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RESEARCH

Shifts in biomass allocation shape yield responses of mung bean (*Vigna radiata* L.) to molybdenum and silicon

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Abstract

Nutrient limitation is a persistent constraint to mung bean in low-input cropping systems, where micronutrient availability plays a critical role in nodulation, biomass allocation, and yield. This study examined the individual and combined effects of molybdenum (Mo) and silicon (Si) on growth, root–nodule, and yield of *Vigna radiata* L. grown under nitrogen-limited soil conditions. A pot experiment was conducted using a completely randomized design with four treatments: control, Si, Mo, and combined Si + Mo. Plant height was not influenced by micronutrient application, indicating limited effects on shoot elongation. In contrast, Mo substantially improved belowground development, resulting in greater root biomass, increased nodule fresh weight, and higher seed number and seed yield compared with the control. Si alone significantly altered root traits and nodulation, demonstrating its capacity to modify belowground allocation. The combined Si + Mo promoted greater allocation to root and nodule biomass relative to individual treatments; however, this response was accompanied by reduced pod number and seed yield relative to Mo alone, indicating an imbalance in assimilates partitioning. Correlation and principal component analysis provided clear insight into traits, that Mo-treated plants were closely associated with yield-related parameters, whereas the combined Si + Mo aligned with root biomass and nodulation. Overall, the findings indicate that Mo is a key micronutrient for optimizing nodulation and reproductive performance of mung bean, while silicon plays a direct role in shaping root and nodule development.

Keywords Legume · Low–input · Micro nutrients · Nodulation · Root traits

1 Introduction

Legume productivity in tropical farming systems is closely tied to the efficacy of biological nitrogen fixation (BNF), which supplies nitrogen for vegetative growth and grain development while reducing dependence on external fertilizer inputs. In short-duration crops such as mung bean (*Vigna radiata* L.), the contribution of BNF is particularly critical because nodulation, canopy establishment, and reproductive development occur within a short period of time (Ge et al. 2025; Kebede 2021). When limitations arise during early vegetative stages, the crop has limited capacity for compensation, often resulting in reduced biomass accumulation and yield potential. In many tropical regions including the Philippines, mungbean is cultivated on weathered acidic soils characterized by strong Fe–Al oxide activity, low organic matter, and restricted availability of certain micronutrients. Under such conditions, nodules frequently exhibit reduced effectiveness and canopy development

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remains modest, leading to unstable or suboptimal yields (Nair et al. 2019; Gatan et al. 2019; Tahir et al. 2020; Zhou et al. 2023a). These patterns indicate that nutrient-mediated constraints at the root–nodule interface are crucial to understanding productivity in these environments. In this scenario, molybdenum (Mo) occupies a key position in this process as a structural component of the Fe–Mo cofactor in nitrogenase and an essential element of nitrate reductase, which determines the catalytic capacity for atmospheric N_2 reduction and nitrogen assimilation (Banerjee et al. 2022; Bursakov et al. 2023). In acidic soils, molybdate availability declines sharply because of strong adsorption onto oxide surfaces, limiting its uptake by plants. Under such conditions, nodules may develop morphologically yet function below their biochemical potential. Applications of Mo have improved nodulation and yield in various legume species (Oliveira et al. 2022; Jamali et al. 2023); however, the responses are not universally consistent, and this variability suggests that enhancing catalytic capacity alone does not always translate into proportional increases in plant growth or grain production.

Consequently, nitrogen fixation is an energy-demanding process that depends not only on enzymatic competence but also on sustained carbon supply and structural integrity of root systems. Meanwhile, silicon (Si), although not classified as an essential nutrient for dicotyledonous crops, has been reported to influence root architecture, maintain photosynthetic stability, and enhance tolerance to oxidative stress (Mišúthová et al. 2021; Khan 2025; Tripathi et al. 2022). In mung bean and other legumes, Si supplementation has been associated with improved vegetative growth, chlorophyll retention, and greater nodule number or mass (Al Murad & Muneer 2022; Shahzadi et al. 2023; Ahmad et al. 2024; Guanzon et al. 2026). These effects indicate that Si may indirectly affect symbiotic performance by improving the host plant's capacity to supply assimilates and maintain favorable physiological conditions for active nodules (Putra 2020; Coquerel et al. 2023). However, in acidic tropical soils where molybdate availability is inherently restricted, and early root growth may be constrained, nodulation efficiency and yield formation likely reflect the integration of catalytic and structural processes (da Silva et al. 2022; Gao et al. 2025). Mo defines the biochemical potential for nitrogen fixation, whereas Si may influence the capacity of the plant to sustain and translate that potential into biomass accumulation. When these functions are not coordinated, improvements in nodulation may not correspond to equivalent gains in vegetative growth or yield (Wysokinski et al. 2022; Awasthi et al. 2025). Despite extensive research on Mo or Si applied separately, their combined influence on the functional relationship among nodulation, biomass production, and grain formation in mung bean remains insufficiently characterized.

Hence, the study aims to assess the individual and combined effects of Mo and Si on vegetative growth, nodulation, biomass allocation, and yield of mung bean grown under acidic soil conditions. It was hypothesized that Mo supplementation would enhance nodulation and growth while Si application would promote root development and vegetative vigor, thereby strengthening assimilatory support; and their concurrent supply would improve the efficiency with which nodulation contributes to biomass accumulation and grain yield relative to single-nutrient application.

