.25	9.12	9.37
T8	0.75	1.84	5.76	8.35	0.22	1.74	1.96	0.41	13.68	14.10

2.3. Plant Material and Growth Conditions

Pearl millet (*Pennisetum glaucum* cv. Souna 3) seeds were sown directly into pots in January, with organic manure mixed into the soil at sowing when applicable. To ensure uniform emergence, three seeds were sown per pot and, one week after germination, seedlings were thinned to one plant per pot. This widely cultivated variety (Souna 3) is well adapted to Sahelian agroecological conditions and commonly used by smallholder farmers in Senegal [18].

2.4. Measurements and Chemical Analysis

Twelve weeks after sowing, shoots and roots were harvested separately. Fresh root subsamples were taken to assess root colonization rates. Roots were initially rinsed with tap water and then thoroughly washed with distilled water. The percentage of mycorrhizal root infection was determined by microscopic observation of fungal colonization after clearing the washed roots in 10% KOH and staining with 0.05% trypan blue in lactophenol (v/v), following the method described by Phillips and Hayman [26]. Mycorrhizal frequency (F%) (*i.e.*, the proportion of root segments containing any AMF structures (hyphae, vesicles, or arbuscules) was calculated using the grid-line intersect method [27]. Shoot biomass was dried in an oven at 55˚C for 96 hours to determine dry weight. All plant material analyses were carried out at the UMR Interaction Soil Plant Atmosphere (ISPA) of INRAE in France. The dried shoot samples were ground to a fine powder. To determine elemental concentrations, the powdered plant material was digested in a mixture of nitric acid and hydrogen peroxide (HNO_3/H_2O_2). For this, a 500 mg aliquot of the powder was combined with 5 mL of the HNO_3/H_2O_2 mixture (4:1, v/v) in a 50 mL Teflon® tube and digested in a graphite block (DigiPREP MS, SCP Science). After digestion, the samples were filtered, and the concentrations of P, K, Ca, Mg, Cu, Mn, Fe, and Ni in the resulting solutions were analyzed by inductively coupled plasma optical emission spectrometry (ICP-OES) using a Thermo Fischer ICAP 6300 instrument. Total nitrogen content in the shoot tissue was measured separately on an elemental analyzer (Thermo Flash, EA 1112) employing dynamic flash combustion.

2.5. Statistical Analyses

The dataset consisted of 45 observations corresponding to 9 treatments with 5 replicates each. Nutrient removal was calculated as the product of shoot dry biomass (g/pot) and nutrient concentration (mg or µg per g dry matter), and expressed as mg/pot for macronutrients (N, P, K, Ca, Mg) and µg/pot for micronutrients (Cu, Mn, Fe, Ni).

To address heteroscedasticity in the nutrient export data, a logarithmic transformation was applied to all nutrient variables. For multivariate analysis, the log-transformed variables and shoot dry weight were standardized to have a mean of 0 and a standard deviation of 1, ensuring comparability across scales. Nutrient use efficiency (NUE) was calculated for N, P, and K using the agronomic efficiency (AE) formula [28]:

$$\frac{\text{Shoot Dry Weight}(\text{treatment})(\text{g})-\text{Shoot Dry Weight }(\text{control})(\text{g})}{\text{Input of X}\left(\text{g}\cdot\text{pot}^{-1}\right)}$$

where $X \in \{N, P, K\}$. Units: AE in $g \cdot g^{-1}$, shoot dry weight in g, nutrient input in $g \cdot pot^{-1}$. NPK (15/10/10) = 15% N, 10% P_2O_5 (=4.36% P), 10% K_2O (=8.3% K); Urea = 46% N; Manure = 0.96% N, 0.29% P, 2.28% K (fresh weight, 12% moisture). Values are expressed as elemental nutrients.

All statistical analyses were performed using R software (version 4.2.2). Data were first tested for normality (Shapiro-Wilk) and homogeneity of variances (Levene's test). When assumptions of normality and homoscedasticity were met, one-way ANOVA followed by Tukey's HSD test ($\alpha = 0.05$) was used to compare treatments. Otherwise, Kruskal-Wallis tests with Dunn's post hoc comparisons (Bonferroni-adjusted) were applied. To assess overall treatment effects on nutrient export patterns, a multivariate analysis of variance (MANOVA) was conducted using the log-transformed dataset. Relationships among variables were further explored using Pearson correlation between AMF colonization rates and nutrient export. A principal component analysis (PCA) was then applied to the standardized dataset to uncover patterns and associations among nutrients and treatments. The first two principal components (PC1 and PC2) were used for K-means clustering to group treatments according to their nutrient removal profiles. The elbow method was employed to determine the optimal number of clusters.

