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A Meta-Analytical Approach on Arbuscular Mycorrhizal Fungi Inoculation Efficiency on Plant Growth and Nutrient Uptake

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Abstract: Arbuscular mycorrhizal fungi (AMF) are obligate symbionts of higher plants which increase the growth and nutrient uptake of host plants. The primary objective was initiated based on analyzing the enormity of optimal effects upon AMF inoculation in a comparative bias between mycorrhizal and non-mycorrhizal plants stipulated on plant biomass and nutrient uptake. Consequently, in accomplishing the above-mentioned objective a vast literature was collected, analyzed, and evaluated to establish a weighted meta-analysis irrespective of AMF species, plant species, family and functional group, and experimental conditions in the context of beneficial effects of AMF. I found a significant increase in the shoot, root, and total biomass by 36.3%, 28.5%, and, 29.7%, respectively. Moreover, mycorrhizal plants significantly increased phosphorus, nitrogen, and potassium uptake by 36.3%, 22.1%, and 18.5%, respectively. Affirmatively upon cross-verification studies, plant growth parameters intensification was accredited to AMF (*Rhizophagus fasciculatus* followed by *Funniliforme mosseae*), plants (*Triticum aestivum* followed by *Solanum lycopersicum*), and plant functional groups (dicot, herbs, and perennial) were the additional vital important significant predictor variables of plant growth responses. Therefore, the meta-analysis concluded that the emancipated prominent root characteristics, increased morphological traits that eventually help the host plants for efficient phosphorus uptake, thereby enhancing plant biomass. The present analysis can be rationalized for any plant stress and assessment of any microbial agent that contributes to plant growth promotion.

Keywords: arbuscular mycorrhizae; inoculation; meta-analysis; plant growth; nutrient uptake

1. Introduction

Arbuscular mycorrhizal fungi (AMF) are important symbionts of plants and having their origins dating back to 400 million years positively serve the host plants for efficient water and nutrient uptake from the soil [1,2]. AMF have copious roles for the host plants ranging from enhanced nutrition [3–5], biofertilizer [6,7], stress tolerance [8,9], and disease resistance mechanisms [10]. Researchers worldwide have familiarized the utility of AMF and the boosting phenomenon elicited upon AMF inoculation having prospective benefits on plant biomass and enhanced nutrient uptake [3,11–13]. The above shift of inoculation efficiency of AMF and plant growth promotion was demarcated as a strategy bring forth as a result of phosphorus (P) uptake upon AMF inoculation [13–18]. The P uptake was proved as an effective mechanism as the patterning of fungal hyphae furthering the zones for rhizosphere depletion possibly can be mediated by widening the root zones for increased P solubilization and uptake of P effectually [16,19].

Relating the mycorrhizal symbiosis and plant growth promotion of the above said facts still requires a clear understanding for comprehending whether the symbiotic association alone or the magnitude of host plant response due to variability patterns need to be reinvestigated. To apprehend this significant scientific perspective, the meta-analysis employing quantitative analysis was embarked on to link the beneficial effects of AMF inoculation to the ecological variables responsible for plant growth promotion. The meta-analysis proves to be a reliable method that quantitatively integrates various independent experimental outcomes that answers extensive scientific problems incorporating variability profiles using the replicable and reproductive nature of results and dissemination of the data analyzing numerous variables [20,21]. Previously, the definitive roles that pertain to connecting AMF inoculation and probable outcomes of plant-pathogen interactions were assessed by making use of the meta-analysis by several soil microbiologists for revealing the common factorial plant improvement [22], impact of increased atmospheric CO_2 and correlated mycorrhiza-plant responses [23], furthering the comparative efficacies of AMF symbiosis to other biocontrol agent interactions in plant growth [24], relation between AMF and insect herbivores variation prototypes [25], and assessment of allometric disparities upon plant biomass established by AMF under diverse stress environments [26,27].