2 Materials and methods

2.1 Soil physico-chemical properties

The pot experiment was conducted from January to May 2025 at the greenhouse research facilities of the Crop Science Department, Pampanga State Agricultural University, Philippines. The experimental site is geographically located at 15°12′58″ N latitude and 120°41′38″ E longitude, at an altitude of 91.2 m above sea level. Prior to experiment establishment, soil samples were collected from the study site and analyzed following standard analytical procedures. The pre-experimental soil analysis revealed the physicochemical properties summarized in Table 1.

2.2 Planting material and potting medium

Mung bean (*Vigna radiata* L.) cv. Pagasa 19 was used as the test crop. This variety is characterized by glossy green seeds, a maturity period of 57–69 days after emergence, and an average seed yield of 1.21–1.27 t ha^{-1}. Prior to sowing, seeds

Table 1 Physico-chemical analysis of agricultural soil

Soil Parameters	Method of Analysis	Result and Interpretation
Soil pH	Potentiometer	6.75 (near neutral)
Total Nitrogen (%)	Kjeldahl method	< 0.01 (very low)
Available Phosphorus (ppm)	Olsen method ($NaHCO_3$)	25.98 (medium)
Exchangeable Potassium (cmol/kg)	Ammonium Acetate Extraction	0.21 (low)
Organic matter (%)	Walkley–Black wet oxidation	1.81 (moderate)
Soil texture	Bouyoucos hydrometer	Loamy Soil

of uniform size were washed twice with distilled water and directly sown in pots containing a prepared growth medium with predetermined physico-chemical soil properties. The soil was subjected to three days of solarization to reduce pathogen load rather than complete sterilization, in order to maintain conditions more representative of field soils. Plants were grown under greenhouse conditions for 70 days. Polyethylene planting bags measuring 43 cm in height and 22 cm in diameter were used each filled with 5 kg of soil. The soil was collected from lowland agricultural fields where mungbean is commonly cultivated.

2.3 Experimental design and greenhouse conditions

The experiment was arranged in a Completely Randomized Design (CRD) with four treatments: control (no micronutrient application), silicon (Si), molybdenum (Mo), and combined Si + Mo. Each treatment consisted of seven pots, with each pot containing two plants and considered as a single experimental unit. All measurements were conducted on a per-pot basis to avoid pseudo-replication. Pots were randomly arranged at the start of the experiment and re-randomized weekly to minimize positional and environmental bias. The greenhouse was maintained under natural light conditions, with temperature ranging from 21.94 to 31.56 °C and relative humidity averaging approximately 78.8%. To further reduce environmental variability within the greenhouse, pots were rotated within rows at seven-day intervals.

2.4 Silicon and Molybdenum Application

Silicon was applied as a commercial Si-containing fertilizer comprising 24% SiO_2 and 11% K_2O at a rate of 600 mg product kg^{-1} soil, following the methodology of Shamshiripour et al. (2022). This application corresponded to 144 mg SiO_2 kg^{-1} soil, equivalent to approximately 67 mg elemental Si kg^{-1} soil. Each pot contained 5 kg of soil, resulting in a total application of approximately 3.0 g fertilizer pot^{-1}. In addition to silicon, the fertilizer supplied approximately 66 mg K_2O kg^{-1} soil. This potassium input was considered minimal relative to crop demand and uniform across treatments receiving silicon; therefore, it was treated as an inherent component of the Si fertilizer rather than as an independent experimental factor. On the other hand, molybdenum was applied as a chelated Mo fertilizer containing 4% Mo. The solution was prepared at a concentration of 52.5 mg Mo L^{-1} by diluting 21 mL of the formulation in 16 L of water, following Guanzon and Tuazon (2026). This preparation provided a total of 840 mg Mo, which was uniformly distributed across seven pots. Consequently, each pot received approximately 120 mg Mo, equivalent to 24 mg Mo kg^{-1} soil based on 5 kg soil per pot. The total dose was split into two equal applications (12 mg Mo kg^{-1} soil per application) and applied at the V2 (second trifoliate) and R1 (early flowering) growth stages of mung bean. The applied Mo rate falls within ranges previously reported to stimulate nodulation in legumes under low native N availability. Soil drenching was selected as the mode of Mo application to ensure direct availability of Mo in the rhizosphere during critical stages of nodulation and biological nitrogen fixation. Although soil Mo concentration was not analytically quantified, the experimental soil exhibited very low total nitrogen (< 0.01%) and moderately acidic pH (6.75), conditions commonly associated with reduced Mo availability in tropical soils. No basal fertilizer was applied to avoid masking Mo- and Si- induced responses and to maintain conditions representative of low-input legume production systems.