3. Results

3.1. Multivariate and Univariate Analysis of Treatment Effects on Nutrient Export

The multivariate analysis of variance (MANOVA) demonstrated a significant overall treatment effect on nutrient export profiles in pearl millet (Wilks' Lambda, $p < 0.001$). Subsequent univariate ANOVA confirmed that the effects of treatments were highly significant for all measured nutrients ($p < 0.0001$), with F-values based on log-transformed data ranging from 25.7 for calcium to 49.3 for N. Post hoc comparisons using Tukey's HSD test revealed treatment-specific differences in nutrient export. Treatment T5 (OM_{600} + AMF) recorded the highest removal values for N (50.8 mg/pot) and K (241.5 mg/pot), while T8 (NPK_5U_4 + OM_{600} + AMF) excelled in P (29.4 mg/pot), calcium (28.6 mg/pot), magnesium (27.1 mg/pot), and copper (20.6 µg/pot). Treatment T3 (AMF) was most effective in enhancing the removal of micronutrients such as manganese (886.0 µg/pot), iron (1648.8 µg/pot), and nickel (71.0 µg/pot). The detailed nutrient removal means across treatments are presented in Table 3.

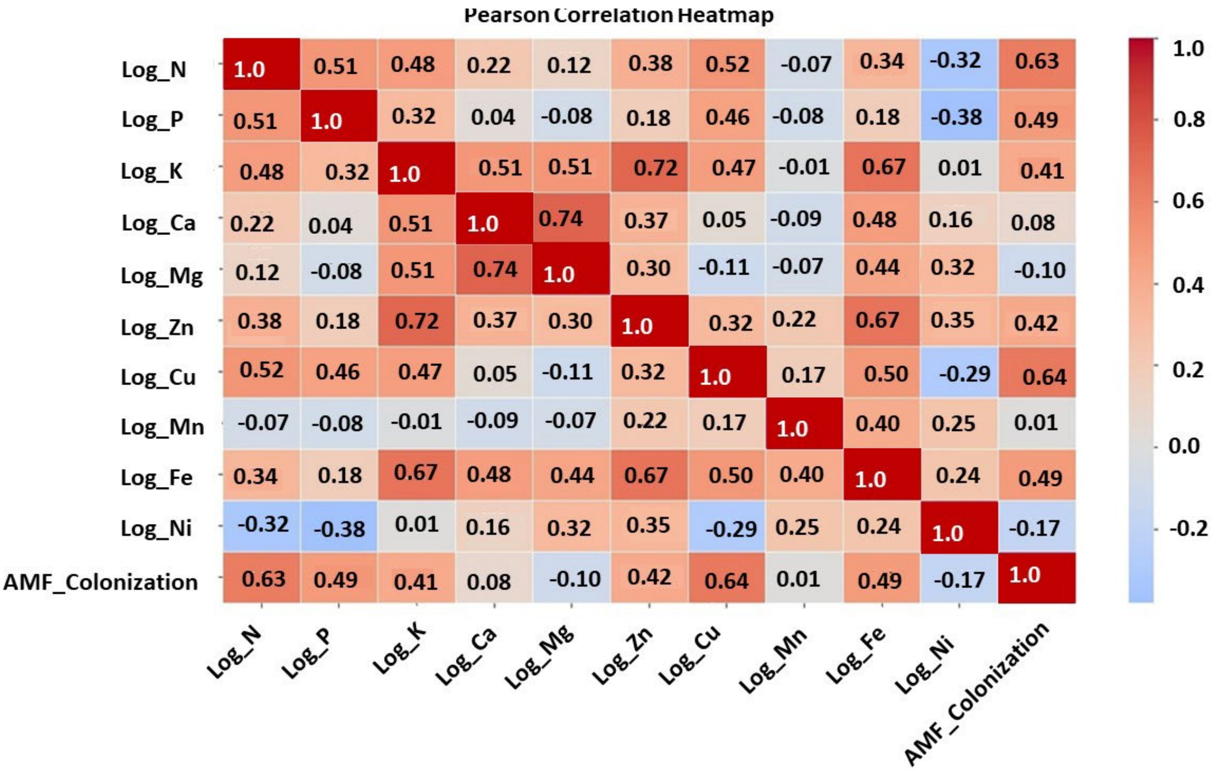
Table 3. Means ± standard deviation by treatment for each nutrient exported (mg/pot for macronutrients and µg/pot for micronutrients).

