



Effectiveness of mycorrhizal inoculation on sweet potato nutrition and NPK fertilization in Cuban Cambisols*

Efectividad de la inoculación micorrízica en la nutrición y la fertilización NPK del camote en suelos Cambisol de Cuba

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Abstract

Introduction. Sweet potato has high nutritional requirements. It is a mycotrophic crop, and in Cuba, its production is limited by the low availability of fertilizers. **Objective.** To evaluate the effectiveness of mycorrhizal inoculation on the nutrition and specific supply of primary macronutrients in two sweet potato cultivars over two planting seasons. **Materials and methods.** Six fertilization response curve experiments were conducted on Eutric Cambisol soils in Santo Domingo, Villa Clara, Cuba, from 2014 to 2016, with two experiments for each macronutrient (nitrogen, phosphorus, and potassium), one during the rainy period and one during the low-rainfall period. Each experiment evaluated five doses of the target macronutrient, with and without inoculation of *Rhizoglyphus irregularis* / INCAM-11, under a fixed background supply of the other two macronutrients. Trials were conducted on the cultivars INIVIT B-2-2005 and CEMSA 78-354 using a split-plot design with four replicates, repeated twice. Yields, macronutrient concentrations, colonization frequency, spores, and fertilizer agronomic efficiency were evaluated. **Results.** Positive and direct effects of inoculation on the yields and nutrition of each macronutrient were found. Inoculation required lower doses of fertilizers to guarantee yields and macronutrient concentrations equal to or higher than those obtained with mineral fertilizers alone, with higher fertilizer agronomic efficiency. Mycorrhizal performance depended on the doses of macronutrients applied. A high and direct relationship was established between the colonization frequency and the yield of the inoculated cultivars, with higher values of both variables in the rainy period. The cultivars always behaved similarly to each other. **Conclusions.** INCAM-11 inoculation of sweet potato cultivars acted directly and positively on the nutrition and fertilization efficiency of each NPK macroelement. The fertilizer doses for these inoculated cultivars growing on Eutric Cambisols were 60, 50, and 75 kg ha⁻¹ of N, P₂O₅, and K₂O for both planting seasons.

Keywords: arbuscular mycorrhizae, *Ipomoea batatas*, mycorrhizal symbiosis, agronomic efficiency, yields.



Resumen

Introducción. El boniato o camote tiene altos requerimientos nutricionales. Es un cultivo micótrofo y en Cuba su producción está limitada por la baja disponibilidad de fertilizantes. **Objetivo.** Evaluar la efectividad de la inoculación micorrízica sobre la nutrición y el suministro específico de macronutrientes primarios en dos cultivares de boniato en dos épocas de plantación. **Materiales y métodos.** Se realizaron seis experimentos de curva de respuesta a la fertilización, dos para cada macronutriente (nitrógeno, fósforo y potasio), uno en el periodo lluvioso y otro en el periodo poco lluvioso, sobre suelos Cambisoles eútricos en Santo Domingo, Villa Clara, Cuba, durante el periodo 2014-2016. En los cultivares comerciales INIVIT B-2-2005 y CEMSA 78-354 se estudiaron cinco dosis del macronutriente correspondiente, con y sin inoculación de *Rhizoglyphus irregularis* / INCAM-11, en presencia de un fondo fijo de los otros dos macronutrientes. Se utilizó un diseño de parcelas divididas, con cuatro réplicas, repetido dos veces. Se evaluaron rendimientos, concentraciones de macronutrientes, frecuencia de colonización, esporas y eficiencia agronómica de los fertilizantes. **Resultados.** Se encontraron efectos positivos y directos de la inoculación sobre los rendimientos y la nutrición de cada macronutriente. Con menores dosis de fertilizantes se garantizaron rendimientos y concentraciones de macronutrientes iguales o superiores a los obtenidos aplicando solo fertilizantes minerales, con mayor eficiencia agronómica del fertilizante. El funcionamiento micorrízico dependió de las dosis de macronutrientes aplicadas. Se estableció una relación alta y directa entre la frecuencia de colonización y el rendimiento de los cultivares inoculados, con valores superiores de ambas variables en el periodo lluvioso. Los cultivares se comportaron de forma similar. **Conclusiones.** La inoculación con INCAM-11 actuó directa y positivamente sobre la nutrición y la eficiencia de la fertilización de cada macroelemento NPK. Las dosis de fertilizantes para estos cultivares inoculados que crecieron en Cambisoles eútricos fueron de 60, 50 y 75 kg ha⁻¹ de N, P₂O₅ y K₂O para ambas épocas de plantación.

Palabras clave: micorrizas arbusculares, *Ipomoea batatas*, simbiosis micorrízica, eficiencia agronómica, rendimientos.

Introduction

Optimal nutrient supply is essential for crops (Witt et al., 2007). In Cuba, nutrient management has traditionally relied on synthetic fertilizers containing nitrogen (N), phosphorus (P), and potassium (K), complemented to some extent by organic manures. However, due to prolonged economic constraints, worsened by the COVID-19 pandemic, fertilizer importation and production have sharply declined, contributing to reduced agricultural yields (Viktorov, 2023). In recent years, national bioproducts, such as biofertilizers and biostimulants, have gained prominence, with promising results in experimental trials and local validations demonstrating satisfactory yields under reduced fertilizer regimes (Departamento de Suelos y Fertilizantes, 2020).

Globally, the use of inoculants with beneficial soil microorganisms in nutrient systems has increased (Antil & Raj, 2020; Baskar et al., 2022), though field-based evidence remains limited. Among these, arbuscular mycorrhizal fungi (AMF) stand out for their symbiosis with 84 % of plant species, exchanging carbon compounds for nutrients (Wipf et al., 2019). Benefits include enhanced nutrient and water uptake (Ortaş & Rafique, 2017; Ye et al., 2022), reduced pathogen damage (Fiorilli et al., 2024), cooperation with other rhizospheric microbes (Basiru et al., 2023), and improved soil aggregation (Lehmann et al., 2017).

The direct effect of AMF on N, P, and K uptake is well documented (Lanfranco et al., 2018; Wipf et al., 2019). Isotopic methods have been decisive in confirming this effect (Fernandez Suárez, 2012; Püschel et al., 2023), though they are rarely used in field trials, which are necessary to establish appropriate fertilizer doses. Nonetheless, it has been argued that, under sufficient phosphorus availability, inoculation-induced increases in other nutrient

concentrations reflect a direct mycorrhizal effect on their uptake, avoiding confounding from improved phosphorus nutrition (Corrêa et al., 2015).

In Cuba, AMF-based inoculants using generalist strains have been developed, with effectiveness influenced by soil pH (Rivera Espinosa et al., 2020). Initial field trials integrated inoculants with fertilizer doses through response curves (with and without inoculation) based on percentages of recommended NPK formulations for each crop. This approach reduced fertilizer needs to reach maximum yields and improved crop performance (Rivera et al., 2007). However, these schemes did not allow independent adjustment of each macronutrient. Later field experiments evaluated response curves for each macronutrient with and without inoculation, while maintaining sufficient levels of the other two (Camejo Hernández, 2016; González et al., 2015). Results showed increased mycorrhizal functioning, higher nutrient concentrations, and reduced fertilizer requirements per macronutrient to reach maximum yields.