Moreover, Tresedar [28] conducted a meta-analysis of AMF response to the increased CO_2 with limited data points, but the data lacked comparative evaluation of AMF inoculation and the host plant response. In 2005, Lekberg and Koide [29] conducted a three-factor analysis of variance (ANOVA) for comparing AMF colonization and various agricultural management practices on crop plants emphasizing the uptake of phosphorus. Multi-factor meta-analyses for reviewing AMF inoculation on host plant responses employing fixed and mixed models for effectuating AMF inoculation benefits resulted inconclusive as the results were statistically insignificant for a complete conclusion upon AMF inoculation [30]. Further, Jayne and Quigley [31] studied AMF inoculation efficiency on plant growth under water stress.

In the present study, I studied the relative importance and magnitude with different predictor variables on plant responses to AMF inoculation using random-effects models. Moreover, it is focused on seven categorical variables: AMF species, plant species, plant family, plant growth habit, plant group (monocot vs. dicot), life cycle (annual vs. perennial), and experimental condition (greenhouse vs. field). The categorical analysis is based on six non-categorical response variables such as shoot, root, and total biomass, nitrogen (N), phosphorus (P), and potassium (K) uptake. More specifically, based on the following questions:

Is mycorrhizal inoculation correlated with variations in plant biomass and nutrient uptake?

In studies where AMF inoculation increased the P, N, and K uptake, is there a relationship on the biomass?

Are there any significant differences in mycorrhizal plant effects based on identities of AMF and plant species?

Is the extent of the effects of AMF inoculation comparable between the plant group (monocot vs. dicot) and life cycle (annual vs. perennial)?

2. Materials and Methods

2.1. Literature Search and Data Collection

As an initial step for the meta-analysis, a literary search carried out in the web of science and other sources and bibliographic analysis was performed to acclaim the nativity of search to build a coherent database. The research articles published from 1999 to 2019 were found in peer-reviewed journal viz., Science, Nature, Elsevier, Springer, and Wiley and Blackwell. The survey of literature was planned to delineate all possible combinatorial searches encompassing the search terms 'mycorrhiza* inoculation, Arbuscular Mycorrhiza* inoculation, Mycorrhiza*/or Arbuscular Mycorrhiza* nutrient uptake, and plant growth. Boolean truncation ('*') character usage limited the search with inclusion criteria composed of "mycorrhizae, mycorrhizas, and mycorrhizal" terminologies. A preliminary Google search brought about 600 research articles, out of which 350 articles had significant statistical data. After meticulous data analysis, 300 articles were excluded from our analysis based on inclusion criteria and confirmed 50 articles for our analysis (File S1).

2.2. Selection Criteria

Data analysis was set to confined categories of inclusion criteria from published resources pertaining to different fixed-factors such as "publication, the taxonomy of the AMF, and host plant, experimental conditions, biomass, and nutrient uptake, as well as statistical data" (File S1).

2.3. Data Acquisition

The meta-analysis requires following statistical information: Mean, standard deviation (SD), and sample size (n) for both the control and treatment. I converted standard errors (SE) to SD using the MetaWin 2.1 Statistical calculator. Data were collected from the graph using the Dexter (GAVO data center) software (http://dc.zah.uni-heidelberg.de/sdexter/).

2.4. Meta-Analysis

The MetaWin v2.1 software was utilized for conducting the meta-analysis. Natural log of the response ratio (further represented as LRR, log response ratio), which is the mean of the treatment (with Arbuscular Mycorrhizal inoculation) divided by the mean of the control (without inoculation) [21,32] was denoted as a metric for the AMF inoculation responses. The meta-analysis integrating the random–effects model was evaluated to calculate the effect size and variance. Statistical inference and LRR computations were arrived employing the following equation:

$$\ln R = \ln\left(\frac{\overline{X}^E}{\overline{X}^C}\right) = \ln\left(\overline{X}^E\right) - \ln\left(\overline{X}^C\right) \tag{1}$$

$$v_{\ln R} = \frac{\left(S^E\right)^2}{N^E\left(\overline{X}^E\right)^2} + \frac{\left(S^C\right)^2}{N^C\left(\overline{X}^C\right)^2} \tag{2}$$

R = Response ratio
X^E = Treatment mean (with inoculation)
X^C = Control mean (without inoculation)
S^E = Treatment standard deviation
S^C = Control standard deviation
N^C = Control replication number
N^E = Treatment replication number