Unit	g/pot	mg/pot					µg/pot			
Treatments	Shoot dry biomass	N	P	K	Ca	Mg	Cu	Mn	Fe	Ni
T0	0.2 ± 0.1^{d*}	0.7 ± 0.2^{d}	0.4 ± 0.1^{e}	1.2 ± 0.7^{d}	0.3 ± 0.0^{d}	0.3 ± 0.1^{f}	0.4 ± 0.1^{e}	2.6 ± 0.9^{e}	16.3 ± 5.4^{c}	0.1 ± 0.0^{d}
T1	3.2. ± 1.6^{bcd}	12.2 ± 4.2^{c}	9.1 ± 2.4^{c}	35.9 ± 19.4^{c}	10.4 ± 3.4^{c}	6.5 ± 2.4^{d}	3.4 ± 1.4^{d}	87.1 ± 37.4^{c}	413.1 ± 137.4^{b}	3.9 ± 1.4^{c}
T2	8.1 ± 5.1^{abc}	49.5 ± 23.5^{a}	17.8 ± 5.4^{b}	192.0 ± 87.4^{a}	14.1 ± 5.4^{b}	11.4 ± 5.4^{c}	17.7 ± 5.4^{a}	95.1 ± 37.4^{c}	1049.4 ± 437.4^{a}	38.8 ± 15.4^{b}
T3	11.7 ± 5.8^{a}	24.6 ± 5.1^{b}	28.3 ± 7.4^{a}	95.0 ± 37.4^{b}	17.9 ± 5.4^{b}	18.5 ± 5.4^{b}	17.5 ± 5.4^{a}	886.0 ± 337.4^{a}	1648.9 ± 537.4^{a}	71.0 ± 25.4^{a}
T4	2.7 ± 0.3^{cd}	28.9 ± 1.2^{b}	3.8 ± 0.4^{d}	34.1 ± 12.4^{c}	8.9 ± 1.0^{c}	4.6 ± 0.4^{e}	6.1 ± 0.4^{c}	135.1 ± 37.4^{c}	558.8 ± 137.4^{b}	4.5 ± 0.4^{c}
T5	8.4 ± 4.7^{abc}	50.8 ± 12.8^{a}	16.8 ± 5.4^{b}	241.5 ± 87.4^{a}	18.6 ± 5.4^{b}	8.1 ± 2.4^{d}	15.9 ± 5.4^{a}	65.2 ± 25.4^{d}	1239.4 ± 437.4^{a}	21.4 ± 5.4^{b}
T6	5.2 ± 2.5^{abcd}	26.4 ± 8.3^{b}	11.3 ± 2.4^{c}	104.0 ± 37.4^{b}	11.5 ± 2.4^{c}	10.0 ± 2.4^{c}	13.2 ± 2.4^{b}	76.0 ± 25.4^{d}	1125.2 ± 437.4^{a}	24.1 ± 5.4^{b}
T7	6.1 ± 2.5^{abcd}	40.3 ± 8.3^{a}	17.0 ± 5.4^{b}	100.8 ± 37.4^{b}	15.6 ± 5.4^{b}	10.9 ± 2.4^{c}	13.0 ± 2.4^{b}	118.7 ± 37.4^{c}	1026.4 ± 337.4^{a}	29.7 ± 5.4^{b}
T8	9.9 ± 3.9^{a}	44.1 ± 7.9^{a}	29.4 ± 7.4^{a}	149.0 ± 37.4^{a}	28.6 ± 7.4^{a}	27.1 ± 7.4^{a}	20.6 ± 5.4^{a}	304.9 ± 87.4^{b}	1128.6 ± 337.4^{a}	6.7 ± 1.4^{c}
F-value	5.55	49.2	33.7	32.6	25.7	29.1	31.1	35.0	37.1	26.4
p-value	<0.001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Letters: Treatments with the same letter for a given nutrient are not significantly different by ANOVA and Tukey's multiple comparison test ($p > 0.05$). Different letters indicate significant differences ($p < 0.05$).

3.2. Correlation between Arbuscular Mycorrhizal Fungi (AMF) Colonization and Nutrient Export

The correlation analysis revealed notable patterns in the relationship between AMF colonization and the export of nutrients by pearl millet, as shown in Figure 1. AMF colonization exhibited strong positive correlations with N (log_N, r = 0.63) and copper (log_Cu, r = 0.64), suggesting that AMF inoculation is associated with increased uptake or accumulation of these nutrients in pearl millet. Moderate correlations were observed with P (log_P, r = 0.49), zinc (log_Zn, r = 0.42), and iron (log_Fe, r = 0.49), indicating a consistent, though less pronounced, influence of AMF on their dynamics. In contrast, AMF colonization showed weak or negligible correlations with calcium (log_Ca, r = 0.08) and manganese (log_Mn, r = 0.01), and a slight negative correlation with magnesium (log_Mg, r = −0.10), suggesting limited AMF involvement in these nutrients' dynamics under the experimental conditions. Among the nutrients, a strong positive correlation between calcium and magnesium (log_Ca and log_Mg, r = 0.74) reflects their shared roles and mobility in soil-plant systems. K (log_K) showed strong correlations with zinc (log_Zn, r = 0.72) and iron (log_Fe, r = 0.67), suggesting possible synergistic uptake or translocation patterns. In contrast, nickel (log_Ni) exhibited mostly weak or negative correlations with other nutrients and AMF colonization (r = −0.17), pointing to distinct regulatory or exclusion pathways. These correlations highlight the role of AMF in modulating nutrient availability, particularly for N and copper, and reinforce the interconnected nature of nutrient dynamics in AMF-inoculated pearl millet systems.