2.5 Growth assessment and biomass determination

Plant height was measured at physiological maturity from the soil surface to the highest growing point of the main stem using a ruler and expressed in centimeters. Root length was determined from tagged plants by carefully excavating the root systems to preserve fine roots. Roots were gently washed under running water to remove adhering soil and measured from the root collar to the tip of the longest root. A total of seven (n = 7) sample plants per treatment were used to assess plant biomass, which was quantified through sequential fresh and dry weight measurements of plant components. Immediately after harvest, shoots and roots were separated, gently blotted to remove surface moisture, and fresh weights were recorded individually using an analytical balance with a precision of 0.01 g. Samples were then placed in labeled paper bags and oven-dried at 70 °C for 24 h or until a constant weight was achieved (Ro et al. 2023). Shoot dry weight and root dry weight were recorded after drying, and total plant biomass was calculated as the sum of shoot and root dry weights. Derived biomass indices were computed from these primary measurements. The root-to-shoot ratio (R:S ratio) was calculated as:

$$R:SRatio = \frac{RootWeight(g)}{ShootWeight(g)}$$

Root mass fraction (RMF), used to assess biomass allocation, was calculated as:

$$RMF = \frac{RootWeight(g)}{TotalPlantBiomass(g)}$$

Nodule biomass was determined concurrently with root sampling to ensure accurate quantification. Following root washing, all nodules attached to the root system of each sampled plant were carefully detached, blotted to remove excess

moisture, and weighed immediately to determine nodule fresh weight (Khanal et al. 2025).

2.6 Yield component measurements

At physiological maturity, reproductive yield components were quantified using the same tagged plants employed for growth and biomass assessments, following the procedure described by Guanzon and Magtoto (2024). The total number of pods per plant was counted manually. Pods from each plant were then air-dried, shelled, and the total number of seeds per plant was determined. Seed yield per plant was obtained by weighing all seeds harvested from each plant using an analytical balance and expressed in grams per plant. For the determination of hundred-seed weight, seeds from each treatment were thoroughly mixed, and four independent subsamples of 100 seeds were randomly selected, counted, and weighed. The mean of these measurements was reported as the hundred-seed weight (Yousefi et al. 2025).

2.7 Statistical analysis

All measured variables were analysed on a per-pot basis. Data were tested for normality using the Shapiro–Wilk test and for homogeneity of variances using Levene's test; both assumptions were satisfied for all parameters. Treatment effects were evaluated using one-way analysis of variance (ANOVA). When significant differences were detected ($p < 0.05$), means were separated using Tukey's Honest Significant Difference (HSD) test. Significant differences among treatments are indicated by different letters in tables and figures. Pearson's correlation coefficients among growth, root, nodulation, and yield traits of mungbean were computed based on pairwise complete observations. The significance of correlations was tested using two-tailed tests, and the results were visualized as a lower-triangular correlation heatmap with significance levels indicated ($p < 0.05$, $p < 0.01$, $p < 0.001$) while principal component analysis (PCA) was performed using standardized (z-score) values to assess multivariate relationships among traits. All statistical analyses and graphical visualizations were performed using R software (version 4.3.2; R Core Team), with correlation heatmaps generated using the ggplot2 package.

3 Result

3.1 Effects of silicon and molybdenum on growth parameters

The effects of silicon, molybdenum, and their combined application on vegetative growth parameters of mungbean are summarized in Fig. 1. Plant height at maturity was not significantly affected by mineral treatments ($p = 0.260$), with mean values ranging from 45.88 to 51.13 cm across treatments. Although plants receiving the combined Si + Mo treatment attained the greatest mean height (51.13 cm), this value did not differ statistically from the control or from individual Si and Mo applications (Fig. 1A).

In contrast, root length differed significantly among treatments ($p = 0.046$). Control plants developed the longest roots (38.24 cm), whereas application of Si, Mo, or their combination resulted in shorter root systems, with mean root lengths ranging from 28.53 to 32.88 cm (Fig. 1C). This reduction in root length under mineral treatments suggests a shift in root growth strategy, potentially favoring increased root biomass density rather than elongation. Mineral treatments significantly influenced biomass partitioning between below- and above-ground components. The root-to-shoot (R:S) ratio varied significantly among treatments ($p = 0.018$; Fig. 1B). The highest R:S ratio was observed under combined Si + Mo application (0.70), followed by Mo alone (0.47), indicating enhanced allocation of assimilates to belowground biomass. Silicon applied alone resulted in the lowest R:S ratio (0.25), while the untreated plants exhibited an intermediate value (0.33). Similarly, root mass fraction (RMF) was strongly affected by mineral application ($p = 0.004$; Fig. 1D). Plants receiving combined Si + Mo showed the greatest proportion of total biomass allocated to roots (0.28), followed by Mo alone (0.21). No significant difference was detected between the control and Si-only treatments, both recording RMF values of approximately 0.12. These results indicate that Mo, particularly when combined with Si, promoted greater biomass investment in root structures.

3.2 Biomass accumulation and nodulation

Shoot and root biomass parameters are presented in Table 2. Shoot fresh weight did not differ significantly among treatments ($p = 0.384$), although mean values ranged from 22.51 g in the control to 27.75 g under combined Si + Mo application. Meanwhile, shoot dry weight was significantly influenced by mineral treatments ($p = 0.005$), with values ranging from 4.80 to 7.78 g. In contrast, root biomass exhibited pronounced responses to mineral application. Root fresh weight differed significantly among treatments ($p = 0.005$). Plants supplied with Mo recorded the highest root fresh weight (7.78 g), followed by the combined Si + Mo treatment (6.07 g), whereas control and Si-only treatments produced significantly lower values. Root dry weight showed a similar trend ($p = 0.013$), with the greatest root dry biomass observed under combined Si + Mo application (3.61 g), followed by Mo alone (2.53 g). Control and Si-only treatments recorded substantially lower root dry weights (1.51–1.72 g). Nodule fresh weight was significantly affected by mineral fertilization ($p = 0.024$). Mo application resulted in the