The analysis of variance for each study was signified as $v_{\ln R}$ and the effect size as ln R (LRR) [21]. Randomization resampling for testing the connotation of moderators was performed with 4999 iterations. The bootstrapping (BS) method incorporated in MetaWin was used to create confidence intervals (95% CIs). Single-factor categorical analyses proceeded, when the homogeneity statistic Q, exceeds the level of significance ($p < 0.05$, chi-square distribution), and the statistics were declared to be heterogeneous. Three Q statistics were created per factor under categorical analyses encompassing the variation within categories (Q_W), the variation among categories (Q_M or Q_B), and the total Q (Q_T), which is the sum within and among categories ($Q_T = Q_W + Q_B$). Q_B rather than Q_W pose potential scientific deliberations according to Gurevitch and Hedges [20]. When the Q_B values are higher than a critical value, the response ratio is bound to depend on an independent variable for prominent impact. Values for Q_B were significant and described at least 10% of the total variation ($Q_B/Q_T \geq 0.1$) for determining response factors to be significant. Percentage change relative to the control was calculated based on the equation (exp (LRR) −1) × 100% and it was used to predict AMF inoculation efficiency.

3. Results

3.1. Overview

I conducted the meta-analysis using 419 independent trials from 50 research articles. The trials included in the meta-analysis were: 82 trials for shoot biomass, 69 for root biomass, 69 for total biomass, 51 for N uptake, 73 for P uptake, and 75 for K uptake (Table 1).

Table 1. Summary of overall heterogeneity analysis.

Response Variable	Effect Size	Number of Trails	95% BS CI	Q-Total	P (Chi-Square)
All studies	0.26	419	0.22 to 0.29	1696.26	0.00000
Shoot Biomass	0.34	82	0.26 to 0.42	221.44	0.00000
Root Biomass	0.27	69	0.18 to 0.37	87.67	0.02166
Total Biomass	0.28	69	0.20 to 0.35	122.65	0.00002
P uptake	0.25	73	0.18 to 0.31	54.83	0.75865
N uptake	0.20	51	0.13 to 0.27	32.45	0.82749
K uptake	0.19	75	0.08 to 0.29	75.56	0.17405

Mycorrhizal inoculation efficiency was explored between AMF species, AMF inoculation, plant species, plant group, growth habit, life cycle, and experimental conditions. Overall, the analysis showed a positive statistical evidence on mycorrhizal inoculation. Overall, inoculation increased positively by 29.7% (n = 419; LRR = 0.26). Furthermore, AMF inoculation positively increased shoot, root, and total biomass by 36.3, 28.5, and 29.7%, respectively (Figure 1). Moreover, the increased P, N, and K uptake by 36.3, 22.1, and 18.5%, respectively, in mycorrhizal plants was compared to those of non-mycorrhizal plants (Figure 1).

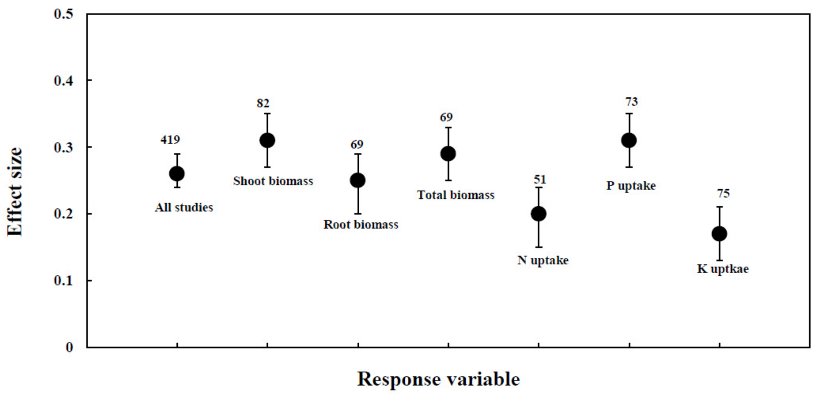

Figure 1. Full data set of arbuscular mycorrhizal inoculation responses. Error bars are means ±95% bootstrap confidence intervals (CIs). Where the CIs do not overlap the horizontal dashed lines, the effect size for a parameter is significant at $p < 0.05$. All response ratios differed significantly from zero. Numbers of trials are shown above the bar.

