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The Dynamics of Seed-Derived Molybdenum Following Seed Priming in Faba Bean (*Vicia faba* L.) and Impact on Nitrogen Accumulation

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ABSTRACT

Molybdenum (Mo) is required for biological nitrogen fixation because it forms part of the FeMo cofactor of nitrogenase. Seed priming has been shown to increase BNF in other legumes, but its effectiveness has not been tested in faba bean (*Vicia faba* L.). This study investigated the dynamics of Mo following seed priming with a Mo solution and whether this improves nodulation or nitrogen accumulation under controlled nitrogen-free conditions. Faba bean seeds were primed with water or 0.4% sodium molybdate for 4 or 16 h. Preliminary seed analyses confirmed that Mo priming substantially increased seed Mo content, from 7- to 17- $\mu\text{g Mo seed}^{-1}$ in water-primed seeds to approximately 395- to 1145- $\mu\text{g Mo seed}^{-1}$ following Mo priming ($F_{7,16} = 5620$, $p < 0.001$), with most Mo initially retained in the testa. Primed seeds were grown in an autoclaved sand–perlite medium supplied with nitrogen- and Mo-free nutrient solution. Across two independent experimental runs ($n = 8$ replicate plants per treatment), nodulation was assessed 30 days after sowing, and biomass, carbon, nitrogen and Mo partitioning were assessed over a 60-day growth period. Mo seed priming had no significant effect on effective nodule number, nodule dry weight, shoot or root biomass, plant nitrogen accumulation or plant carbon accumulation (all $p > 0.05$). However, inferences from mass balance patterns suggest that Mo was progressively mobilised from the testa and redistributed to roots and shoots, particularly following 16-h Mo priming. These results demonstrate that seed-derived Mo is retained in the testa and progressively redistributed to vegetative tissues during early growth but that this redistribution did not translate into improved nodulation or nitrogen accumulation under the conditions tested.

1 | Introduction

Faba bean (*Vicia faba* L.) can contribute to more sustainable arable systems through biological nitrogen fixation (BNF), reducing reliance on synthetic nitrogen (N) fertilisers and supporting rotational N inputs (Köpke and Nemecek 2010). However, BNF is a nutrient-demanding process. In addition to the macronutrients required for plant growth and nodule function, phosphorus (P) and sulphur (S) are frequently reported to colimit

N fixation alongside Mo, because P supports the high energetic cost of nitrogenase activity and nodule development, whereas S is required for the iron–sulphur clusters of nitrogenase and for ferredoxin-mediated electron transport to the enzyme complex (Sulieman and Tran 2015; O'Hara 2001). Several micronutrients are also directly involved in BNF.

Molybdenum (Mo) is of particular importance because it is a structural component of the FeMo cofactor of nitrogenase, the

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enzyme responsible for symbiotic reduction of atmospheric N₂ to ammonia within root nodules (Kim and Rees 2002). Distinct from this symbiotic role, Mo is also required as a cofactor for nitrate reductase, which catalyses the first step of nitrate assimilation in nonsymbiotic N metabolism, and for other molybdoenzymes involved in wider plant N and redox metabolism (Williams and Fraústo da Silva 2002). These are functionally separate Mo-dependent pathways: Nitrogenase activity governs BNF specifically, whereas nitrate reductase activity governs the plant's capacity to assimilate mineral N when it is available. Because plants in the present study were grown under N-free conditions, nitrate reductase-dependent pathways are not expected to have contributed materially to plant N status, and any influence of seed-derived Mo on N accumulation observed here is more plausibly linked to nitrogenase-dependent BNF. This distinction links Mo supply to both symbiotic and nonsymbiotic N acquisition pathways (Banerjee and Nath 2022). Plants take up Mo predominantly as molybdate (MoO₄²⁻) from the soil, after which it must be transported to tissues with high Mo demand, including nodules (Bursakov et al. 2023).

Seed priming is a controlled presowing hydration treatment that allows seeds to initiate pregerminative metabolic processes without radicle emergence (Paparella et al. 2015). When micronutrients are included in the priming solution, they may be taken up into seed tissues and subsequently become available to the developing seedling.

Additional Mo, primarily delivered through seed priming, has been shown to improve BNF in other legumes. For example, in common bean (*Phaseolus vulgaris*), Majda et al. (2019) reported that seed priming with 0.1% ammonium molybdate for 10 h substantially increased seed Mo concentration and was associated with increased BNF, enhanced CO₂ assimilation and a reported 115% increase in grain yield. Similarly, in chickpea (*Cicer arietinum*), Umair et al. (2011) compared seed priming with 0.02% and 0.04% sodium molybdate for 5 h and reported increases in seed yield, dry matter production, N accumulation and BNF parameters relative to untreated controls. Notably, these and other previously reported studies of Mo seed priming were conducted in field soils rather than under controlled, Mo-free conditions; background soil Mo availability was therefore not consistently reported or controlled, making it difficult to establish whether the observed benefits of priming reflect correction of soil Mo deficiency or a more general effect of seed Mo supply independent of soil status.

