



Revisiting Legume Response to Inoculation with Arbuscular Mycorrhizal Fungi and/or Rhizobia: What a Meta-analysis Tells Us?: A Review

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ABSTRACT

Plant co-inoculation with different beneficial microbes, such as rhizobia (RH) and arbuscular mycorrhizal fungi (AMF), is a promising technology for improving crop yield and quality and contributing to sustainable agriculture. This is why the use of mixed microbial inoculants, rather than single inoculants, has increased, with remarkable success in some parts of the world. However, we do not have an overview of the effects of dual inoculation of AMF + RH on plant growth. Sometimes, experimental results show synergistic, additive, negative or no effect on plant growth even reduced growth. In this context, the present study aimed to quantify through a meta-analysis the effects of RH+AMF co-inoculation on nutrient uptake and growth of legume yield (crop, weeds and tree) and to discuss the key mechanisms that underpin enhanced plant growth promotion. A literature search was conducted across Scopus, Web of Science and Google Scholar, focusing on studies examining RH and AMF co-inoculation's impact on nutrient uptake and biomass. The mean effect sizes were calculated using Cohen's *d* at 95% confidence intervals (CIs). A total of 59 articles was analyzed. Our results show that inoculation and particularly co-inoculation significantly enhanced plant nutrient uptake, root infection and plant biomass yield (N and K uptake, $p < 0.001$; shoot and root biomass, $p < 0.0001$). Similarly, dual inoculation effects were significant at 95% CIs. This analysis provides a clearer understanding of the co-inoculation process, highlighting its benefits for leguminous plants and suggesting potential solutions for sustainable agriculture amidst climate change.

Key words: Arbuscular mycorrhizal fungi, Co-inoculation, Legumes, Rhizobia.

Legumes play pivotal roles due to their multi-functional characteristics and especially their role in cropping systems. The Leguminosae family, with 800 genera and 20,000 species, includes weeds, trees and crops which are used for human consumption, animal feed and soil fertility improvement in agricultural and agroforestry systems (Yanni *et al.*, 2024). In addition, legumes provide sustainable options for delivering multiple benefits in cropping systems. In natural ecosystems, they are associated with multiple symbionts concurrently, including rhizobia bacteria and arbuscular mycorrhizal fungi (AMF+RH). Rhizobia and AMF colonize the roots of legumes and allow the latter to fix atmospheric nitrogen and mobilize phosphorus respectively (Soumare *et al.*, 2020, 2021). Hence, the success of legumes can largely be attributed to their ability to form arbuscular mycorrhizal and nitrogen-fixing symbioses (Balachandar *et al.*, 2007; Shi *et al.*, 2017). Farmers exploit this relationship through crop rotation or agroforestry (Charakas and Khokhani, 2024). According to Farquharson *et al.* (2012), about 40 million tons of nitrogen are fixed annually by 185 million hectares of crop legumes and 150 million hectares of pasture legumes around the world. In addition, the leguminous plants are highly dependent on mycorrhizal fungi that can resolve the problem of phosphorus limitation (Kumari *et al.*, 2021). These two important groups of plant root symbionts are abundantly present in the rhizosphere of leguminous plants

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even if they are not always effective. Numerous publications have reported that co-inoculation of legumes with selected AMF and rhizobial strains resulted in greater benefits for the plants and symbionts which can influence the dynamics of both host and symbiont populations (Mugabo *et al.*, 2024; Qin *et al.*, 2022). Rhizobia provide additional nitrogen to support efficient colonization rates of AMF while, AMF