Pearson Correlation Heatmap

	Log_N	Log_P	Log_K	Log_Ca	Log_Mg	Log_Zn	Log_Cu	Log_Mn	Log_Fe	Log_Ni	AMF_Colonization
Log_N	1.0	0.51	0.48	0.22	0.12	0.38	0.52	-0.07	0.34	-0.32	0.63
Log_P	0.51	1.0	0.32	0.04	-0.08	0.18	0.46	-0.08	0.18	-0.38	0.49
Log_K	0.48	0.32	1.0	0.51	0.51	0.72	0.47	-0.01	0.67	0.01	0.41
Log_Ca	0.22	0.04	0.51	1.0	0.74	0.37	0.05	-0.09	0.48	0.16	0.08
Log_Mg	0.12	-0.08	0.51	0.74	1.0	0.30	-0.11	-0.07	0.44	0.32	-0.10
Log_Zn	0.38	0.18	0.72	0.37	0.30	1.0	0.32	0.22	0.67	0.35	0.42
Log_Cu	0.52	0.46	0.47	0.05	-0.11	0.32	1.0	0.17	0.50	-0.29	0.64
Log_Mn	-0.07	-0.08	-0.01	-0.09	-0.07	0.22	0.17	1.0	0.40	0.25	0.01
Log_Fe	0.34	0.18	0.67	0.48	0.44	0.67	0.50	0.40	1.0	0.24	0.49
Log_Ni	-0.32	-0.38	0.01	0.16	0.32	0.35	-0.29	0.25	0.24	1.0	-0.17
AMF_Colonization	0.63	0.49	0.41	0.08	-0.10	0.42	0.64	0.01	0.49	-0.17	1.0

Figure 1. Pearson correlation heat map: AMF colonization vs. log-transformed nutrient removal.

3.3. Nutrient Use Efficiency (NUE): Agronomic Efficiency of N, P, and K

Agronomic efficiency (AE) was calculated to assess the nutrient use efficiency of N, P, and K. Values for N (AE_N), P (AE_P), and K (AE_K) across all treatments are presented in Table 4. Due to heteroscedasticity, Kruskal-Wallis tests were used, revealing significant effects of treatment on all three nutrients (AE_N: H = 14.07, p = 0.029; AE_P: H = 15.32, p = 0.018; AE_K: H = 18.95, p = 0.004). N efficiency was highest in T1 (3 g NPK + 2 g urea/pot) and T2 (600 g OM/pot), which received a low NPK dose or only organic matter, respectively (Table 4). This indicates that targeted, lower mineral fertilizer doses or moderate organic inputs can maximize N utilization. Although the global Kruskal-Wallis test was significant, post-hoc Dunn's comparisons did not reveal specific pairwise differences, likely due to high variability within treatments and the conservative adjustment for multiple comparisons. P efficiency followed a different pattern. T2 (OM$_{600}$) achieved the highest AE_P, significantly exceeding T6 (2 g NPK + 1 g urea + 200 g OM/pot + AMF) and T7 (3 g NPK + 2 g urea + 400 g OM/pot + AMF) (Table 4). This suggests that P uptake depends not only on the amount applied but also on a balanced nutrient regime. Treatments combining high organic matter with smaller mineral inputs were less effective at promoting P use. P efficiency showed the clearest separation among treatments. The high-efficiency group, including T1 (3 g NPK + 2 g urea/pot), T2 (OM$_{600}$), and T4 (3 g NPK + 2 g urea + AMF), received balanced mineral fertilization without excessive organic matter and achieved AE_K values of 8.33 - 15.80 g/g. In contrast, treatments with high organic matter inputs (T5, T6, T7, T8) exhibited drastically reduced AE_K (0.26 - 0.94 g/g), indicating nutrient co-limitation, likely from N or P shortages, which limited biomass accumulation and prevented efficient K utilization. These results demonstrate that maximal nutrient use efficiency is achieved under balanced fertilization. While high organic matter increased total nutrient supply, it disrupted nutrient balance, particularly reducing K efficiency. These findings underscore that excessive application of a single nutrient, without addressing potential deficiencies in others, leads to inefficient resource use and diminished agronomic returns.