Ipomoea batatas (sweet potato) is cultivated in over 100 tropical and subtropical countries, mainly in developing regions. It is the world's second-largest root crop (Food and Agriculture Organization of the United Nations, n. d.). In Cuba, sweet potatoes are widely consumed for their flavor and texture, and rapid biomass conversion, and can reach 25–35 t ha⁻¹ of edible roots in five months (Espinosa-Cuéllar et al., 2023). It also serves as animal feed (Rodríguez et al., 2020). Sweet potatoes are typically grown under irrigation during the rainy or dry seasons, with lower temperatures and yields in the latter (Espinosa-Cuéllar et al., 2023), and at least ten commercial cultivars are used (Ministerio de la Agricultura, 2022).

Despite this potential, recent national average yields have remained around 9 t ha⁻¹ (Oficina Nacional de Estadística e Información, 2023), highlighting a significant gap between attainable and actual productivity. One contributing factor is insufficient nutrient supply. Potassium is the most extracted nutrient (5.6 kg t⁻¹), followed by nitrogen (4.4 kg t⁻¹), both far exceeding phosphorus (0.62 kg t⁻¹) (Ruiz Martínez et al., 2012). Recommended fertilizer doses for high yields are 90-75-150 kg ha⁻¹ of N, P₂O₅, and K₂O, respectively (Instituto de Investigaciones de Viandas Tropicales [INIVIT], 2007), although these values vary according to soil fertility.

Sweet potato is a mycotrophic crop (Yuan et al., 2023). In Cuba, a positive yield response to mycorrhizal inoculation and increases in mycorrhizal performance have been obtained using response curves with percentages of the NPK formulation for high yields (Ruiz Martínez et al., 2012). Inoculation reduced the fertilizer needed to achieve the highest yields by 50 % on Eutric Cambisols. However, the effects of inoculation on the specific supplementation of each macronutrient for optimal effectiveness, higher yields, improved fertilization efficiency, and the influence of planting time remain unstudied. Therefore, this work aimed to evaluate the effectiveness of mycorrhizal inoculation on the nutrition and specific supply of primary macronutrients in two sweet potato cultivars over two planting seasons.

Materials and methods

Location and characterization of the experiment

Six field experiments were conducted between 2014 and 2016 in areas of the Instituto de Investigaciones de Viandas Tropicales (INIVIT), located at 22°35'1.2"N, 80°13'11.9"W, and 40 m above sea level in the municipality of Santo Domingo, Villa Clara province, Cuba. Each experiment evaluated the response of two sweet potato cultivars to five doses of one primary macronutrient (N, P, or K), applied with and without inoculation with arbuscular mycorrhizal fungi (AMF). Three of these experiments, one for each macronutrient, were carried out during the rainy season, and the other three followed the same structure during the low-rainfall season. Experiments were repeated once. Details on the experimental design, treatments, and cultivars are provided in the following sections.

The experiments were conducted on soils previously classified as Eutric Cambisols with carbonates (Espinosa-Cuéllar et al., 2023), according to the WRB system (IUSS Working Group WRB, 2022). Chemical characterization of the 0–20 cm layer (Table 1) showed typical features: slightly alkaline pH-H₂O (7.0–7.3), high exchangeable Ca, and medium levels of exchangeable Mg and K. Available phosphorus (P) was moderate, and organic matter content was low, likely due to degradation from continuous cultivation. Mycorrhizal spore abundance remained consistently low (1.2 spores g⁻¹), probably affected by fertilization and long-term soil exploitation (Guo et al., 2020). Overall, these results align with those reported by Espinosa-Cuéllar et al. (2019) and Simo González et al. (2020).

Table 1. Initial chemical and mycorrhizal spore characterization at the beginning of the experiments in an Eutric Cambisol with carbonates (0-20 cm depth). Santo Domingo, Villa Clara. 2014-2016.

Cuadro 1. Caracterización química y de esporas micorrízicas al inicio de los experimentos en un suelo Pardo mullido con carbonatos (0-20 cm profundidad). Santo Domingo, Villa Clara. 2014-2016.

	pH H ₂ O ¹	OM ² (g kg ⁻¹)	P ³ (mg kg ⁻¹)	⁴ Ca ²⁺	⁴ Mg ²⁺	⁴ K ⁺	AMF ⁵ Spores in 50 g
Rainy period							
Repetition 1	7.00	17.30	7.64	27.20	4.10	0.53	70
Repetition 2	7.20	19.00	11.13	35.62	4.66	0.54	65
Low-rainy period							
Repetition 1	7.30	18.70	10.91	31.14	4.89	0.57	57
Repetition 2	7.10	18.80	7.73	27.21	4.11	0.53	60

pH-H₂O: pH measured in water. **OM:** Soil organic matter. **P:** Available phosphorus in soil. **Ca, Mg, Na, K:** Exchangeable cations. **AMF spores:** Mycorrhizal spores. Repetition 1 and 2 refer to the first and second executions of the experiments within each crop cycle climatic conditions. Each value represents the average of four replicates from the three experiments conducted during that execution. Chemical determinations in soil according to Paneque Pérez et al. (2010). Spore determinations according to Torres-Arias et al. (2015). / **pH-H₂O:** pH medido en agua. **OM:** Materia orgánica del suelo. **P:** Fósforo disponible en el suelo. **Ca, Mg, Na, K:** Cationes intercambiables. **AMF spores:** Esporas micorrízicas. Repetición 1 y 2 se refieren a la primera y segunda ejecución de los experimentos dentro de cada condición climática del ciclo de cultivo. Cada valor representa el promedio de las cuatro réplicas provenientes de los tres experimentos realizados durante esa ejecución. Las determinaciones químicas en el suelo de acuerdo con Paneque Pérez et al. (2010). Las determinaciones de esporas de acuerdo con Torres-Arias et al. (2015).

Climatic data were collected directly from Meteorological Station No. 326 of the Cuban Institute of Meteorology (INSMET), located at INIVIT, through in-person review of daily records. Based on the 55-year average (1969–2023), the experimental area exhibits a dry tropical climate, with an annual total precipitation of 1363.7 mm and a mean annual temperature of 24.4 °C. The rainy season (May to October) typically accounts for about 78 % of the yearly rainfall and presents mean temperatures approximately 4.8 °C higher than those recorded during the low-rainfall season (November to April). During the study years, the average total rainfall was 1259.2 mm and the mean temperature was 24.4 °C, both within the historical range of variability for these climatic variables.