Faba bean differs from the smaller seeded legumes in which Mo seed priming has previously been tested, such as common bean, chickpea and mung bean, in having a substantially larger seed mass and a proportionally larger testa. These anatomical differences may alter both the capacity of the seed to take up and retain Mo during priming and the relative contribution of seed-derived Mo reserves to early seedling and nodule Mo demand, such that findings from smaller seeded legumes may not translate directly to faba bean. No published study has evaluated Mo seed priming as a strategy for improving nodulation and symbiotic N acquisition in faba bean, nor has any study determined where primed Mo is initially localised within the seed or how it is redistributed during plant development. The aim of this study

was to characterise the localisation and mobilisation of seed-derived Mo following priming and to determine whether the resulting increase in Mo availability influences nodulation and plant N accumulation under controlled, N-free conditions. We hypothesised that seed-derived Mo would accumulate within the seed during priming and be progressively mobilised from the testa to roots and shoots during early development and that enhanced Mo availability would increase nodulation and plant N accumulation, as demonstrated in other legumes.

2 | Materials and Methods

2.1 | Plant Material and Seed Priming Treatments

Faba bean (*Vicia faba* L. cv. Vertigo) seeds were used throughout. Seeds were selected to be uniform in size and free from visible bruchid beetle (*Bruchus rufimanus*) damage. Mean seed weight of cv. Vertigo was 0.69 g (five-seed mass: 3.45 ± 0.05 g). Prior to priming, unprimed seeds contained low endogenous Mo reserves (approximately 5- to 17-μg Mo seed⁻¹; Section 3.1), which is relevant to interpreting whether endogenous seed Mo reserves were already sufficient to meet early plant Mo demand (see Section 4). Before priming, seeds were surface-sterilised in 1% (v/v) sodium hypochlorite for 5 min and rinsed six times with ultrapure water. All seed handling, priming and tissue separation (e.g., testa/embryo dissection) was carried out using washed glassware and single-use gloves, with seeds rinsed three times in ultrapure water after priming, to minimise the risk of cross-contamination with environmental Mo.

Sodium molybdate dihydrate (Na₂MoO₄·2H₂O; ≥99% purity) was used as the Mo source. Sodium molybdate was selected rather than ammonium molybdate to avoid introducing additional N during priming. A 0.4% (w/v) sodium molybdate solution was prepared in ultrapure water. Seeds were primed at a solution-to-seed ratio of 1:5 (w/v) (Majda et al. 2019).

Five seed treatments were used: unprimed control, water-primed for 4 h, water-primed for 16 h, Mo-primed with 0.4% sodium molybdate for 4 h and Mo-primed with 0.4% sodium molybdate for 16 h. The two Mo treatments were selected from preliminary seed-loading experiments because 0.4% Mo for 4 h produced a lower Mo treatment, whereas 0.4% Mo for 16 h produced a high Mo treatment. Water-primed treatments were included to distinguish effects of hydration from those of Mo addition. After priming, seeds were rinsed three times with ultrapure water. Average moisture content was 33.6% and 31.6% for the 4 h water- and Mo-primed seeds respectively and 48.1% and 47.4% for the 16-h treatments.

2.2 | Preliminary Determination of Seed Mo Loading and Localisation

A preliminary seed analysis was conducted to confirm that the selected priming treatments produced contrasting seed Mo contents and to determine the initial localisation of Mo within the seed. Seeds were primed with water or 0.4% sodium molybdate for either 4 or 16 h. After priming and rinsing, seeds were manually separated into testa and embryo tissues. These parts were

dried at 60°C to constant weight, milled to a fine powder and analysed for Mo concentration by ICP-MS (NexION 1000, Perkin Elmer Inc., Shelton, USA) using a calibration curve prepared with Mo standards at 0, 25, 50, 100, 200 and 400 ppb. Mo content was calculated from dry biomass and Mo concentration.