Table 4. Agronomic efficiency (AE, g/g) of nitrogen (N), phosphorus (P), and potassium (K) for pearl millet under different treatment regimes. Values represent mean ± standard deviation (n = 3).

Treatment	AE_N (g/g)	AE_P (g/g)	AE_K (g/g)
T0 Control	NA	NA	NA
T1 (NPK)$_3$U$_2$	6.67 ± 3.78^{a*}	10.00 ± 5.67^{ab}	10.00 ± 5.67^{a}
T2 OM$_{600}$	3.51 ± 2.25^{a}	15.80 ± 10.10^{a}	15.80 ± 10.10^{a}
T3 AMF	NA	NA	NA
T4 (NPK)$_3$U$_2$ + AMF	1.85 ± 0.26^{a}	8.33 ± 1.17^{ab}	8.33 ± 1.17^{a}
T5 OM$_{600}$ + AMF	1.42 ± 0.81^{a}	4.71 ± 2.68^{bc}	0.60 ± 0.34^{b}
T6 (NPK)$_2$U$_1$ + OM$_{200}$ + AMF	0.81 ± 0.40^{a}	2.46 ± 1.21^{c}	0.35 ± 0.18^{b}
T7 (NPK)$_3$U$_2$ + OM$_{400}$ + AMF	0.78 ± 0.34^{a}	2.52 ± 1.09^{c}	0.38 ± 0.17^{b}
T8 (NPK) $_5$U$_4$ + OM$_{600}$ + AMF	1.16 ± 0.46^{a}	4.95 ± 1.97^{bc}	0.71 ± 0.28^{b}
Dunn	NS	T2 > T6, T2 > T7	T1, T2, T4 > T5, T6, T7, T8

Values followed by different lowercase letters within a column are significantly different based on Kruskal-Wallis and post-hoc Dunn's test ($p < 0.05$). NS = Not significant. NA = Not applicable.

3.4. Patterns in Nutrient Export and Their Relationship with Shoot Biomass

Principal component analysis performed on log-transformed nutrient export variables and shoot dry biomass revealed three well-defined clusters that reflected profound differences in growth and nutrient acquisition strategies among treatments (**Figure 2**, PCA biplot). The first principal component (PC1), explaining 89.7% of the total variance, was dominated by a strong opposition between shoot dry biomass (negative loadings) and the export of nearly all measured nutrients (positive loadings). This pattern demonstrates a striking trade-off: treatments achieving the highest biomass removed the least nutrients per unit of dry matter, whereas those exhibiting the greatest nutrient export suffered severe biomass penalties.

The control (T0) formed an isolated cluster on the negative side of PC1(cluster1: low biomass, low export), characterized by the lowest shoot dry biomass (0.2 g·pot^{-1}) and, consequently, extremely low absolute nutrient removal (e.g., 0.7 mg N·pot^{-1}, 2.6 µg Mn·pot^{-1}). In contrast, treatments receiving any mineral NPK + urea fertilizer (T1, T4, T5, T6, T7, T8) clustered tightly on the far positive side of PC1. Despite producing significantly higher biomass than the control in several cases, these treatments consistently displayed the highest tissue nutrient concentrations and, in many instances, elevated total export (e.g., T8 reached 29.4 mg P·pot^{-1} and 28.6 mg Ca·pot^{-1}). However, their shoot dry weights remained substantially lower than those of purely organic or biological treatments, resulting in a clear growth-for-nutrients trade-off suggestive of fertilizer-induced physiological stress, luxury uptake, or ion toxicity.

A distinct intermediate cluster (Cluster 2: high biomass, balanced to high export, exceptionally high Mn), separated upward along PC2 primarily by exceptionally high manganese export, comprised only T2 (600 g cow manure alone) and T3 (AMF inoculation alone). These two treatments achieved the highest shoot biomass of the entire experiment (8.1 and 11.7 g·pot^{-1}, respectively) while simultaneously exporting large absolute quantities of nutrients, particularly Mn (95.1 and 886.0 µg·pot^{-1}), Fe (1049 and 1649 µg·pot^{-1}), and Ni (38.8 and 71.0 µg·pot^{-1}). Notably, AMF alone (T3) outperformed all other treatments in micronutrient removal, confirming the powerful role of mycorrhizal symbiosis in enhancing the acquisition of relatively immobile elements in acidic sandy soils.

Surprisingly, combinations of high organic manure with mineral fertilizers and/or AMF (T5, T6, T7, T8) did not capitalize on the beneficial effects observed in T2 and T3 (Cluster 3: moderate to high biomass but strongly shifted toward macronutrient luxury uptake). Instead, they fell into the mineral-fertilizer cluster, exhibiting biomass reductions and nutrient export patterns dominated by excessive macronutrient accumulation rather than balanced enhancement. This indicates that mineral NPK and urea, even at microdosing rates, disrupted the positive plant-soil-microbe interactions promoted by either cow manure or AMF when applied separately.