Experimental design and studied factors

A randomized block design with a split-plot arrangement and four replications was used in the six experiments. Factor A, with two levels corresponding to sweet potato cultivars, was assigned to the main plots. Subplots included all combinations of the two levels of Factor B (with and without AMF inoculant) and the five levels of Factor C (specific macronutrient fertilizer doses). Each experiment comprised 20 treatment combinations, replicated across four blocks. All experiments were conducted twice under similar conditions to ensure consistency.

The two cultivars used as Factor A were ‘INIVIT B-2-2005’ and ‘CEMSA 78-354’, two of the most productive and widely cultivated Cuban sweet potato varieties (Espinosa-Cuéllar et al., 2023). For the inoculated level of Factor B, a solid formulation based on *Rhizoglyphus irregularis* [Błaszk., Wubet, Renker & Buscot] Sieverd., G.A. Silva & Oehl], isolate INCAM-11/DAOM711363, was applied. This inoculant is recommended for sweet potato cultivation under the edaphic conditions of the study site (Espinosa-Cuéllar et al., 2023).

Factor C always consisted of five nutrient dose levels. In nitrogen experiments, the doses were 0, 30, 60, 90, and 120 kg ha⁻¹ of N; in phosphorus experiments, 0, 25, 50, 75, and 100 kg ha⁻¹ of P₂O₅; and in potassium experiments, 0, 75, 150, 225, and 300 kg ha⁻¹ of K₂O. A fixed background of the other two macronutrients was applied in all experiments, with doses of 90 kg ha⁻¹ N, 75 kg ha⁻¹ P₂O₅, and 150 kg ha⁻¹ K₂O, respectively. These doses ensure sufficient availability of the two background nutrients (INIVIT, 2007), so that only the nutrient under study may be present in limiting conditions within each experiment.

The experiments were planted between May 12–16 (2014 and 2015) during the rainy season, and between November 10–15 of the same years during the low-rainfall period. Vegetative planting material consisted of apical and sub-apical stem cuttings (commonly referred to as tip and pre-tip), measuring 25–30 cm in length. The planting frame was 0.90 × 0.25 m for the rainy season and 0.90 × 0.23 m for the low-rainfall period, following INIVIT recommendations (INIVIT, 2007). Each experimental plot comprised five furrows, six meters in length, covering a total area of 27 m².

Preparation and inoculant application

The inoculant was produced at the National Institute of Agricultural Sciences, Cuba, following the protocol used by Espinosa-Cuéllar et al. (2023). The product contained 25 to 30 spores g⁻¹ and undetermined amounts of mycelium. Inoculation was performed by coating the lower third of the vegetative seeds with sufficient inoculant suspension (Ruíz Martínez et al., 2012). The suspension was prepared at a 0.125 kg of inoculant to 600 mL of water ratio. The seeds were shade-dried for two hours before planting. This application corresponded to 35 kg ha⁻¹ of inoculant.

Fertilizer application and field management

Fertilizers were applied 25–30 days after planting, in bands adjacent to the furrows, using urea (46–0–0), simple superphosphate (0–20–0), and potassium chloride (0–0–60) as carriers of nitrogen, phosphorus, and potassium, respectively. Irrigation during the low-rainfall period consisted of applications of 300 m³ ha⁻¹ every seven days up to 45 days after planting, and every ten days thereafter, suspended 15 days before harvest (INIVIT, 2007). In the rainy season, irrigation was applied using the same criteria when rainfall did not meet the required thresholds. Cultural practices were carried out according to the technical instructions for sweet potato cultivation (INIVIT, 2007).

Soil sampling and chemical determinations

For soil analysis at the beginning of each experimental cycle, two composite samples (0–20 cm depth) were taken per replication. Each experiment had 8 samples per year; this corresponded to a total of 96 samples overall. The methods used for the chemical determinations were: pH-H₂O, extraction in soil/water ratio of 1/5, and measured on pH-meter; organic matter by the Walkley-Black method; available P by extraction with solution of (NH₄)₂CO₃ 10 g L⁻¹, pH 9.0, soil/solution ratio of 1/10, blue color development with molybdate solution, and colorimetric measurement; and exchangeable cations were extracted with NH₄ Ac 1 M and pH 7, with a soil to solution ratio of 1:5 and were determined by flame photometry (Paneque Pérez et al., 2010).

Evaluated variables and response indicators

The evaluated variables and response indicators are listed below in an order that facilitates clarity and coherence in the presentation and does not necessarily reflect the chronological sequence of measurements.

Yield (t ha⁻¹) determination

Harvesting took place 120 days after planting. For yield estimation, the plants corresponding to the three central furrows were used in each plot, excluding the two border plants at the beginning and end of the furrows. Yield was expressed in t ha⁻¹ of harvested roots weighing more than 115 g. This threshold corresponds to the one commonly used for determining commercial yield in sweet potato production. Accordingly, throughout this document, the term 'yield' refers exclusively to this commercial category.

Frequency of mycorrhizal root colonization (%)

The sampling procedure was conducted in all experiments approximately 90 days after the sweet potato planting. Composite samples of fine roots were collected from six plants within each of the 960 subplots (six experiments, two yearly repetitions, two cultivars, two inoculants, five fertilizer levels, and four replicates). The samples were oven-dried from the collected roots, weighing 200 mg at 70 °C until a constant mass was achieved. Subsequently, the roots were stained following the protocol outlined by Phillips and Hayman (1970). The evaluation process was performed using a stereomicroscope in line with the method described by Giovannetti and Mosse (1980).

Mycorrhizae spores count (number in 50 g of soil)

The evaluations were conducted at the onset of the experiments, utilizing the initial soil sampling, and at the harvest stage. During the latter, composite rhizospheric soil samples were taken, comprising six subsamples (0-20 cm) from all 960 subplots. Spores were extracted in water by the wet-sieving method according to the modifications described by Torres-Arias et al. (2015). Spores were counted on Doncaster plates using a stereomicroscope and expressed as spores in 50 g of soil.

Macronutrient NPK concentrations in organs and plants (g kg⁻¹)

Six plants per plot were sampled and divided into leaves, stems, and tubers in each experiment at harvest. The total fresh mass of each organ with a precision of 0.01 g was determined. Samples of 200 g were taken, and dry mass was determined in an oven at 65 °C, after which the total dry mass (kg/plot) was estimated. Part of the dry matter was ground, and nitrogen, phosphorus, and potassium concentrations were determined for each organ in each plot. Determinations were made by wet digestion with H₂SO₄ 98 % + Se. Nitrogen was determined by visible spectrometry using Nessler's reagent, and phosphorus by color development with ammonium molybdate solution. Potassium was measured by flame photometry.

The concentration of macronutrients in the plants of each plot was estimated from the concentrations in the organs and the respective dry masses. Equation 1 enables the estimation of macronutrient concentrations, as illustrated by nitrogen concentration in the plot plants.

$$N = (Nl * Ml + Ns * Ms + Nr * Mr) / (Ml + Ms + Mr) \quad (1)$$

Where N represents nitrogen concentration (g kg^{-1}) in the plot plants, while Nl , Ns , and Nr correspond to nitrogen concentration (g kg^{-1}) in leaves, stems, and roots (tubers), respectively, and Ml , Ms , and Mr represent the dry mass (kg) of different organs in each plot. The estimation for phosphorus and potassium was done similarly with the respective concentrations of one or the other macronutrient.