improve rhizobial symbiosis efficiency by increasing phosphorus uptake (Gorgia and Tsikou, 2025). This translates into an increase in legume nodulation when colonized by AM fungi (He *et al.*, 2024). Furthermore, the dual inoculation can have a synergistic effect on the uptake of nutrients, soil aggregate formation and stabilization (Mpongwana *et al.*, 2024). Thus, understanding the synergistic interactions in legume-AMF-rhizobium systems through a holistic view is necessary in order to change our agronomic practices. Nowadays, efforts are being made to promote the technology in agricultural practice under nutrient-limiting conditions and other adverse climatic conditions, such as drought, soil salinity and waterlogging. Through their functions, AMF and RH symbionts influence the belowground traits of plants and regulate plant-plant interactions (Tederloo *et al.*, 2020). Although there are many studies on the AM and N-fixing symbioses, the co-inoculation with AMF and RH is not yet well adopted on a large scale. Some results report positive effects, others negative or neutral effects and there is a lack of quantitative estimation (Ossler *et al.*, 2015; Gorgia and Tsikou, 2025). With this vast amount of information in published journals, it is difficult to keep up to date without spending many hours searching and reading articles. The aim of this meta-analysis is to i) provide an overview of the effects of co-inoculation with RH and AMF on growth, nutrient content and root colonization of legumes, ii) to summarize the latest evidence and iii) to discuss the key mechanisms that underpin these effects.

Data collection

Data used in the present study were collected in 2025 from published research articles from Scopus (<https://www.scopus.com/home.uri>, Netherland), Web of Science (<https://mjl.clarivate.com/home>, Thomas Reuters, Canada) and Google Scholar (<https://scholar.google.com>, United States) databases. The research was conducted at the Laboratory of Agroforestry and Ecology, Assane Seck University of Ziguinchor, Senegal. The following keywords were used in the literature search: “Co-inoculation RH-CMA”, “dual inoculation AMF-RH”, “mixed inoculation AMF-RH”, “Tripartite Rhizobium-legume-AM symbiosis” or “legumes symbiosis”. The publication year and publication language were not considered as exclusion criteria during the literature search. Our criteria for inclusion were that the study (1) included a legume plant, (2) co-inoculation with RH-CMA and (3) experimental data. Whereas, the studies where co-inoculation or single inoculation was combined with additives such as fertilizers or fungicides were excluded. The search strategy and data collection were designed according to the PRISMA reporting guidelines (Liberati *et al.*, 2009). From the selected articles, the assessment of microbial inoculation effect was focused on the following most common studied plant traits: root infection (mycorrhization and nodulation), shoot, root and/or total biomass and nutrition (P, K and N).

Statistical analysis

Data was analyzed by one-way analysis of variance and the significant difference between treatments was compared with Tukey's HSD at the 5% level. All analyses were conducted using R (version 4.2.1) and the graphs were generated using the “ggplot2” package (Hadley, 2016). The effect size was calculated using the Metafor package (Viechtbauer 2010). They were calculated using Cohen's *d* (Cohen 1992). The effect of the inoculation treatment on the studied variable (roots infection, shoot, root and/or total biomass and nutrition) was considered significant when the 95% CIs of each group did not overlap.

An effect size summarizes the effect of intervention, manipulation or observation of some phenomenon being studied.

Literature survey

Our search strategy yielded 102 articles, of which 55 (accounting for 54%) were obtained from Google Scholar, 24 (23.5%) from Web of Science (WoS) and 23 (22.5%) from Science Direct (Fig 1). After reviewing titles, abstracts and full texts' relevance to the subject, applying eligibility criteria and deduplication, only 59 articles were selected for further analysis. These articles were published in 45 different journals. All collected articles were published between 1991 and 2024 with a record publication in 2021.

Bibliometric analysis

The meta-analysis included 59 articles from 26 countries around the world (data not shown). More than 80% of publications have an SJR indicator greater than zero and were indexed in Scopus and/or WoS (Fig 2A and 2B). Data presented in these selected publications were obtained from greenhouse (61%), field (30%) and both greenhouse and field studies (9%, Fig 2C). Overall, 43 legume species including tree, herbaceous crop and herbaceous weeds were recorded from these 59 articles. The legume species were dominated by trees, followed by herbaceous crops and weeds accounting for 45.23%, 30.95% and 23.81% respectively (Fig 2D). *Acacia* is the dominant genus for trees, *Vigna* for crops and *Cytisus* for weeds.