The highest nutrient export coupled with superior biomass production, the most desirable outcome for both productivity and nutrient cycling, was achieved exclusively through purely organic (600 g cow manure) or biological (AMF inoculation) inputs. Any inclusion of mineral NPK + urea shifted the system toward high nutrient removal at the cost of growth, highlighting a fundamental incompatibility between conventional microdosing of inorganic fertilizers and optimal performance of pearl millet in this low-pH, low-fertility Sahelian sand. These findings strongly advocate for standalone organic or mycorrhizal-based strategies to simultaneously maximize yield and nutrient offtake in resource-constrained dryland cropping systems.

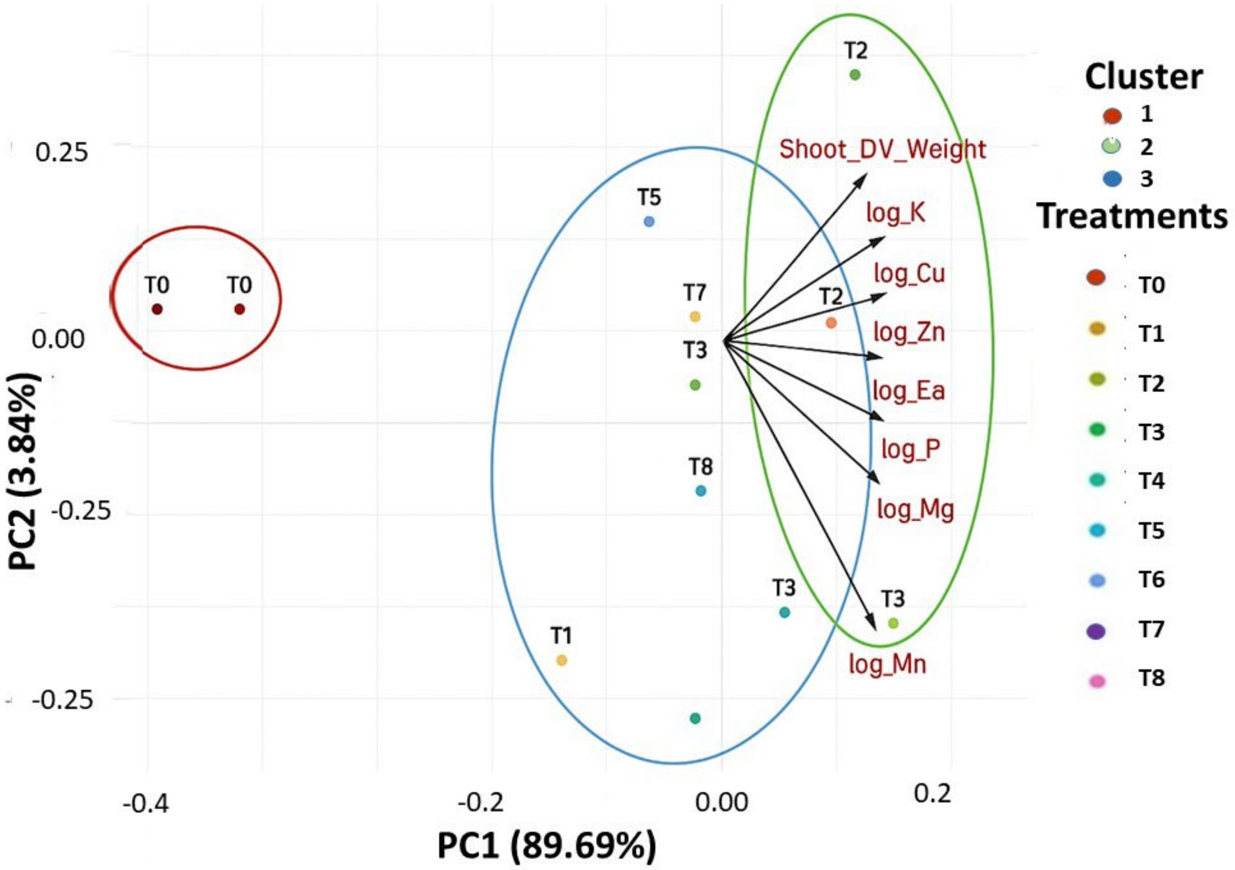


Figure 2. PCA biplot: log-transformed nutrient removal and shoot dry weight with k-means clusters.

4. Discussion

This study highlights the critical role of arbuscular mycorrhizal fungi (AMF) in optimizing nutrient uptake and improving agronomic efficiency in pearl millet cultivated under greenhouse conditions. In the context of the Sahel, where soils are typified by low P availability and high sand content, and where rainfall is both sparse and erratic, sustainable nutrient management strategies are urgently needed [11]. The integration of AMF with microdosing offers a promising pathway to enhance nutrient use efficiency (NUE) while addressing the challenges of nutrient depletion and low productivity in the Sahel.