Yield response (%)

In each of the experiments, the relative yield responses (%) to inoculation were determined by comparing the highest yield obtained in the inoculated fertilized treatment (AMFF1) with the yield of its non-inoculated counterpart (F1). Both treatments received the same dose of NPK fertilizer. Equation 2, originally proposed by Janos (2007) to define responsiveness under sterile conditions, was applied here to non-sterile soils without modification.

$$\text{Yield response (\%)} = [\text{Yield(AMFF1)} - \text{Yield(F1)}] * 100 / \text{Yield(F1)} \quad (2)$$

Yield responses (%) to sweet potato inoculation were identified as NYR, PYR, or KYR for nitrogen, phosphorus, or potassium experiments.

Concentration response (%)

Similarly, in each experiment, the response of the macroelement concentration studied to AMF inoculation was calculated using Equation 3, based on the macroelement concentration (M) in the plot plants (Equation 1) corresponding to the AMFF1 and F1 treatments:

$$\text{Concentration - response (\%)} = [M(\text{AMFF1}) - M(\text{F1})] * 100 / M(\text{F1}) \quad (3)$$

The concentration responses to AMF inoculation were represented as NCR, PCR, or KCR for nitrogen, phosphorus, or potassium.

Agronomic efficiency (AE) (kg kg^{-1})

The agronomic efficiency (AE) of fertilizer was determined for each macronutrient using the data from the two corresponding experiments. It was calculated for the two best treatments, with or without mycorrhizal inoculation, which achieved higher yields with lower fertilizer doses in each of the eight combinations (cultivars-planting time-annual repetition). This allowed a direct comparison of fertilizer AE with or without inoculation for each macronutrient. The AE of fertilizer (kg kg^{-1}) was estimated using Equation 4, as described by Hammond et al. (2009). This estimation was performed under fixed background levels of the other two macronutrients, as defined in the experimental setup.

$$AE = [\text{Yieldmax} (t \text{ ha}^{-1}) - \text{Yield0} (t \text{ ha}^{-1})] * 1000 / F (kg \text{ ha}^{-1}) \quad (4)$$

Yieldmax refers to the yield obtained with the best fertilizer dose, with or without inoculation, while Yield0 represents the yield of the treatment without fertilization or inoculation, which remained the same for AE calculations in both inoculated and non-inoculated treatments. F denotes the macroelement fertilizer doses used

in each treatment. These doses exclude the fixed background and only account for the quantities specific to the studied macronutrient (kg ha^{-1} of N, P_2O_5 , or K_2O). Depending on the macronutrient assessed, AE was designated as NAE, PAE, or KAE.

Data analysis

For statistical analysis, an analysis of variance (ANOVA) was conducted on experimental data. Differences among means were assessed using Duncan's test ($p \leq 0.05$) or 95 % confidence intervals. In the tables and figures showing information on selected treatments, mean comparisons were calculated based on the $\text{SE}\bar{X}$ obtained with all treatments. Additionally, linear or polynomial regression and Pearson correlation analyses were conducted to establish better relationships between variable pairs. The significance of regression and correlation coefficients was determined using t-student tests. Data processing was carried out using the statistical package SPSS version 21.0.

Results

Yields

In the six experiments, a significant yield response to mineral fertilization was found in the non-inoculated treatments for both cultivars in each repetition and during the two growth periods. The highest yields obtained in each case corresponded to the doses of 90 kg ha^{-1} of N, 75 kg ha^{-1} of P_2O_5 , and 150 kg ha^{-1} of K_2O for the experiments with doses of nitrogen, phosphorus, and potassium fertilizers, respectively (Table 2). Higher doses in each experiment did not increase yield. Detailed information on the results obtained in each experiment is presented in Supplementary Tables S1, S2, S3, S4, S5, and S6.

In the inoculated treatments, a significant response to apply macronutrients was also found. However, in these cases, the maximum yields were always seen with lower fertilizer doses, corresponding to 60 , 50 , and 75 kg ha^{-1} of N, P_2O_5 , and K_2O , respectively. Higher doses in each experiment did not increase yield. The maximum yields obtained for the inoculated cultivars were higher ($p \leq 0.05$) than those found in the non-inoculated homologous treatments (same fertilizer doses) and numerically higher (7 to 10 %), although no significant differences were observed compared with the maximum yields obtained with the treatments that only received mineral fertilizer, which received higher fertilizer doses.

The yields of the cultivars in each treatment were similar ($p \leq 0.05$) to each other. Moreover, the maximum experimental yields obtained with the inoculated cultivars in the rainy period (32.4 to 36.96 t ha^{-1}) were higher ($p \leq 0.05$) than those found in the low-rainy period (29.12 to 32.25 t ha^{-1}). In these soils, the least deficient macronutrient was potassium since the treatments without potassium fertilizer guaranteed about 60 % of the maximum experimental yield, while the treatments without nitrogen or phosphorus fertilizer guaranteed about 45 %, with slightly higher percentages in the rainy period.

The maximum yields reached by the inoculated cultivars in each experiment also showed a high and significant relation ($R^2 = 91.6 \%$) with the maximum yields reached in the absence of inoculation (Figure 1). Although the cultivars responded positively to inoculation, guaranteeing high yields with lower doses of fertilizers (Table 2) and achieving yields slightly higher than the maximum yields reached in the absence of inoculation, the behavior presented by inoculated cultivars was not independent of the maximum yields reached by the cultivars in the non-inoculated treatments. The greater the experimental yields in the absence of inoculation, the higher the maximum yields of the inoculated cultivars were, and vice versa.

Table 2. Summary of the yields (t ha⁻¹) obtained in selected treatments of the six fertilization experiments in the presence or absence of INCAM-11 inoculation. Average data from the two repetitions. Santo Domingo, Cuba. 2014-2016.

Cuadro 2. Resumen de los rendimientos (t ha⁻¹) obtenidos en tratamientos seleccionados de los seis experimentos de fertilización en presencia o ausencia de la inoculación con INCAM-11. Datos promedio de las dos repeticiones. Santo Domingo, Cuba. 2014-2016.