Overall, the categorical analysis showed that among AMF species, *Rhizophagus fasciculatus* (n = 42, LRR = 0.46, 58.4%) followed by *Funnilieforme mosseae* (27.1%) had a significant effect on plant growth (Figure 2a). Mixed inoculation (36.4%) on plant growth showed a more positive effect than those of single inoculation (28.4%) (Figure 2a). Among the plant functional group, dicot plants (35.1%) had more positive effects on plant growth than those of monocot plants (18.5). The life cycle analysis showed that perennial plants (37.7%) had more positive effects than those of annual plants (24.6%) in AMF inoculated plants (Figure 2b). Among the plant growth habit, herbaceous plants (53.7%) had more positive effects on plant growth in AMF inoculated plants. Among the plant family, Fabaceae family (47.7%) indicated a significant plant growth (Figure 2c). There was no significant difference among the soil type, but the sandy soil (32.3%) is slightly positive than the sandy loam soil (30.1%). Among the experimental condition, field studies (58.4%) showed a more positive effect than those of greenhouse studies (28.4%). Due to the low sample size (field studies), consider the results with caution (Figure 2d).

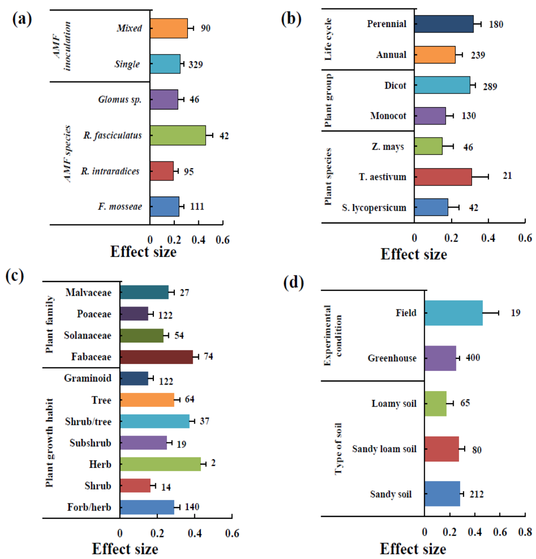

Figure 2. Effect sizes of plant biomass. Error bars are means ±95% bootstrap confidence intervals (CIs). Categorical analysis for trials grouped into (**a**) AMF species, (**b**) plant species and functional groups, (**c**) plant family and habit, (**d**) type of soil and experimental condition. Where the CIs do not overlap the horizontal dashed lines, the effect size for a parameter is significant at $p < 0.05$. Numbers of trials are shown above the bar.

There were no significant correlations between P uptake and total biomass for AMF inoculations. The correlation analysis of P uptake was positively correlated with total biomass and K uptake ($R^2 = 0.002$) and N uptake ($R^2 = 0.01$). Similarly, K uptake had positive correlations with N uptake ($R^2 = 0.1$) (Figure 3). Moreover, our results showed a positive linear relationship between the degree of mycorrhizal colonization and mean effect size of P (Figure 4). Mycorrhizal colonization also found a positive relationship for biomass and K uptake, while a very weak relationship was found between the degree of mycorrhizal colonization and N uptake.