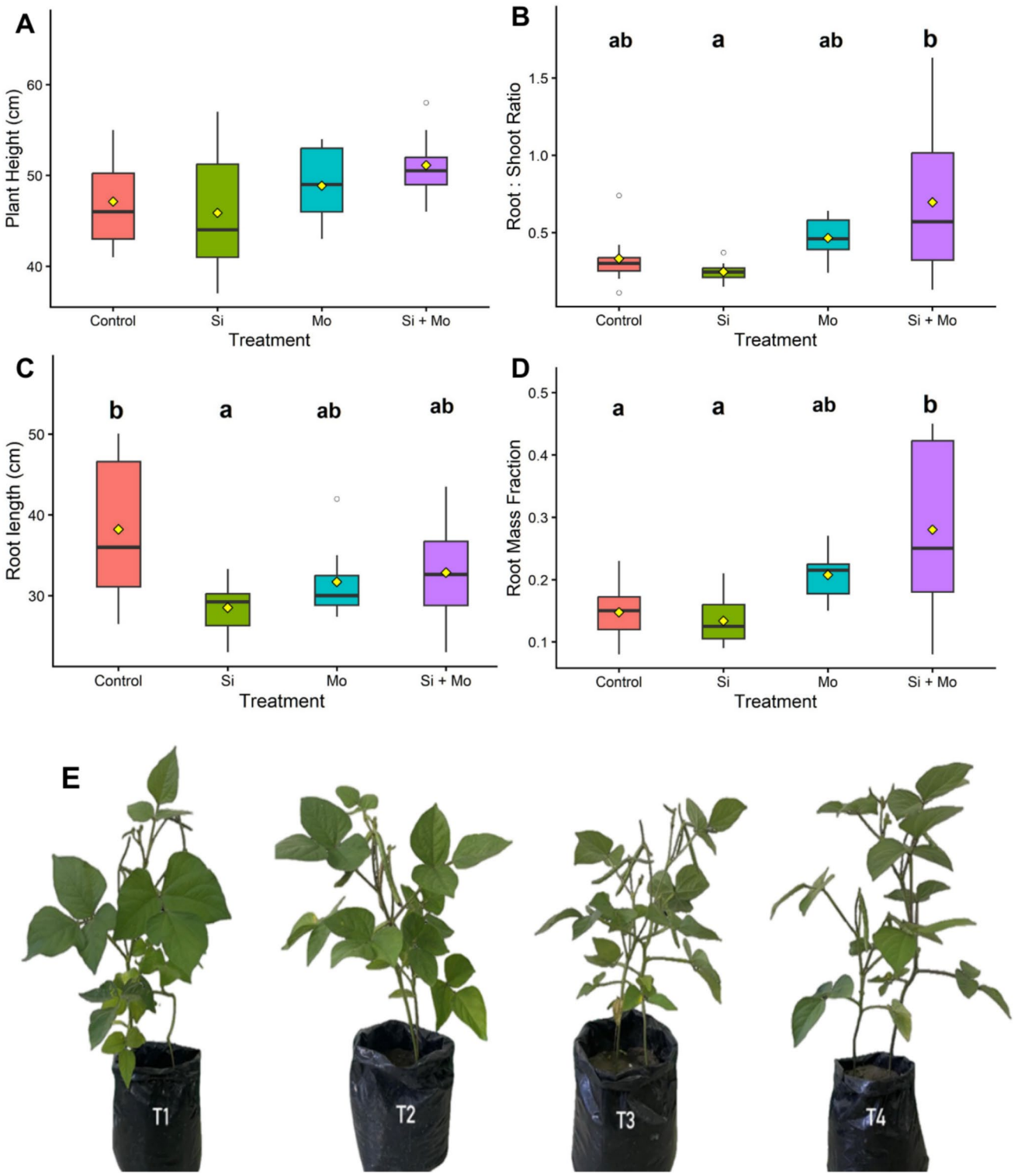


Fig. 1 Plant growth and root partitioning of mungbean and representative morphology of mung bean plants grown under different micronutrients at the reproductive stage. Treatments include T1: control (no micronutrient input), T2: silicon (Si), T3: molybdenum (Mo), and T4: combined silicon and molybdenum (Si + Mo)

Table 2 Biomass accumulation and partitioning of mungbean as affected by silicon, molybdenum, and their combined application

Treatment	Shoot Fresh Weight (g)	Shoot Dry Weight (g)	Root Fresh Weight (g)	Root Dry Weight (g)	Nodule Fresh Weight (mg)
Control	22.51 ± 1.46 [a]	4.80 ± 0.63 [a]	4.04 ± 0.22 [a]	1.72 ± 0.10 [a]	19.93 ± 1.29 [a]
Silicon (Si)	25.76 ± 0.95 [a]	4.27 ± 0.59 [a]	4.27 ± 0.20 [a]	1.51 ± 0.07 [a]	22.78 ± 1.19 [ab]
Molybdenum (Mo)	24.97 ± 1.22 [a]	7.78 ± 0.78 [b]	7.78 ± 0.36 [b]	2.53 ± 0.14 [ab]	28.40 ± 2.05 [b]
Si + Mo	27.75 ± 1.24 [a]	6.07 ± 0.79 [ab]	6.07 ± 1.06 [ab]	3.61 ± 0.32 [b]	26.47 ± 2.27 [ab]
p value	0.384	0.005	0.005	0.013	0.024

Means ± SE followed by the same letter within a column are not significantly different at $p \leq 0.05$ according to Tukey's HSD test.

highest nodule biomass (28.40 mg plant^{-1}), followed closely by the combined Si + Mo treatment (26.47 mg plant^{-1}). Silicon alone produced a moderate increase relative to the control, which recorded the lowest nodule fresh weight (19.93 mg plant^{-1}). These results confirm the strong role of Mo in enhancing nodulation, with Si contributing modestly when applied alone.