Selected treatments	Rainy period		Low-rainy period	
	‘INIVIT B-2-2005’	‘CEMSA 78-354’	‘INIVIT B-2-2005’	‘CEMSA 78-354’
0 kg ha ⁻¹ N	15.1 ± 1.76	15.1 ± 1.76	12.7 ± 1.47	12.5 ± 1.47
60 kg ha ⁻¹ N	26.5 ± 1.76	26.9 ± 1.76	25.1 ± 1.47	25.0 ± 1.47
60 kg ha ⁻¹ N + AMF	34.8 ± 1.76	34.5 ± 1.76	31.3 ± 1.47	31.1 ± 1.47
90 kg ha ⁻¹ N	31.8 ± 1.76	31.9 ± 1.76	28.9 ± 1.47	28.9 ± 1.47
0 kg ha ⁻¹ P ₂ O ₅	16.6 ± 1.47	15.6 ± 1.47	13.6 ± 1.27	12.7 ± 1.27
50 kg ha ⁻¹ P ₂ O ₅	28.2 ± 1.47	27.6 ± 1.47	25.2 ± 1.27	24.8 ± 1.27
50 kg ha ⁻¹ P ₂ O ₅ + AMF	34.1 ± 1.47	33.9 ± 1.47	29.6 ± 1.27	29.1 ± 1.27
75 kg ha ⁻¹ P ₂ O ₅	31.9 ± 1.47	31.9 ± 1.47	27.9 ± 1.27	27.6 ± 1.27
0 kg ha ⁻¹ K ₂ O	22.1 ± 1.57	21.6 ± 1.57	17.5 ± 1.47	17.9 ± 1.47
75 kg ha ⁻¹ K ₂ O	27.7 ± 1.57	27.5 ± 1.57	25.5 ± 1.47	24.6 ± 1.47
75 kg ha ⁻¹ K ₂ O + AMF	35.3 ± 1.57	35.1 ± 1.57	31.8 ± 1.47	31.3 ± 1.47
150 kg ha ⁻¹ K ₂ O	32.3 ± 1.57	32.5 ± 1.57	29.5 ± 1.47	28.5 ± 1.47

All yield values are expressed in t ha⁻¹. **AMF:** Inoculation with *R. irregulare* / INCAM-11. In each experiment, fixed amounts of the other two primary macroelements were applied at rates of 90, 75 or 150 kg ha⁻¹ of N, P₂O₅ and K₂O, respectively. ± 95 % confidence interval. / Todos los valores de rendimiento están expresados en t ha⁻¹. **AMF:** Inoculación con *R. irregulare* / INCAM-11. En cada experimento se aplicaron fondos fijos de los otros dos macroelementos primarios en las dosis de 90, 75 y 150 kg ha⁻¹ de N, P₂O₅ y K₂O, respectivamente. ± intervalo de confianza al 95 %.

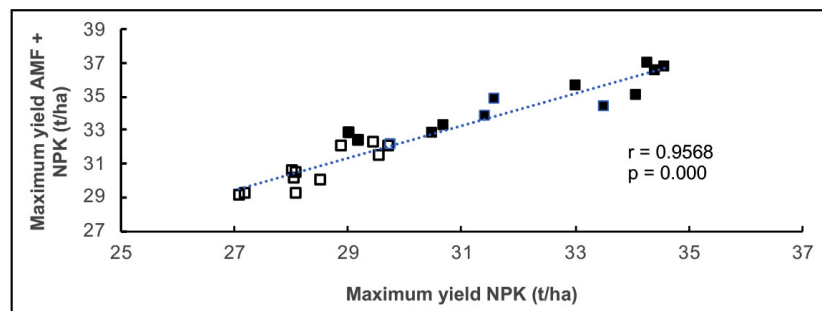


Figure 1. Relationship between maximum experimental yields of cultivars with and without AMF inoculation. Santo Domingo, Cuba. 2014-2016.

Data from the six experiments. Black filled: rainy period; unfilled: low-rainy period. N = 24.

Figura 1. Relación entre los rendimientos máximos experimentales de los cultivares con y sin inoculación micorrízica. Santo Domingo, Cuba. 2014-2016.

Datos de los seis experimentos. Relleno en negro: periodo lluvioso; sin relleno: periodo poco lluvioso. N = 24.

It should be noted that the NPK fertilizer doses received by the treatments corresponding to the maximum experimental yields in the absence of inoculation were the same for all six experiments and correspond to 90, 75, and 150 kg ha⁻¹ of N, P₂O, and K₂O, respectively (N90P75K150). Thus, the groupings of these yields reflect first the differences between the two growth periods (12 values each) and, within these, between the two annual repetitions (6 values each). The differences between the two-year repetitions were more marked in the rainy period, possibly related to the more significant differences found in the climatic conditions between these in comparison with differences found in the climatic conditions in the low-rainy period.

Frequency of colonization and spores

In the inoculated treatments and the fertilization response zone of each experiment corresponding to doses of 0 to 60 kg ha⁻¹ of N, 0 to 50 kg ha⁻¹ of P₂O₅, and 0 to 75 kg ha⁻¹ of K₂O, respectively, a positive and significant correlation ($p = 0.000$) was found between colonization frequency and yield (Figure 2) with a high coefficient. This correlation integrates the information from the different experiments for both cultivars and growth periods, and establishes a strong relationship between these two variables. In each experiment, the values reached in each treatment (same dose, inoculation, and cultivar) and in each repetition were higher in the rainy period than in the low-rainy period, while cultivars showed similar values.

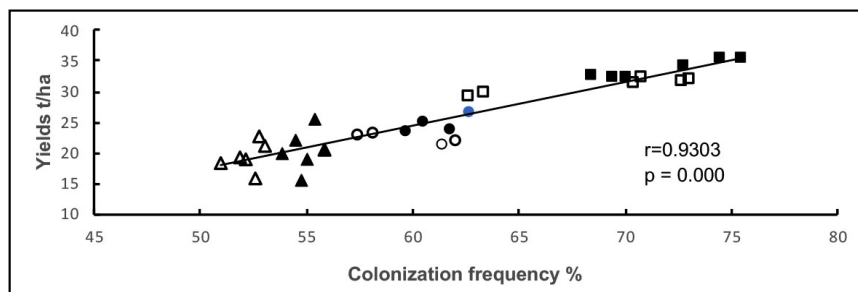


Figure 2. Correlation between the frequency of mycorrhizal colonization and yield of cultivars inoculated with INCAM-11 at selected fertilizer levels in both growth periods. Santo Domingo, Cuba. 2014-2016.

Fertilizer levels, N experiments: N0, N30 and N60; P experiments: P0, P25 and P50, and K experiments: K0 and K75. Each average value of the two cultivars. Legend: □ treatments with N60, P50 or K75; ○ treatments with N30 or P30; △ treatments with N0, P0 or K0. Black filled: rainy period; unfilled: low-rainy period. N = 32.

Figura 2. Correlación entre la frecuencia de colonización micorrízica y el rendimiento de los cultivares inoculados con INCAM-11 en niveles de fertilizantes seleccionados en ambos periodos de crecimiento. Santo Domingo, Cuba. 2014-2016.

Niveles de fertilizantes, experimentos de N: N0, N30 y N60; experimentos de P: P0, P25 y P50, y experimentos de K: K0 y K75. Cada valor promedio de los dos cultivares. Leyenda: □ tratamientos con N60, P50 o K75; ○ tratamientos con N30 o P30; △ tratamientos con N0, P0 o K0. Relleno en negro: periodo lluvioso; sin relleno: periodo poco lluvioso. N = 32.