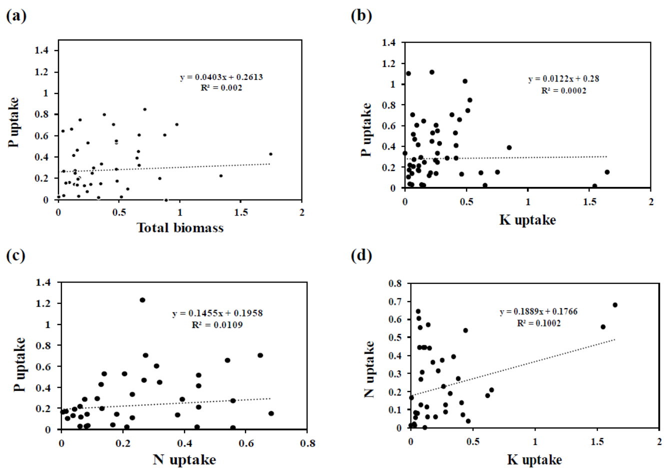

Figure 3. Correlation analysis of response variables. (**a**) P uptake vs. total biomass, (**b**) P uptake vs. K uptake, (**c**) P uptake vs. N uptake, (**d**) N uptake vs. K uptake.

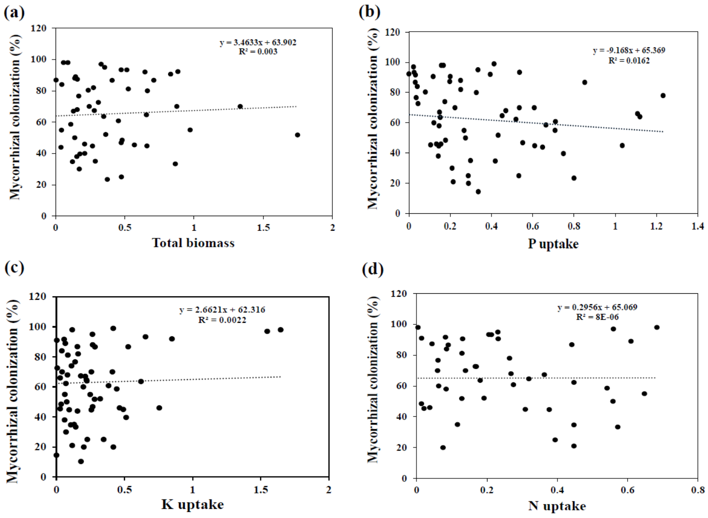

Figure 4. Relationship between mycorrhizal colonization (%) and (**a**) total biomass, (**b**) P uptake, (**c**) K uptake, (**d**) N uptake.

3.2. Effect of AMF Inoculation on Biomass

Our analysis showed that mycorrhizal inoculation significantly increased total biomass (LRR = 0.29) whereas there was no significant difference between shoot (LRR = 0.31) and root biomass (LRR = 0.25) in mycorrhizal plants (Figure 1). The three-factor categorical analysis amongst AMF species depicted a plethora of significance for the three most utilized *Glomus* sp. inoculum in all the studies. Most of the studies used the following AMF species such as *F. mosseae*, *R. intraradices*, and *R. fasciculatus*. Among AMF species, *R. fasciculatus* showed a more positive impact on plant growth than *F. mosseae* and *R. intraradices* (Figure 5a).