3.3 Yield-related traits of mung bean

Yield components and agronomic traits are presented in Table 3. Pod number per plant differed significantly among treatments ($p = 0.023$). The control produced the highest pod number (18.29), while the lowest was recorded under combined Si + Mo application (10.29). Optimum pod numbers were observed under individual Si and Mo treatments. Total seed number per plant was also significantly affected by mineral application ($p = 0.020$). Plants treated with Mo produced the highest number of seeds (72.00 plant^{-1}), whereas the combined Si + Mo treatment recorded the lowest value (45.88 plant^{-1}). Control and Si-only treatments produced intermediate seed numbers. Seed yield per plant varied significantly among treatments ($p = 0.040$). Molybdenum application resulted in the highest seed yield (4.59 g plant^{-1}), followed by the control (3.49 g plant^{-1}). Silicon alone and combined Si + Mo treatments produced comparatively lower yields (3.13–3.22 g plant^{-1}). In contrast, hundred-seed weight was not significantly influenced by mineral treatments ($p = 0.160$), with mean values ranging from 6.22 to 6.99 g across treatments.

3.4 Pearson correlation heatmap

The correlation analysis revealed distinct functional linkages among vegetative growth traits, root system attributes, and yield components in mung bean (Fig. 2). Plant height (PH) exhibited a moderate to strong negative correlation with root shoot ratio (RSR; $r = -0.39$) and root mass fraction (RMF; $r = -0.55$), indicating that taller plants tended to allocate proportionally less biomass to belowground structures. Notably, PH was strongly and negatively associated with shoot dry weight (SDW; $r = -0.69$, $p < 0.05$), which signifies that increased vertical growth did not necessarily translate into greater structural biomass accumulation. Root length (RL) displayed a positive correlation with RSR ($r = 0.50$), but was negatively correlated with SDW ($r = -0.57$) and seed yield per plant (SYPP; $r = -0.35$). Among all traits, root shoot ratio (RSR) emerged as a dominant structural trait, showing an exceptionally strong positive correlation with RL ($r = 0.89$, $p < 0.001$) and root dry weight (RDW; $r = 0.76$, $p < 0.01$). However, RSR was negatively associated with SYPP ($r = -0.51$), indicating that greater proportional investment in roots occurred at the expense of reproductive output. A similar trend was observed for RMF, which showed negative correlations with yield-related traits. Nodule weight (NW) exhibited a strong positive correlation with NP ($r = 0.65$, $p < 0.05$) while shoot fresh weight (SFW) was negatively associated with number of seeds per plant ($r = -0.83$, $p < 0.001$), suggesting that excessive vegetative growth may reduce assimilate partitioning toward seed development.

Table 3 Effects of silicon, molybdenum, and combined Si + Mo application on yield-related traits of mungbean

Treatment	Pod Number	Seed Number	Seed Yield (g)	100 seed weight (g)
Control	18.29 ± 0.83 [b]	51.13 ± 0.51 [ab]	3.49 ± 0.28 [ab]	6.23 ± 0.28 [a]
Silicon (Si)	15.83 ± 0.53 [ab]	52.63 ± 0.32 [ab]	3.13 ± 0.03 [a]	6.28 ± 0.03 [a]
Molybdenum (Mo)	12.14 ± 0.68 [ab]	72.00 ± 0.41 [b]	4.59 ± 0.16 [b]	6.22 ± 0.16 [a]
Si + Mo	10.29 ± 0.49 [a]	45. 88 ± 0.38 [a]	3.22 ± 0.06 [ab]	6.99 ± 0.06 [a]
P value	0.023	0.020	0.040	0.160

Means ± SE followed by the same letter within a column are not significantly different at $p \leq 0.05$ according to Tukey's HSD test.