Inoculation effect on biomass, root infection and nutrient contents of the plant

The results show that inoculation with AMF and/or RH significantly increased legume shoots and roots biomass ($P < 0.0001$), nodule number ($p < 0.0001$), AMF colonization rate ($p < 0.001$) and plant N, P and K content ($p < 0.001$) compared to uninoculated control (Fig 3). Additionally, co-inoculation with AMF + RH resulted in higher mycorrhizal colonization and nodulation compared to single inoculation (Fig 3). The “RH+CMA” treatment was generally followed by the “CMA” treatment for most of the variables assessed. The hierarchical analysis grouped them (Fig 4, cluster 1). This cluster contrasts with cluster 2 and cluster 3, which showed low values for all variables (Fig 4). Furthermore,

the effect size statistics confirmed the statistical significance of these findings for all attributes evaluated. The effect size distribution of roots and shoots biomass (95% CIs, $n = 25$), AMF colonization (95% CIs, $n = 13$), nodule number (95% CIs, $n = 27$), N and K (95% CIs, $n = 23$ and 09 respectively) showed clear

differences (Fig 5). For these variables, the strength of effects was overall higher for RH+AMF treatments compared to AMF or RH treatment alone. Positive effects, without statistically significant differences, were also noted between treatments for total biomass and P content (Fig 5).

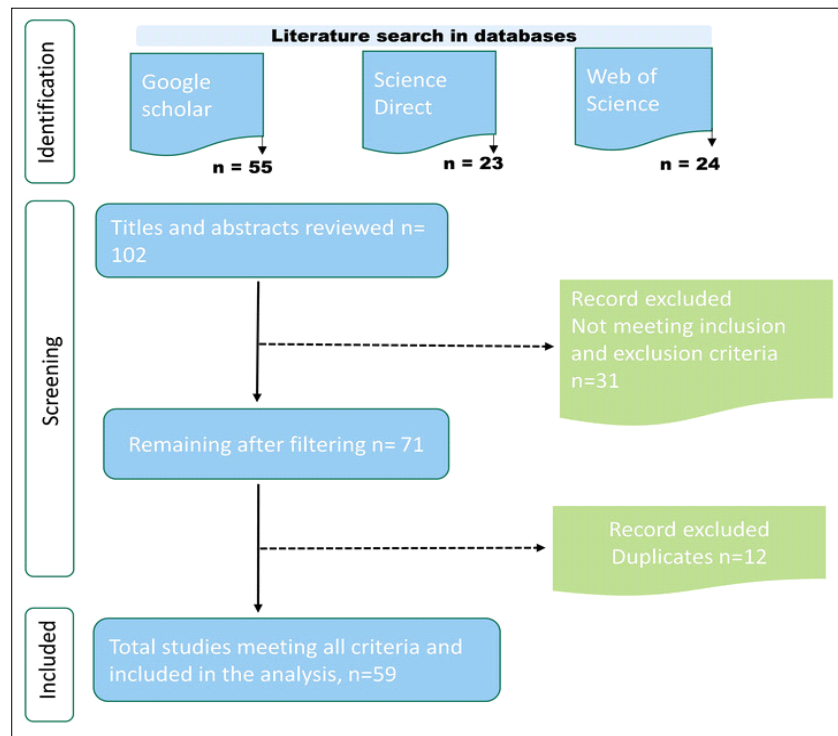


Fig 1: Process of selecting articles for data collection using inclusion and exclusion criteria, following the PRISMA flowchart of literature search.