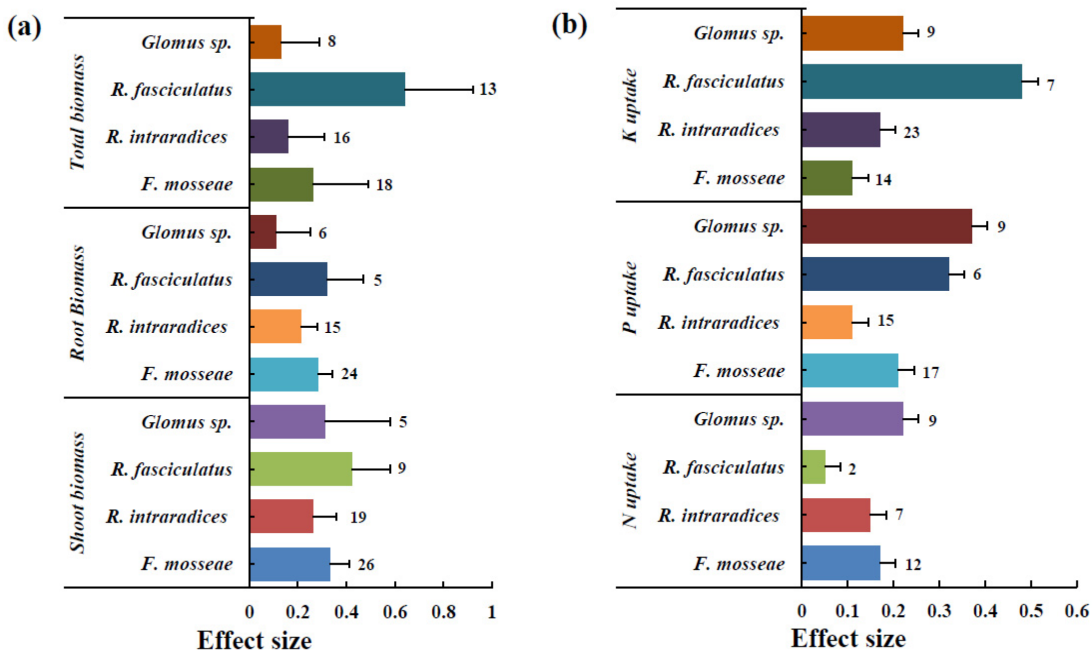

Figure 5. Effect sizes of AMF categorical analysis. (**a**) Plant biomass categorical analysis. (**b**) Nutrient uptake categorical analysis. Error bars are means ±95% bootstrap confidence intervals (CIs). Where the CIs do not overlap the horizontal dashed lines, the effect size for a parameter is significant at $p < 0.05$. Numbers of trials are shown above the bar.

A significant difference was evident between these three AMF inoculum treatments on total biomass ($Q_B/Q_T = 0.27$; $p < 0.05$). Significant variations on shoot and root biomass were also observed among monocot vs. dicot ($Q_B/Q_T = 0.11$; $p = 0.003$ and $Q_B/Q_T = 0.17$; $p < 0.05$). Moreover, shoot and total biomass showed a significant variation on annual vs. perennial plants, whereas there are no significant variations on root biomass.

3.3. Effect of AMF Inoculation on P Uptake

Our meta-analysis showed that AMF inoculation significantly increased P uptake by 36.3% compared to those of non-inoculated plants. Moreover, significant variations among studies ($n = 73$; LRR = 0.31; $p < 0.05$). Among the categorical analysis, AMF inoculation ($p < 0.05$) had a significant effect on P uptake. Among AMF species, *R. fasciculatus* showed a more positive effect size than *F. mosseae* and *R. intraradices* (Figure 5b). Across studies, plant families such as Fabaceae (LRR = 0.37) had greater P uptake than Poaceae and Solanaceae. Moreover, herbaceous plants had a more positive effect than tree and graminoid plants. Annual vs. perennial plants responded favorably to mycorrhizal inoculation; however, annual species showed more P uptake than perennial (Figure 6a).