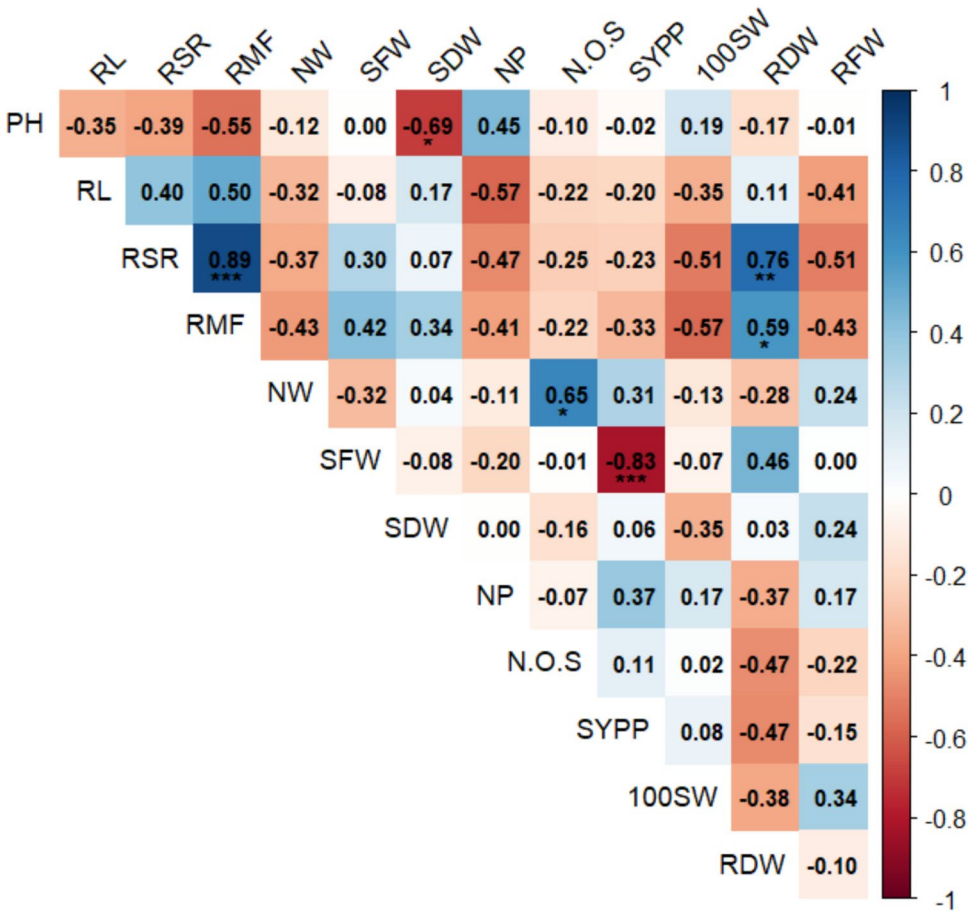


Fig. 2 Pearson correlation matrix among growth, root traits, nodulation, and yield components in mung bean PH- plant height; RL- root length; RSR- root shoot ratio; RMF- root mass fraction; NW- nodule weight; SFW- shoot fresh weight; SDW- shoot dry weight; NP- number of pods; N.O.S- number of seeds; SYPP- seed yield per plant; 100SW- hundred seed weight; RDW- root dry weight

3.5 Scree plot and principal component analysis (PCA)

The scree plot showed that PC1 accounted for 30.9% of the total variance, while PC2 explained 13.0%, giving a cumulative variance of 43.9% for the first two components (Fig. 3). The third and fourth components contributed 10.5% and 9.7%, respectively. The remaining

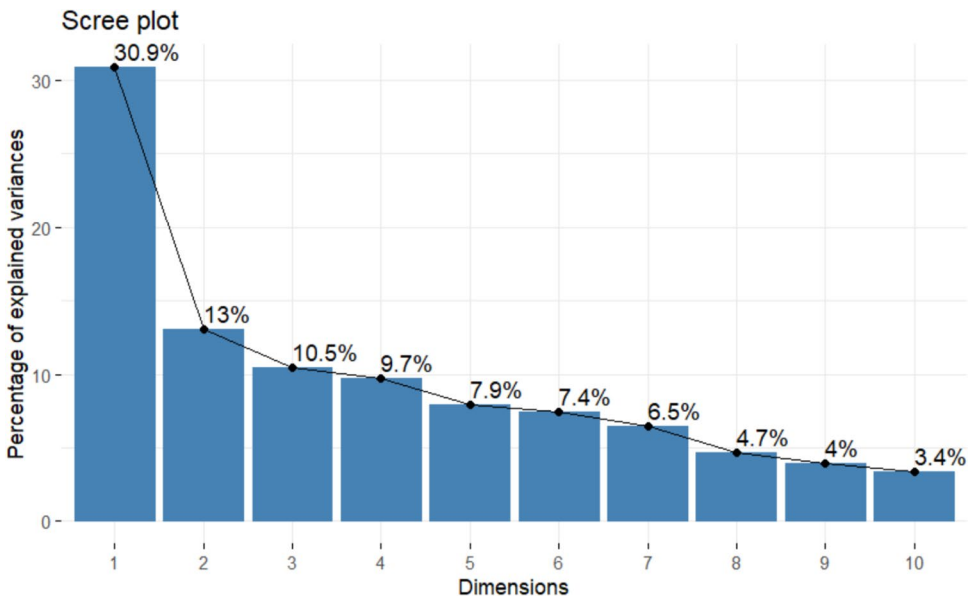


Fig. 3 Scree plot showing the percentage of variance explained by each principal component

components each explained less than 8% of the total variance, with progressively smaller contributions from PC5 (7.9%) to PC10 (3.4%).

The PCA revealed that the first two principal components together accounted for 43.9% of the total variation (Fig. 4). Along the positive side of PC1, the Si + Mo treatment was distinctly separated from the other treatments and showed strong alignment with root fresh weight, root dry weight, root mass fraction, and root–shoot ratio, as indicated by the direction and length of the corresponding vectors. These traits clustered closely together, which shows similar loading patterns along this axis. In contrast, the control treatment was positioned predominantly on the negative side of PC1 and oriented toward seed yield per plant and root length, which were projected in the lower-left quadrant of the biplot. The silicon (Si) treatment was located in the upper region of the ordination space and was associated with plant height, nodule weight, and shoot dry weight toward positive PC2 values. Meanwhile, the molybdenum (Mo) treatment occupied an intermediate location between the control and Si + Mo treatments and aligned with 100-seed weight and shoot fresh weight, which extended toward the central-right region of the plot. PC2 provided additional separation among traits, distinguishing plant height and nodulation-related variables (positive direction) from root length and seed yield per plant (negative direction). Root biomass-related traits were largely concentrated along PC1 with relatively smaller dispersion along PC2.