4.1. Role of AMF in Micronutrient Uptake

The results demonstrate that AMF inoculation significantly enhanced the removal of micronutrients, notably manganese (Mn), iron (Fe), and nickel (Ni), particularly under treatment T3 (AMF). The remarkable performance of treatment T3 (AMF), which exhibited the highest colonization rate (56.4%), supports previous findings that highlight AMF's capacity to enhance the acquisition of poorly mobile elements [29]. This is particularly relevant for sandy soils of the Sahelian zone, where the natural abundance of micronutrients is limited and their mobility is constrained by low organic matter and weak retention capacity [17]. These elements, while required in trace amounts, are indispensable for various physiological processes, including enzymatic function, chlorophyll synthesis, and overall plant metabolic health [30]. Their increased availability in mycorrhizal treatments confirms the capacity of AMF to mobilize less accessible soil nutrients, particularly under low-input systems [29]. It is important to note that while shoot Fe concentration is a valuable indicator of plant nutrient status and soil export, further research is needed to confirm the translocation of these micronutrients to the edible grain, which is the ultimate goal of biofortification efforts. The moderate improvement in P, magnesium (Mg), and calcium (Ca) further aligns with the well-established role of AMF in enhancing P acquisition, especially in soils with critically low available P (3.1 ppm), as commonly found across the Sahel [20]. Interestingly, N and K uptake were only marginally influenced by AMF. This is consistent with prior work suggesting that AMF symbioses are less effective for highly mobile nutrients such as nitrate and K ions [31]. This finding suggests the need for complementary strategies, such as the integration of legumes or the application of split fertilizer applications, to enhance macronutrient availability in such soils [21].

4.2. Complementarity between AMF and Fertilization Strategies

The observed divergence in nutrient removal patterns between treatments dominated by biological inputs (e.g., T3: AMF) and those with higher mineral or organic matter applications (e.g., T5: OM_{600} + AMF, T8: NPK_5U_4 + OM_{600} + AMF) suggests a complementary relationship between AMF inoculation and fertilization. Treatment T3, which exhibited the highest AMF colonization (56.4%), significantly enhanced micro-nutrient removal (Mn: 885.9 µg/pot, Fe: 1648.8 µg/pot, Ni: 71.0 µg/pot) and improved the nutritional profile of harvested biomass without exacerbating macronutrient mining [29]. In contrast, T5 and T8, which promoted greater biomass accumulation, exhibited the highest macronutrient removal (e.g., T5: N 50.77 mg/pot, K 241.46 mg/pot; T8: P 29.38 mg/pot), likely due to higher nutrient availability from organic and mineral inputs [24]. However, this high removal raises concerns about long-term nutrient depletion in fragile Sahelian soils, where replenishment through organic or mineral amendments is often limited [13]. Notably, P uptake showed a moderate correlation with AMF colonization (r = 0.47), underscoring AMF's role in enhancing P acquisition in low-P soils (3.1 ppm). This is a critical factor given the limited access to chemical fertilizers for smallholders in the Sahel [17]. These findings highlight the potential of integrating AMF with judicious nutrient management to optimize both growth and nutritional quality of pearl millet while minimizing soil fertility decline [32].

4.3. Enhancing Crop Performance through NPK Microdosing and AMF Synergy

The agronomic efficiency (AE) analysis using the Kruskal-Wallis test followed by Dunn's post hoc comparisons revealed significant treatment effects for P and K, but not for N (**Table 4**). AE_P was significantly higher in T2 (OM600) relative to T6 and T7, while AE_K was greater in T1, T2, and T4 than in T5 - T8. These findings demonstrate that moderate inputs—particularly organic manure alone (T2) and NPK microdosing combined with AMF (T4)—achieved higher nutrient use efficiency than high-input regimes. The results also underscore the positive contribution of organic manure to K availability in sandy soils. In contrast, treatments receiving combined high mineral and organic inputs (T5 - T8) displayed reduced AE values, indicating diminishing returns under excessive nutrient supply. Such declines are consistent with nutrient losses through leaching or immobilization when application exceeds plant uptake capacity [33]. These findings emphasize the importance of synchronizing nutrient supply with crop demand, a central principle of sustainable intensification [21]. They also align with earlier studies showing that mycorrhizal inoculation paired with moderate NPK microdosing can improve nutrient use efficiency [24], whereas excessive inputs may depress recovery efficiency if not supported by biological agents like AMF [32].