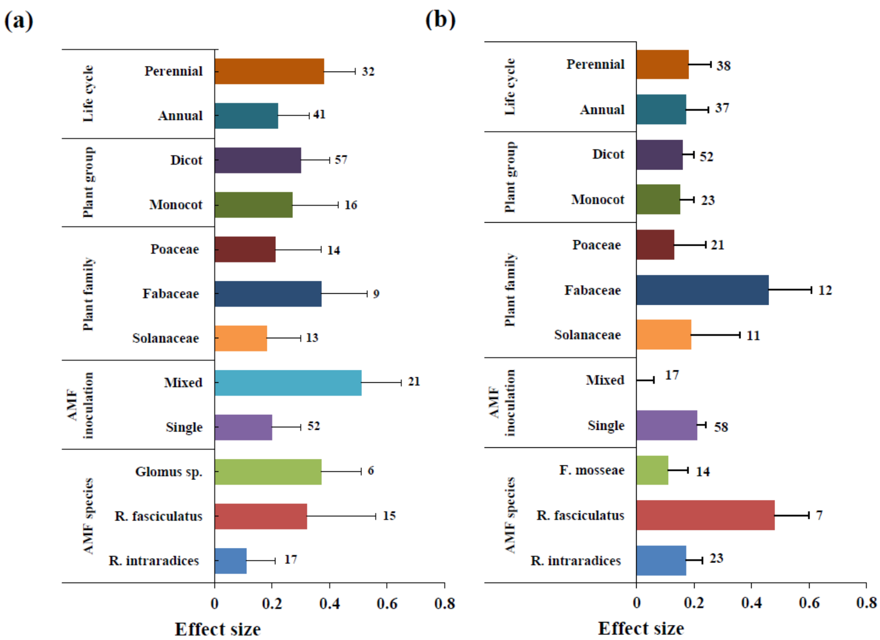

Figure 6. Effect sizes of nutrient uptake categorical analysis. Categorical analysis for trials grouped into (**a**) P uptake, and (**b**) K uptake. Error bars are means ±95% bootstrap confidence intervals (CIs). Where the CIs do not overlap the horizontal dashed lines, the effect size for a parameter is significant at $p < 0.05$. Numbers of trials are shown above the bar.

3.4. Effect of AMF Inoculation on N Uptake

AMF inoculation significantly increased N uptake by 22.1% compared to those of non-inoculated plants. Moreover, significant variations among studies ($n = 51$; LRR = 0.2; $p < 0.05$). Categorical analysis of N uptake with AMF inoculation ($p < 0.05$) was found to have a significant positive effect on plant growth. Among AMF species, *F. mosseae* had a more positive effect than *R. intraradices* (Figure 5b).

3.5. Effect of AMF Inoculation on K Uptake

In our analysis, K uptake exhibited a significantly positive impact on mycorrhizal plants (18.5%) and also found significant variation among studies ($n = 74$; LRR = 0.16; $p < 0.05$). Categorical analysis of AMF species showed positive responses. Among AMF species, *R. fasciculatus* had better K uptake than *R. intraradices* and *R. mosseae* (Figure 5b). In addition, herbaceous plants ($n = 8$; LRR = 0.53) had a more positive effect on K uptake than graminoid plants (n = 21; LRR = 0.13). Moreover, mycorrhizal perennial plants (n = 38; LRR = 0.18) were marginally greater than annual plants (n = 37; LRR = 0.17) (Figure 6b).

4. Discussion

The meta-analysis corresponds to a comprehensive compilation and analysis of data of particular interest to evaluate the nobility of research perspectives and potential outcomes across various studies and to confirm the convincing factors contributing to variable effects associated with the studies [33]. Our meta-analyses on mycorrhizal inoculations highlighted the simultaneous important contributions of mycorrhizal inoculation on plant biomass and nutrient uptake. Research analyses of individual studies revealed the outcomes to be optimistic. The results prove worthy of benefits and could act as a launchpad and furthering profound insights onto mycorrhizal functions dependence on specific AMF and plant species, and pose areas for future research that could a bridge the gap of understanding the multifaceted association between plant roots and obligate fungal symbionts.

Mycorrhizal colonization facilitated the plants to grow healthier than the non-mycorrhizal plants as evident from the rigorous analysis. The overall AMF inoculation response of plants was more positive than non-mycorrhizal plants. The AMF inoculation mediated enrichment on plant biomass was higher than non-mycorrhizal plants. The shoot and root biomass were significantly greater in mycorrhizal plants than non-mycorrhizal plants. Our results are similar to previous studies [5,34–37]. The increase of mycorrhizal inoculation response in shoot biomass among the three most studied AMF species are ranked as *R. fasciculatus* (52.2%) > *F. mosseae* (39.1%) > *R. intraradices* (29.7%), and *R. fasciculatus* (37.7%) > *F. mosseae* (32.3%) > *R. intraradices* (23.4%), for root biomass. In this study, plants inoculated with *R. fasciculatus* (89.6%) had higher total biomass production than that of the uninoculated plants.