4 Discussion

The present study evaluated the individual and combined effects of silicon and molybdenum on growth, biomass allocation, nodulation, and yield of mung bean under controlled greenhouse conditions. The results demonstrate that micronutrient supplementation primarily altered belowground traits and biomass partitioning rather than producing uniform increases in shoot growth or reproductive output. These findings underscore the micronutrient effects in short-duration legumes. Plant height was not significantly affected by Si or Mo application, despite clear differences in root biomass and nodulation. This response is consistent with previous reports showing that micronutrient supply can modify internal assimilate allocation and physiological efficiency without increasing final plant stature (Karaman and Türkay 2024). Such outcomes suggest that Si and Mo influenced functional growth processes rather than structural shoot elongation. Root length was reduced under Si, Mo, and combined Si + Mo treatments compared with the control, whereas root biomass, root-to-shoot ratio, and root mass fraction increased, particularly under Mo and Si + Mo application. This pattern indicates a shift from root elongation toward increased root thickening, branching, or fine-root proliferation rather than growth inhibition. Similar architectural adjustments have been reported in legumes and other crops where improved nutrient availability promotes greater biomass density per unit root length, enhancing absorptive capacity without extending maximum root depth (Ramírez-Olvera et al. 2021; Sadhanandan et al. 2025). Such modifications reflect adaptive root plasticity aimed at optimizing nutrient uptake and symbiotic interactions.

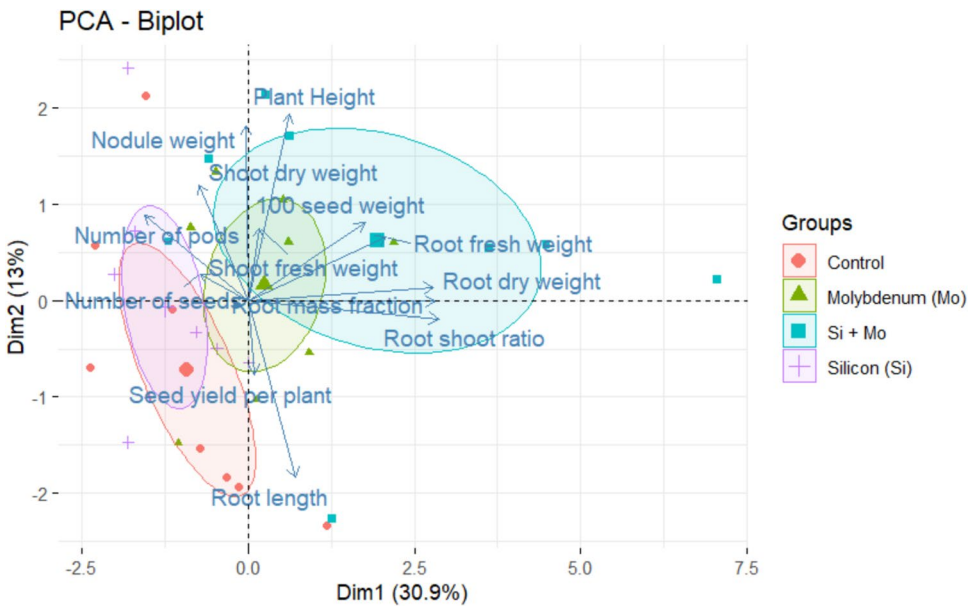


Fig. 4 PCA biplot illustrating the multivariate relationships among growth, biomass allocation, and yield-related traits of mung bean under silicon (Si), molybdenum (Mo), and combined Si + Mo treatments. The first two principal components (PC1 and PC2) explain 30.9% and 13.0% of the total variance, respectively. Arrows represent variable loadings, while points and ellipses denote treatment group scores and dispersion

The substantial increase in root biomass and nodule fresh weight under Mo application aligns with the established role of Mo as a key cofactor of nitrogenase and nitrate reductase, directly supporting BNF and nitrogen assimilation (Banerjee et al. 2022; Bursakov et al. 2023; Threatt et al. 2023). Enhanced nodulation under Mo treatment likely reflects improved functional symbiosis with rhizobia, increasing nitrogen acquisition potential (Bhavana et al. 2025; Guanzon and Tuazon 2026). Larger nodules are often associated with higher nitrogenase activity and leghemoglobin content, which improve the efficiency of N_2 fixation (Luan et al. 2025; Li et al. 2023; Zulfiqar et al. 2025). However, responses to Mo are strongly dose-dependent, and several studies indicate that benefits plateau or decline at higher application rates (Zhou et al. 2023b).