The treatments that received the optimal fertilizer doses for the inoculated cultivars yielded the highest yields (Table 2) and exhibited the highest colonization frequencies, with values ranging from 64.8 % to 76.3 %. The N0, P0, and K0 treatments showed the lowest colonization frequencies (51.1 % to 57.6 %) and were associated with the lowest yields (Table 2). However, the K0 treatments showed higher values of both variables than those corresponding to N0 or P0. The treatments that received intermediate doses of N and P showed intermediate values of both variables.

In the inoculated cultivars, mycorrhizal spores were closely associated with colonization frequencies. In the fertilization response zone of each experiment (Figure 3), the relation was high ($R^2 = 75.7\%$) and significant ($p = 0.000$). Values for both indicators increased with dose, with the highest spore values (470 to 625 spores in 50 g) associated with the treatments receiving the optimum fertilizer doses for mycorrhization in each experiment (N60, P50, and K75). Also, the values corresponding to the rainy period were higher for each dose. In each treatment, the cultivars showed similar values. The relation between these variables remained significant ($p = 0.04$) when information on fertilization doses that decreased the response to inoculation was included, although the regression coefficient was lower ($r = 0.644$).

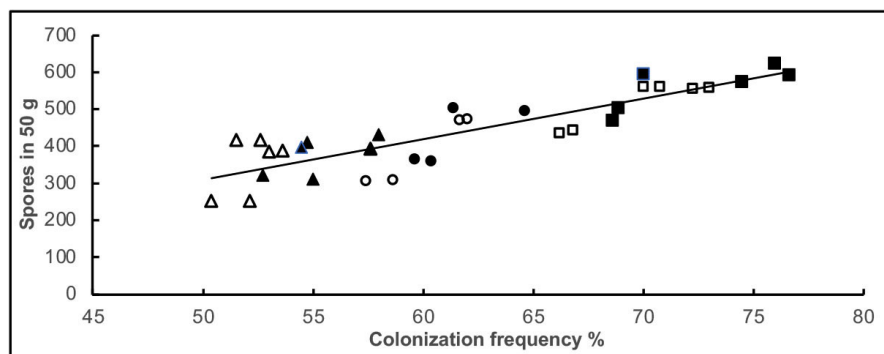


Figure 3. Relationship between colonization frequencies and spores of cultivars inoculated with INCAM-11 at selected fertilizer levels in both growth periods. Santo Domingo, Cuba. 2014-2016.

Fertilizer levels, N experiments: N0, N30 and N60; P experiments: P0, P25, and P50, and K experiments: K0 and K75. Each average value of the two cultivars. Legend: □ treatments with N60, P50 or K75; ○ treatments with N30 or P30; △ treatments with N0, P0 or K0. Black filled: rainy period; unfilled: low-rainy period. N = 32.

Figura 3. Correlación entre frecuencias de colonización y esporas de los cultivares inoculados con INCAM-11 en niveles de fertilizantes seleccionados en ambos periodos de crecimiento. Santo Domingo, Cuba. 2014-2016.

Niveles de fertilizantes, experimentos de N: N0, N30 y N60; experimentos de P: P0, P25 y P50, y experimentos de K: K0 y K75. Cada valor promedio de los dos cultivares. Leyenda: □ tratamientos con N60, P50 o K75; ○ tratamientos con N30 o P30; △ tratamientos con N0, P0 o K0. Relleno en negro: periodo lluvioso; sin relleno: periodo poco lluvioso. N = 32.

In all experiments, the colonization frequency and spores values in the non-inoculated treatments were lower ($p \leq 0.05$) than those in the inoculated treatments. They were similar among the different experiments, cultivars, and growth periods. In the case of colonization frequency, values ranged between 8.5 and 12.5 %, with no significant effect of fertilization doses. Spores ranged from 51 to 95 in 50 g, with the highest values ($p \leq 0.05$) observed at the intermediate fertilizer doses.

N, P, and K macronutrient concentrations

In each experiment, the fertilizer-inoculation combinations that maximized both yield and mycorrhizal performance indicators (N60AMF, P50AMF, and K75AMF) significantly increased ($p \leq 0.05$) the concentrations of nitrogen, phosphorus, and potassium, respectively, compared with their non-inoculated counterparts and with the best-performing treatments based solely on mineral fertilization, consistently across both cultivars (Figure 4). These increases were found in both rainy and low-rainy periods, except for K concentrations in cultivar C-78354, which in the low-rainy period were similar to those obtained with the optimum fertilization treatment. For the

inoculated treatments in the different experiments, the cultivars presented similar values ($p \leq 0.05$) of the NPK macroelements, except for the nitrogen concentration in the rainy period.

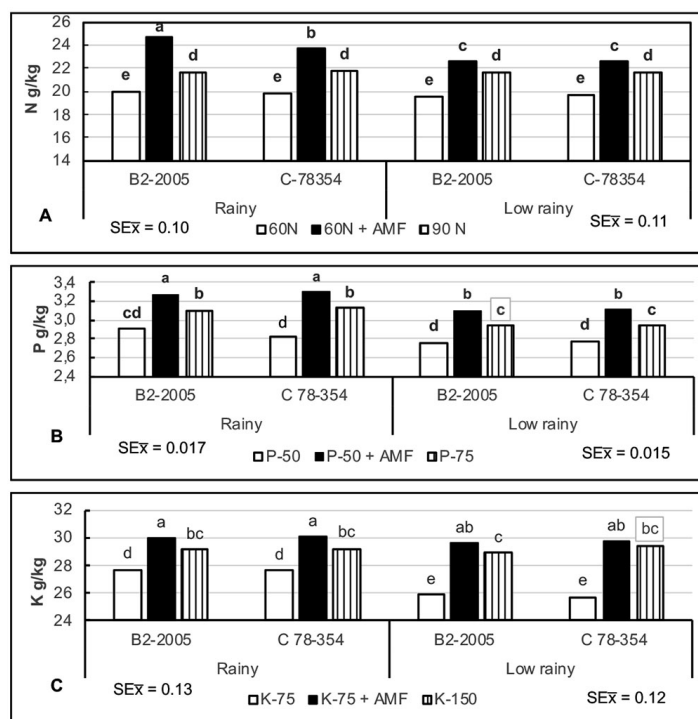


Figure 4. Concentrations of macroelements: A) nitrogen experiments, B) phosphorus experiments, and C) potassium experiments for both cultivars and growth periods in selected treatments. Santo Domingo, Cuba. 2014-2016.

Each average value of the two repetitions. The means were compared based on the 95 % confidence intervals calculated for each growing period. Different letters indicate significant differences ($p \leq 0.05$) between treatments.

Figura 4. Concentraciones de macroelementos: A) experimentos de nitrógeno, B) experimentos de fósforo, y C) experimentos de potasio para ambos cultivares y periodos de crecimiento en tratamientos seleccionados. Santo Domingo, Cuba. 2014-2016.