Each AMF species differ in their response. The AMF–host plant interaction was proved responsible for aiding plant growth promotion after a comparative assessment for efficiency of *R. fasciculatus* inoculation than *R. intraradices* and *F. mosseae* inoculation. Previous studies have stated that the efficiency of AM symbiosis could differ according to the genotype of the two symbionts, plants, and AMF, as well as the combination of the both [38–40]. Croll et al. [41] described a solid fondness for AM fungal genotype by host plants. In his study, *R. intradices* showed significant preferences to different host plant species. In addition, Angelard et al. [42] studies showed functional differences by genotype among AMF isolates for host plants. Moreover, different genotypes of plant had different impacts on plant growth [43,44]. AMF species functional diversity studies showed that plants can respond differently to AMF, not only at the level of colonization, nutrient uptake, and growth, but also at the level of gene expression [40]. Numerous researches revealed that AMF-inoculated plants exhibit better growth than non-inoculated plants [5,12,14,45]. Despite overall positive effects, the AMF inoculation effect on plant biomass was greatly dependent on plant functional groups ($p < 0.05$). AMF inoculation had a strong relationship with herbaceous plants than woody plants. The extensive rooting system with extensive soil volume of several herb/forbs give an edge over woody plants. Moreover, mycorrhizal perennial plants had improved plant growth and they responded more positively than annual species. These results can be corroborated to the possible accumulation in persistent roots and habitual shoots [31]. AMF-mediated growth promotion in plants was increased particularly by the P and K uptake from the adjoining soil [3,8,18,26,28,46].

Our meta-analysis revealed that AMF significantly increased the P uptake (36.3%). Among categorial analysis, AMF and plant species had a significant impact on the uptake of P ($p < 0.01$). Among AMF species, *R. fasciculatus*, *F. mosseae*, and *R. intraradices* were found to be more efficient in P uptake. Our results are similar with previous studies of AMF inoculation responses [13,18,38,47,48]. Establishment of a wide hyphal structure for exploring a wide soil volume enriches the uptake of more P in mycorrhizal plants than uninoculated plants [17,49,50]. Moreover, AMF inoculation supported the formation of lateral roots which in turn produced more fine roots thus increasing the uptake of water and nutrients from the soil [17,50]. Across studies, I found that perennial and woody plants had increased the uptake of P than those of other mycorrhizal plants. AMF inoculation not only influenced the root morphology but also the physiological condition in host plants. These results confirm that the enhanced growth of mycorrhizal plants is largely associated with the enrichment of P nutrition.

AMF inoculation can help improve N absorption in mycorrhizal plants [3,5]. Mycorrhizal inoculation on plants showed an increased uptake of N and thereby increasing the synthesis of chlorophyll in plants [3,51]. However, I did not find any significant variation among groups indicating discrepancies among categorical variables for N uptake. Furthermore, the exact mechanism through which AMF enhances N uptake is not yet clearly understood. Moreover, the K^+ ion is one of the most important cations important for stomatal movement and protein synthesis and is also considered as an osmotic regulator. In the present study, mycorrhizal plants showed a significant increase in K uptake compared to the non-mycorrhizal plants. Mycorrhizal mediated higher K^+ ion uptake than the non-AMF control providing a hint for better K^+ ion uptake in the root xylem of mycorrhizal plants [5,50,52]. Mycorrhizal plants increased the accumulation of K^+ ion in plants that render an appropriate environment by maintaining osmotic balance and K^+ ion mediated cytosolic enzyme activities and cell regulation [5,52].

5. Conclusions

This meta-analysis study, provides a unique evidence about AMF inoculation, particularly about plant growth and improved nutrition (higher P and K uptake) in mycorrhizal plants. Among the studied AMF species, better results were found with the inoculation of *R. fasciculatus* as compared with *F. mosseae* and *R. intraradices* for most of the non-categorial variables. The positive effects of mycorrhizal inoculation on plant growth promotion have been largely attributed to more P uptake. An enhanced root nutrient uptake (especially P) by AMF is ascribed to changes in root traits such as the elongation and formation of lateral roots, root hairs, increased root surface area, and root volume. Further, the active AM root likely holds up greater quantities of nutrients, leading to the enrichment of plant biomass production. However, further studies including soil and environmental characteristics and analyzing more categories under diversified soil conditions are vital to further authenticate the efficacy of AM inoculation to sustainable agriculture.

Supplementary Materials: The following are available online at http://www.mdpi.com/2077-0472/10/9/370/s1, File S1: Dataset and datasheet for meta-analysis.

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