Silicon applied alone resulted in modest changes in root biomass and nodulation, consistent with its classification as a beneficial rather than essential element for legumes. Recent mechanistic studies demonstrate that Si can enhance nodule functioning by modifying the nodule ionome and proteome, stabilizing antioxidant systems, and improving cellular homeostasis, thereby indirectly supporting nitrogen fixation (Coquerel et al. 2023, 2024; Etesami and Shafiei. 2020). Importantly, the positive effects of Si on nodulation and N_2 fixation appear to be highly dependent on the environment and are most pronounced under nutrient deficiency, abiotic stress, or when rhizobial efficiency is low (Putra et al. 2022; Etesami 2024; Guanzon et al. 2026). The relatively limited response to Si observed in the experiment suggests that such stress-mitigating benefits were not fully expressed under the controlled growth conditions. The combined Si + Mo produced the greatest allocation of biomass to roots and relatively high nodule biomass; however, this response did not translate into increased yield. Instead, crop yields were reduced relative to Mo alone and, in some cases, the control. This outcome is consistent with a root–reproductive sink trade-off, a well-documented phenomenon in legumes. Nodules are strong carbon sinks, and increased investment in root and nodule biomass can reduce assimilate availability for reproductive development when carbon supply is finite (Parvin et al. 2020; Dwivedi et al. 2021). Under short-duration conditions, such trade-offs may be amplified, leading to enhanced belowground investment at the expense of pod and seed formation.

The superior yield performance observed under Mo alone indicates that Mo supply optimized nodulation efficiency and nitrogen assimilation without imposing excessive carbon demand on belowground sinks. In legumes, BNF constitutes a substantial metabolic cost, and its benefit to reproductive development depends on a finely regulated balance between carbon availability and sink activity (Yang et al. 2024; Putra et al. 2022). In this study, Mo appeared to enhance this balance, allowing improved nitrogen metabolism to be effectively coupled with seed set and biomass partitioning toward reproductive organs (Hasanah et al. 2024; Guanzon and Rivera 2025). In contrast, the combined Si + Mo treatment may have intensified root and nodule sink strength beyond the threshold that maximizes reproductive return. Enhanced root proliferation and nodular biomass, while physiologically advantageous under stress, can redirect assimilates away from developing pods when conditions are non-limiting. The relatively high Mo rate used here may also have approached supra-optimal levels, particularly in the presence of Si-mediated improvements in root uptake efficiency (Sinky et al. 2023; Coquerel et al. 2025). When micronutrient uptake is amplified, tissue Mo concentrations may increase beyond the range that sustains efficient enzymatic activity, potentially perturbing micronutrient homeostasis or rhizosphere microbial equilibrium. Recent studies indicate that excessive Mo availability can disrupt nutrient interactions and microbial functioning, resulting in neutral or even negative plant responses (Zhou et al. 2023a; Özkan et al. 2024). Such physiological and microbiological imbalances may partly explain the diminished yield observed under combined Si + Mo application.

The PCA further substantiated these findings by resolving distinct multivariate trajectories. The Si + Mo combination clustered predominantly with root biomass allocation variables, whereas Mo alone was more closely aligned with nodulation efficiency and yield-related traits. This separation reflects coordinated trait syndromes rather than functional synergy. In other words, the enhanced vegetative investment under Si + Mo constituted a divergent allocation strategy, not an additive pathway toward reproductive enhancement (Zhou et al. 2023a). This finding provides an important conceptual clarification: increased nodulation or root biomass should not be interpreted automatically as a proxy for yield improvement, particularly when carbon economy becomes the limiting integrator of plant performance. Yield responses to micronutrient supplementation in legumes are inherently nonlinear and context-dependent (Cun et al. 2025; Ali et al. 2023). Within this framework, the present results suggest that Mo fertilization operates within an optimum response window, beyond which incremental inputs—especially when combined with elements that stimulate root vigor—may shift the source–sink balance away from reproductive efficiency. The positive effects of Mo alone on seed number and seed yield per plant are consistent with established evidence that Mo enhances nitrate reductase activity, symbiotic nitrogen fixation, photosynthetic efficiency, and reproductive development in legumes grown on Mo-deficient soils (Banerjee et al. 2022; Jamali et al. 2023; Gonzalez-Porras et al. 2024).

Conversely, the absence of yield enhancement under Si + Mo application underscores that structural improvements in root architecture or nodulation intensity do not inherently translate into greater reproductive output under

controlled greenhouse conditions, where abiotic stress mitigation—one of silicon's primary functional advantages—may not be a limiting factor. Collectively, these findings advance the concept that micronutrient synergy is conditional rather than universal, governed by carbon allocation thresholds and nutrient homeostasis. This nuanced perspective helps refine nutrient management strategies in legumes by emphasizing that optimal performance depends not simply on maximizing physiological traits, but on synchronizing them with whole-plant carbon economics and reproductive priorities.

5 Conclusion

The study showed that silicon (Si) and molybdenum (Mo) differentially regulate biomass partitioning and yield in mung bean under greenhouse conditions. Responses were more pronounced in belowground traits than in shoot growth, indicating that mung bean is particularly sensitive to shifts in root–nodule allocation rather than overall vegetative expansion. Mo alone consistently increased root biomass, nodule fresh weight, seed number, and seed yield per plant, supporting its established role in nitrogen fixation and assimilation. These results indicate that Mo availability can constrain productivity in low-input systems and that its targeted application enhances reproductive output. In contrast, Si alone had limited influence under non-stress conditions. Notably, the combined Si + Mo treatment increased plant biomass allocation to roots and nodules but reduced pod number and seed yield, representing an allocation trade-off where enhanced belowground sink strength did not translate into reproductive gain. Thus excessive partitioning to nodules may impose a metabolic cost, particularly when micronutrient supply approaches supra-optimal levels. The combined application of Si and Mo did not confer additional yield benefits and may reduce reproductive performance when biomass is shifted toward belowground sinks. Meanwhile, further work should quantify nitrogen fixation, define optimal Mo application rates, and validate these responses under field conditions.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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