Cada valor promedio de dos repeticiones. La comparación de medias fue realizada con base en los intervalos de confianza al 95 % calculados para cada periodo de crecimiento. Letras diferentes indican diferencias significativas ($p \leq 0,05$) entre tratamientos.

For the inoculated treatments, nitrogen and phosphorus concentrations in the cultivars were higher ($p \leq 0.05$) in the rainy period (24 g kg^{-1} and 3.27 g kg^{-1}) than in the low-rainy period (22.3 g kg^{-1} and 3.10 g kg^{-1}). In the case of potassium, there were no differences between the concentrations of the inoculated cultivars in both periods, and they ranged between 29.6 and 30.05 g kg^{-1} . The concentrations of these macroelements were ordered from highest to lowest as follows: $K > N \gg P$.

Yield and concentration responses to inoculation

Each experiment positively responded to inoculation on yields (NYR, PYR, or KYR) and concentrations (NCR, PCR, or KCR), respectively. Yield responses were higher in the rainy period, in which NYR and KYR were

similar (30 %) and higher than PYR (22 %). In the low-rainfall period, KYR was higher (26 %) than the others (16.5 %). NCR was higher in the rainy period (22 %) vs 14.5 % in the low-rainfall period, and PCR was similar in both periods (14 %). KCR was lower in the rainy period (8.5 %) vs 15 % in the low-rainfall period. The cultivars showed similar values. N and P responses correlated significantly ($p \leq 0.05$), $r = 0.796$ and $r = 0.652$, respectively, but not for potassium responses.

Agronomic efficiency (AE) of fertilizers

Inoculation also increased the AE of the three fertilizers (Figure 5) when comparing the AE obtained for the best treatments with or without inoculation in the two experiments for each macroelement. Inoculation increases in AE for nitrogen and phosphorus fertilizers were similar, with values between 60 % and 80 %. The increases in potassium fertilizer AE were higher, between 130 % and 180 %. NAE and PAE values for the inoculated cultivars were similar and ranged between 210 and 440 kg kg⁻¹, while KAE values were lower and ranged between 118 and 250 kg kg⁻¹.

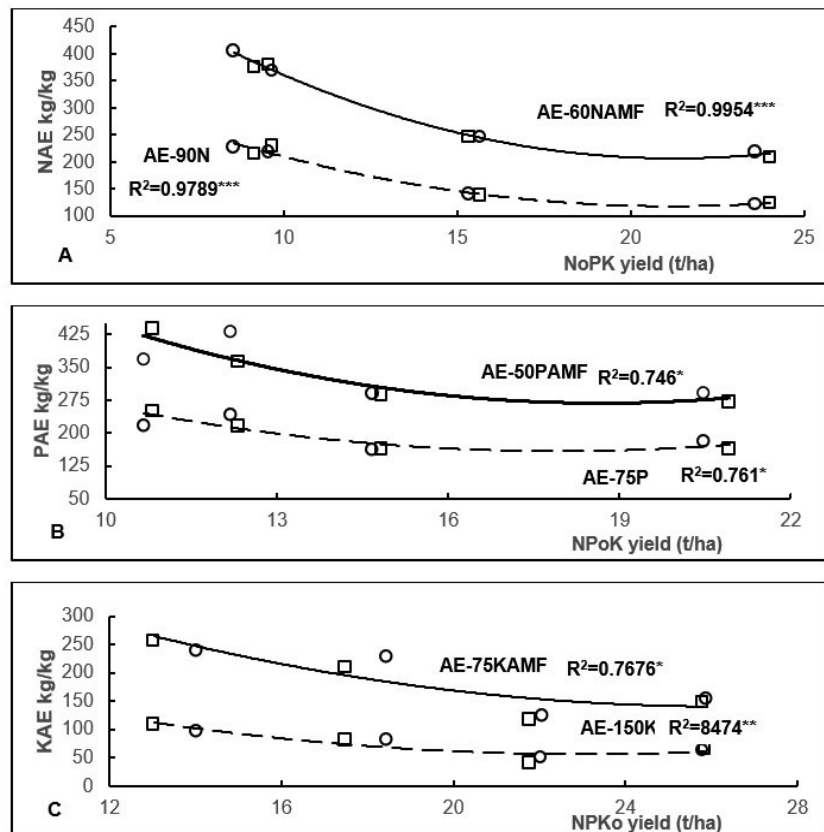


Figure 5. Relationships between the agronomic efficiency (AE) of fertilizers for the best inoculated and non-inoculated treatments and the yield of the control treatment for both cultivars and growth periods. **A)** Nitrogen experiments, **B)** phosphorus experiments, and **C)** potassium experiments. Santo Domingo, Cuba. 2014-2016.

Solid line: inoculated treatments; dashed line: non-inoculated treatments. □ 'INIVIT B2-2005'; ○ 'CEMSA 78-354'.

Figura 5. Relaciones entre la eficiencia agronómica (EA) de los fertilizantes para los mejores tratamientos inoculados y no inoculados y el rendimiento del tratamiento testigo para ambos cultivares y periodos de crecimiento. **A)** Experimentos de nitrógeno, **B)** experimentos de fósforo, y **C)** experimentos de potasio. Santo Domingo, Cuba. 2014-2016.

Línea continua: tratamientos inoculados; línea discontinua: tratamientos no inoculados. □ 'INIVIT B2-2005'; ○ 'CEMSA78-354'.

For each macronutrient, the AE was inversely and significantly related to the yield of the control treatment in each experiment, so that as the control yield increased, for example, in the rainy period, the AE decreased, and vice versa. The coefficient of determination was high for each macroelement, and great values were achieved in the nitrogen experiments. The cultivars always showed similar AE values in the different experimental conditions evaluated.

Discussion

The reduction through inoculation of the necessary quantities of each of the three macroelements to ensure high yields ($t\ ha^{-1}$), which were never lower than the maximum yields obtained with higher fertilizer doses, together with the increases observed in the concentrations of nitrogen, phosphorus, and potassium, as well as in both types of response and agronomic efficiency (AE), evidenced direct effects of mycorrhizal inoculation on the nutrition of each macroelement. In the different experiments, only one macroelement was studied under limiting conditions, and the others in sufficient quantities. Thus, the positive effects obtained in each experiment can be associated with improved nutrition of the macronutrient studied.

The results meet the criteria established by Corrêa et al. (2015) and are enriched by including positive responses in yield, mycorrhizal functioning, and increases in fertilization efficiency of each studied macroelement. The latter indicators are necessary to evaluate the effectiveness of inoculation. Other studies conducted in the country with similar experimental schemes but in different crops and soil types have also found positive effects on yields and NPK macronutrient concentrations, with lower inputs of each macronutrient in cassava and *Urochloa* species (Camejo Hernández, 2016; González et al., 2015). These authors also consider these results to be direct effects of mycorrhization on the nutrition of these elements.