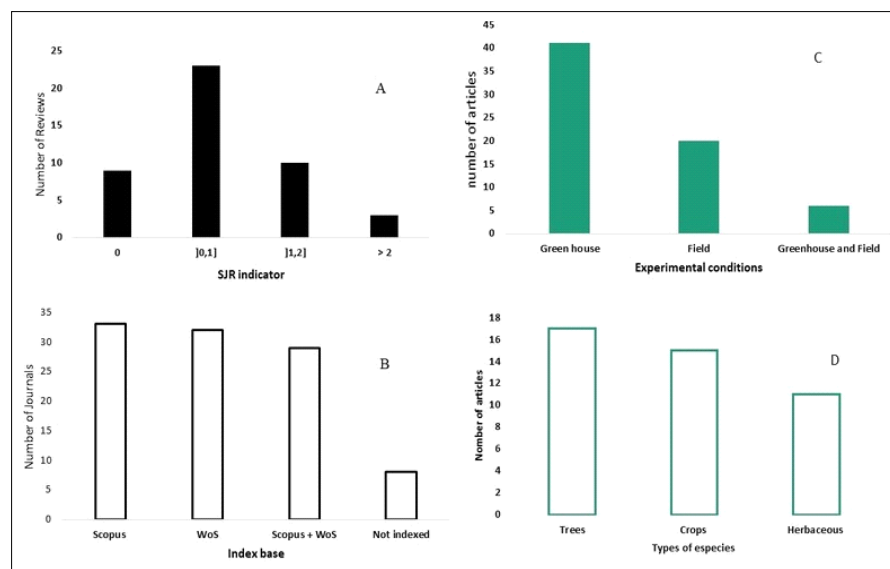


Fig 2: Number of articles according to SJR indicator (A), Index base (B), Experimental conditions (C) and the type of legume species (D).

The meta-analysis revealed that AMF and RH exhibited greater benefits for host plant growth especially when they are co-inoculated. The combined effect of dual inoculation with AMF and RH primarily manifests in promoting nitrogen and phosphorus element uptake/utilization by the plants

which results in plant growth and development. In this regard, several studies have shown that, an increase in P content in legume tissue due to association with AMF has been consistently associated with an increase in N content and N productivity in legumes associated with or without

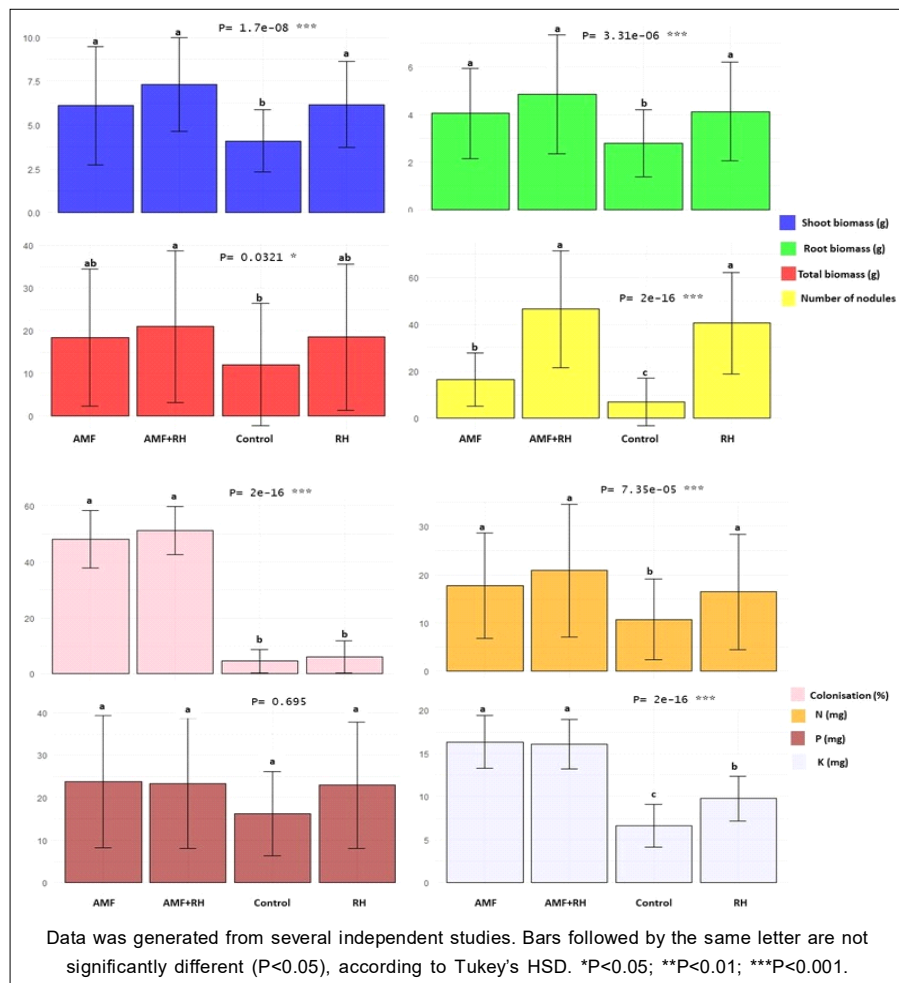


Fig 3: Effect of single inoculation and co-inoculation with rhizobia and AMF.