Although high-manure (T2) and AMF-only (T3) treatments produced the highest shoot biomass and micronutrient uptake, their substantial export of N, P, K, Mn, and Fe raises concerns about long-term sustainability. Without external replenishment, such nutrient removal may accelerate soil nutrient mining—already a major challenge in Sahelian agroecosystems. These results therefore highlight the need for integrated practices that match organic and biological inputs with modest mineral fertilization or legume diversification to sustain soil fertility.

4.4. Optimizing Plant Nutrition through the Synergy of Growth and Symbiosis

The PCA results provided a compelling visualization of how nutrient removal patterns are governed by two principal axes: one driven by biomass accumulation (associated with macronutrients and shoot dry weight), and the other by AMF colonization (associated with micronutrient uptake). This duality is indicative of the trade-offs and complementarities inherent in plant nutrient strategies. Treatments such as T5 and T8 favored high growth rates, whereas T3 optimized micronutrient acquisition through symbiotic efficiency. These distinct strategies underline the need for context-specific nutrient management that considers both yield targets and nutritional quality, as emphasized by Beggi *et al.*, who noted similar trade-offs in pearl millet under low-P Sahelian conditions [2].

High macronutrient removal in the most productive treatments represents short-term gains but also heightens the risk of nutrient mining in sandy soils with low cation exchange capacity and slow natural replenishment. To prevent long-term fertility decline, management strategies should incorporate explicit nutrient budgeting and replenishment through periodic organic inputs, targeted nutrient replacement, or soil-restoring rotations

4.5. Implications for Agroecological Transition

Treatment clustering revealed three functional strategies with relevance for agroecological design. T0 (Control) exemplified low-input production with minimal nutrient export. T3 (AMF) represented a biologically intensive pathway that improved micronutrient content, particularly relevant for biofortification efforts addressing hidden hunger in vulnerable populations [10]. The third group (T2, T5 - T8) reflected strategies that enhance biomass and yield but require higher external inputs.

These patterns underscore the value of integrating AMF inoculation, organic amendments, and moderate fertilization to improve nutrient use efficiency and support sustainable crop production in degraded Sahelian soils [11]. Such approaches align closely with climate-smart agriculture goals and SDG 2 on Zero Hunger [33].

AMF inoculation showed considerable potential for micronutrient enhancement, as treatments such as T3 and T2 consistently increased shoot concentrations of Fe and Mn. Translating this potential into practical, farmer-relevant outcomes will require: 1) multi-location field trials to confirm effects on grain micronutrient concentrations; 2) development of robust, low-cost AMF inoculant formulations adapted to Sahelian soils; 3) simple, scalable delivery methods such as seed coatings or granular inoculants for smallholder use; and 4) economic and adoption studies to ensure feasibility under real-world conditions. Advancing these steps will help move AMF-based biofortification and nutrient-management innovations from greenhouse validation toward successful field implementation.

5. Conclusion

This greenhouse study demonstrated that AMF inoculation substantially influenced nutrient removal in pearl millet, especially for micronutrients. The AMF-only treatment (T3) significantly enhanced the removal of Mn, Fe, and Ni, underscoring the role of AMF in improving the nutritional quality of harvested biomass. In terms of agronomic efficiency, the combination of NPK microdosing with AMF (T4) produced the most favorable outcomes, indicating that moderate mineral inputs combined with AMF can optimize nutrient use efficiency while avoiding the inefficiencies associated with high-input systems. Conversely, high-input treatments increased macronutrient removal but showed lower AE values, suggesting a trade-off between biomass production and nutrient efficiency in coarse-textured Sahelian soils. This controlled environment study, with its robust replication ($n = 5$) and significant statistical outcomes, provides clear evidence of the synergistic effects of AMF and microdosing on nutrient dynamics in pearl millet. Although this study provides clear evidence of AMF-microdosing interactions on nutrient removal and agronomic efficiency, several limitations must be acknowledged. First, the experiment was conducted in a controlled greenhouse using pots. Such conditions cannot fully represent field-scale processes in Sahelian agroecosystems. Second, nutrient dynamics observed in pots, particularly leaching, AMF colonization stability, and nutrient depletion, may differ under field conditions where soil volume, rainfall patterns, and biological activity are more complex. Third, the absence of multi-location replication restricts the generalization of the observed trends. For these reasons, the findings should be considered preliminary. A key limitation of this study is the use of sterilized soil, which removes native microbial communities and alters natural plant-microbe interactions; thus, AMF establishment and nutrient dynamics may differ under field conditions where complex microbial networks are present. To confirm these findings under real-world conditions, multi-location and multi-season field trials are recommended. Future research should validate these results under multi-year field trial conditions to assess scalability, long-term nutrient cycling, and AMF persistence. Particular attention should be paid to nutrient losses in high-input treatments, given the sandy texture and low organic matter content of Sahelian soils.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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