The optimum doses of each macronutrient were the same in both planting seasons, even though yields and nutritional requirements were significantly higher in the rainy season. This can be explained by the higher contribution of soil nutrients to plant nutrition in the rainy season due to the higher intensity of microbiological and chemical processes when temperatures increase and soils are rewetted (Ruan et al., 2023), and by the greater root absorption capacity associated with increased crop growth, exemplified by higher yields of unfertilized treatments. However, in the low-rainy season, with lower temperatures, although crops grew and produced less, soil nutrient availability and plant nutrient uptake capacity were also lower, and supplementary doses remained the same.

Increased NPK concentrations may explain yield increases in inoculated cultivars compared to their non-inoculated counterparts and the slight increases obtained when maximum yields with and without inoculation were compared. However, there may be improvements in the nutrition of other essential elements, such as micronutrients, which may also be constraining experimental yields and whose uptake may be increased by mycorrhizae (Moreno Jiménez et al., 2024). It should be noted that inoculation as a component of nutrient delivery systems does not increase the crop's yield potential but reaches it or reduces the difference with experimental yields. The latter explains the high coefficient of determination between the maximum yields with optimal fertilization doses without inoculation and the maximum yields obtained in the inoculated cultivars.

The high correlation between colonization frequency and the yields of the inoculated cultivars in the fertilization response zone, integrating the results of all experiments, expresses the relationship between crop requirements, mycorrhizal performance, and nutrient supply. An optimal nutrient supply is necessary to achieve satisfactory mycorrhizal performance; lower or higher nutrient supplies limit or diminish mycorrhization, even in the presence of effective inoculum, as also pointed out by Rivera et al. (2007). However, since these studies did not use different experimental conditions that significantly varied crop productivity and nutrient requirements, they failed to demonstrate the importance of these variations for mycorrhizal functioning and only related mycorrhizal performance to nutrient supply at a single expected yield level.

Including two planting dates with different maximum yields shows that, in the presence of this optimal nutrient supply, the higher yields reached by the inoculated cultivars, e.g., in the rainy season, demanded higher performance from the mycorrhizae. In this case, the higher colonization frequency was a consequence of the increased crop demand, and vice versa. A similar behavior, when working with 17 inoculated sweet potato cultivars at two planting times, was reported by Espinosa-Cuéllar et al. (2023). This is consistent with the reciprocal rewards/reciprocity approach, in which partners deliver resources to each other in response to resources they receive (Bunn et al., 2024), e.g., higher fungal structures (receiving more C) and plants achieving higher yields (receiving more nutrients).

The high relationship between colonization frequencies and spores demonstrated the potential of spores as an indicator of mycorrhizal performance. Although spores are part of the survival mechanisms of fungi, their production in each growing season is directly related to mycorrhizal performance (Willis et al., 2013). Several authors have also found that spore values are directly and closely associated with colonization frequency in different types of experiments with inoculated crops (Espinosa-Cuéllar et al., 2023; González Cañizares, 2014; Simo González et al., 2020). Other authors have recommended spores as indicators of mycorrhizal performance (Koch et al., 2017; Zangaro & Rondina, 2016), while González Cañizares (2014) recommended them as a criterion for reinoculation in forage areas planted with *Urochloa* species.

Although sweet potato nutrient requirements are ranked from highest to lowest ($K > N \gg P$), the relatively high levels of exchangeable potassium in the soil made it the least limiting element under these conditions. Nevertheless, this did not prevent a clear response to mycorrhizal inoculation in terms of potassium nutrition and yield. The relatively high availability of K in the soil may explain the lower response in potassium concentration (KCR) during the rainy period compared to the response observed in the less rainy period, and these differences likely account for the absence of a relationship between KYR and KCR when results from both periods are integrated.

The AE was a suitable indicator to reflect the effects of the inoculation on reducing the quantities of macronutrients supplied to achieve maximum yields. The highest AE values were found in the low-rainfall period, which can be explained by the lower participation of soil nutrients in plant nutrition in this period. KAE values were lower, possibly due to the higher availability of soil potassium and the higher doses of potassium applied to achieve maximum yields compared to nitrogen and phosphorus doses. Although results using these indicators are not abundant for AMF-inoculated crops, Camejo Hernández (2016) and González Cañizares (2014) found similar results working with the fertilizer utilization coefficient and the productivity factor (Hammond et al., 2009).

The successful integration of results from six experiments suggests that the individual supply of nitrogen, phosphorus, and potassium modulates mycorrhizal functioning, as reflected in colonization frequency. This, in turn, directly influences macroelement concentrations, agronomic efficiency, and yields. The evidence supports the direct nutritional effect of mycorrhization and corroborates its impact on potassium uptake (Fernandez Suárez, 2012), confirming its inclusion among elements responsive to inoculation under limiting conditions. It also reinforces the view of mycorrhizae as a root extensor system (Lanfranco et al., 2018), facilitating nutrient uptake according to plant demand and soil availability (Rivera Espinosa et al., 2023).

Several authors working with similar experimental schemes in other crops have recommended fertilizer doses for inoculated crops based on selecting the most effective doses of the macronutrient studied in each experiment (Camejo Hernández, 2016; González et al., 2015). From this point of view, the recommendations for these sweet potato cultivars would be 60, 50, and 75 kg ha⁻¹ of N, P₂O₅, and K₂O, respectively. However, as each of the macronutrient doses was obtained independently and in the presence of a single limiting element, it would be advisable to verify the validity of this approach in the short term, as under this recommendation all three macronutrients would be in limiting conditions.

The cultivars 'INIVIT B-2-2005' and 'CEMSA 78-354' showed similarly high yields, as reported by Espinosa-Cuéllar et al. (2023). Although the cultivars also showed analogous yields when inoculated and required equal

fertilizer doses to obtain the highest mycorrhizal performance, this fertilizer recommendation does not necessarily apply to other less productive cultivars, which may be more suitable under different conditions or production systems. For this reason, it is recommended to carry out similar experiments with at least two commercial cultivars with contrasting yields (25 and 35 t ha⁻¹) to relate macronutrient doses with different cultivar productivities, as well as to verify the direct effect of inoculation on the nutrition of these macronutrients in other cultivars.

Conclusions

Inoculation of sweet potato cultivars with *Rhizoglyphus irregularis* / INCAM-11 acts directly and positively on mycorrhizal performance, yield, nutrition, and fertilization efficiency of each NPK macroelement. Regardless of the higher yields in the rainy period, the most effective doses of each macroelement for the inoculated cultivars were the same in both periods. These doses were 60, 50, and 75 kg ha⁻¹ of N, P₂O₅, and K₂O for ‘INIVIT B-2-2005’ and ‘CEMSA 78-354’. In the presence of an effective inoculant, the needs or requirements of the cultivar determine the intensity of mycorrhizal functioning, which requires an adequate nutrient supply to express itself. This adequate nutrient supply was lower than that required by the non-inoculated cultivars. Under- or over-supplementation limits mycorrhizal performance and the effectiveness of inoculation.

Interests conflict

The authors declare no conflicts of interest.

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