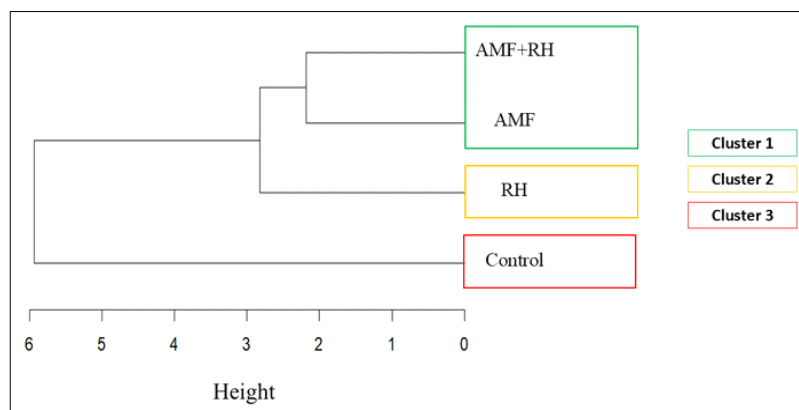


Fig 4: Hierarchical clustering of treatments based on bibliometric analyses.

RH (Kebede, 2021; Soumare *et al.*, 2015, Abeer *et al.*, 2025). The incremental increase in N, P and K uptake could be attributed to RH and AMF roots infection and their efficiency in boosting plant nutrition. In fact, AMF's hyphal networks attract essential nutrients including P to the rhizosphere and thereby increase nodulation and the efficiency of symbiotic nitrogen fixation (Mortimer *et al.*, 2008; Atakli *et al.*, 2022) and allow the transfer of symbiotically fixed N between similar or dissimilar plant species (Soumare *et al.*, 2020). According to He *et al.* (2024), an increase in nodulation, occurs since these symbionts select the competent rhizobia in the rhizosphere. Unfortunately, the mechanisms underlying these fungal hyphae facilitation for N-fixing rhizobia remain less well-understood. However, we hypothesize that AMF would modify the flavonoids in such a way as to favor the rhizobial strains that are the most efficient. Indeed, it is known that some AMF possess genes associated with the flavonoid biosynthesis pathway (Mohanta, 2020). AMF can act indirectly by modifying the root exudates and thereby shape the composition and structure of the rhizosphere microbial community (Zhang *et al.*, 2018). Through this process, AMF can regulate the establishment and function of nitrogen-fixing symbiosis (Gorgia and Tsikou, 2025). On the other hand, bacteria can also be beneficial to AMF symbiosis. In fact, symbiotic nitrogen fixing bacteria enhance the excretion of flavonoids in legumes which have positive effects on hyphal branching and spore germination (Abdel-Lateif *et al.*, 2012; Dakora and Phillips, 2002). Further work to elucidate the mechanisms underlying these microbe-microbe and microbe-plant interactions is needed.

Moreover, the highest amount of phosphorus (P) was correlated with the highest AMF colonization in plants inoculated with AMF alone. The amount of P in plants with dual inoculation is statistically comparable to that in the other treatments. This can be explained by the fact that in co-inoculation, the mobilized P is shared between the plant and the rhizobial symbiont which needs P for nitrogen fixation as previously highlighted in Raklami *et al.* (2019) on faba bean (*Vicia faba* L.). However, AMF and RH interactions aren't always synergistic. Some studies have reported that single inoculation had a greater effect than dual inoculation (Kavadia *et al.*, 2021).

Beyond these the macronutrients (N, P and K), AMF efficiently and directly increase other macro and micronutrients such as K, Mg, Fe, Cu, Zn and Mn especially in nutrient-limited conditions (Meding and Zasoski, 2008; Zhang *et al.*, 2024). Although required in small quantities, micronutrient content in soil is often insufficient for enhancing crop growth and yield due to changes induced by leaching (Mugabo *et al.*, 2024). In addition, some studies have shown that co-inoculation promotes photosynthetic capacity through increasing nodule leghemoglobin concentrations and nitrogenase activities (Yu *et al.*, 2024; Zhang *et al.*, 2024). However, this variable was not included in this meta-analysis because of limited publications. Besides their direct effect, RH and AMF symbionts indirectly diminish the inhibitory effects of various pathogens on plant development and enhance soil properties as well (Gopalakrishnan *et al.*, 2020; Tariq *et al.*, 2020).

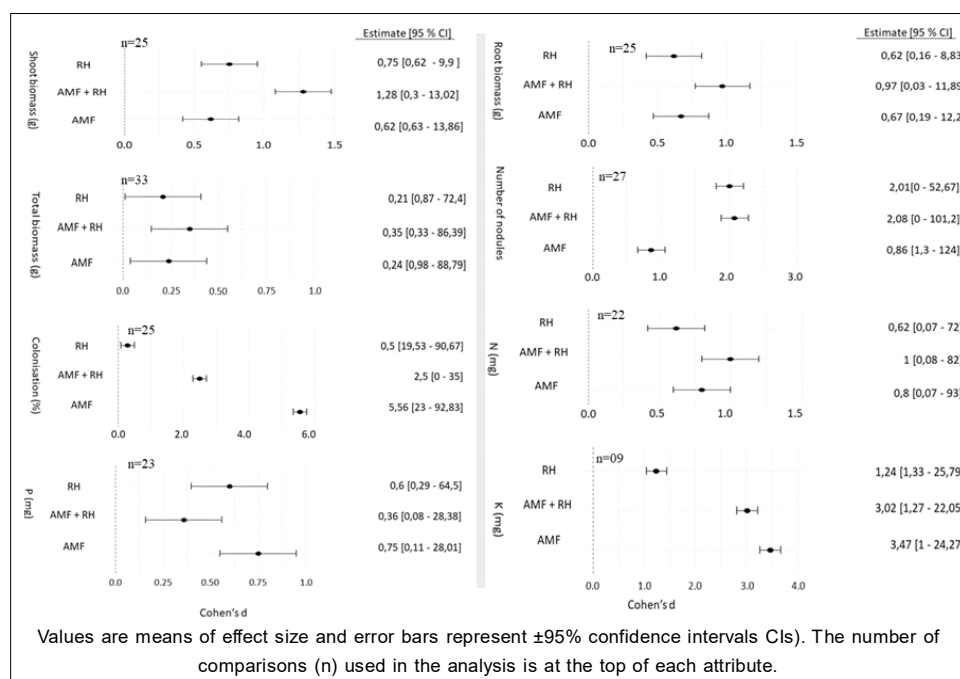


Fig 5: Mean effect size of inoculation on shoot roots biomass and total (i), AM colonisation (ii), number of nodules (iii), plant nutrition (P, N and K).

CONCLUSION

The meta-analysis of 59 studies highlights that co-inoculation with RH and AMF significantly improves plant nutrient content and biomass yield compared to single inoculation. The findings suggest that dual inoculation with AMF and RH can provide a synergistic effect, resulting in yield advantages in most cases. However, the mechanisms behind these interactions are not fully understood, highlighting the need for further research. Current knowledge of legume-AMF-RH interactions is limited and more studies are required to predict the outcomes of this symbiosis under both stress and non-stress conditions. This research offers valuable insights into microbial engineering in the rhizosphere and its potential to improve nutrient use efficiency. It also shows positive impacts on various leguminous species, including trees, herbaceous plants and weeds, offering promising implications for sustainable agriculture, especially amid global climate change.

Declarations

Author declares that all works are original and this manuscript has not been published in any other journal.

Author contributions

All authors contributed to data collection, analysis, drafting and revising the paper. They also agree to its submission for publication.

Conflict of interest

The author declare that they have no conflicts of interest to report regarding the present study.

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