2.3 | Growth Medium, Nutrient Solution and Rhizobial Inoculation

Plants were grown in a 1:1 (v/v) mixture of autoclaved horticultural sand and perlite. The growth medium was selected to minimise background N and Mo availability. The perlite component had a neutral pH of 7 and a particle size of 2–5 mm; cation exchange capacity of the growth medium was not measured. Plants were supplied with a modified N-free Hoagland nutrient solution adapted from Broughton and Dilworth (1971), with the Mo-containing salt omitted. Phosphorus and sulphur were supplied via monopotassium phosphate (KH_2PO_4) and sulphate salts ($\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, K_2SO_4 and trace metal sulphates), respectively. Based on the stock solution composition (five stock solutions combined at 2.5 mL each per 5 L of final solution), the working nutrient solution contained approximately 0.50-mM phosphorus and 0.50-mM sulphate, with an estimated total ionic strength of approximately 5.3 mM. The final solution pH was adjusted to 6.6–6.8 using 1-M NaOH. Each pot received 100-mL nutrient solution once per week, and additional deionised water was supplied as required.

Following priming and rinsing, seeds were not dried back to their original moisture content before sowing; instead, primed and unprimed seeds were transferred directly to pregermination trays containing autoclaved horticultural sand and pregerminated for 10 days. Uniform seedlings were selected for transplanting. Seedlings were inoculated immediately before transplanting by dipping roots into a suspension of *Rhizobium leguminosarum* bv. viciae strain JHI24, originally isolated by Maluk et al. (2022), to ensure a uniform rhizobial background. Strain JHI24 was previously shown to perform effectively with faba bean cv. Vertigo in a sand-vermiculite growth medium supplied with an N-free nutrient solution (Maluk et al. 2022); its effectiveness had not, however, been specifically evaluated under Mo-deficient conditions, and the present study additionally imposed a Mo-free nutrient solution, which was not a feature of the strain's original validation. Inoculum density was standardised across preparation batches by optical density (OD_{600}) prior to inoculation, minimising batch-related variation in rhizobial dose between treatments.

2.4 | Experimental Design and Plant Growth Conditions

Each experimental unit consisted of one pot with one plant. For each experimental run, pots from each seed treatment were allocated to one of two destructive harvests. Half of the pots were harvested at 30 days after sowing for nodulation assessment, and the remaining half were harvested at 60 days after sowing for biomass, C and N accumulation. Each harvest therefore included the five seed treatments with four replicate pots per treatment, giving 20 pots per harvest per run. The entire

experimental run was repeated twice, such that each treatment had eight replicates in total.

Plants were grown under controlled glasshouse conditions at Harper Adams University, Shropshire, UK. The first run began on 5 September 2025 and the second on 6 October 2025. Glasshouse conditions during the first run were approximately 22°C day and 17°C night under a 14-h photoperiod. During the second run, conditions were approximately 18°C day and 15°C night, also under a 14-h photoperiod. Pots of 1-L volume were placed on individual saucers to prevent cross-contamination and arranged in a completely randomised design.

2.5 | Nodulation Assessment

At 30 days after sowing, plants were carefully removed from pots and roots were washed free of growth medium. Nodules were counted and classified as effective or ineffective based on internal colour. Nodules were dried at 60°C to constant weight and weighed to determine total nodule dry biomass. Mean nodule dry weight was calculated by dividing total nodule dry biomass by nodule number. Testas were recovered and retained for Mo analysis.

2.6 | Biomass, C and N Analysis

At 60 days after sowing, shoot height was measured from the growth medium surface to the terminal bud. Plants were separated into shoots and roots, dried at 60°C to constant weight and weighed. Testas were recovered and retained for Mo analysis. Dried shoot and root samples were milled to a fine powder using a hammer mill fitted with a 1-mm sieve. C and N concentrations were determined by dry combustion using a LECO CN-828 analyser (LECO Corp., USA). Shoot, root and total plant C and N contents were calculated from dry biomass and tissue C or N concentration. Samples of the sand-perlite growth medium were analysed before sowing and after 60 days for background N and Mo concentrations.

2.7 | Mo Analysis and Tissue Partitioning

Mo concentrations were quantified in testas at Day 0 and in testas, roots and shoots at 30 and 60 days after sowing. Samples were dried, milled and digested before analysis by ICP-MS as previously described. Mo content was expressed as Mo content in each tissue and as the proportional distribution of total recovered plant Mo among testa, root and shoot tissues. All Mo concentrations in all treatments and tissues were above the analytical detection limit of the ICP-MS method used.

2.8 | Statistical Analysis

All statistical analyses were conducted in R version 4.3.1. Graphs were generated using ggplot2. Preliminary seed Mo localisation data were analysed using one-way ANOVA across tissue-treatment combinations. Nodulation, biomass, C and N parameters were analysed using two-way ANOVA, with seed treatment and

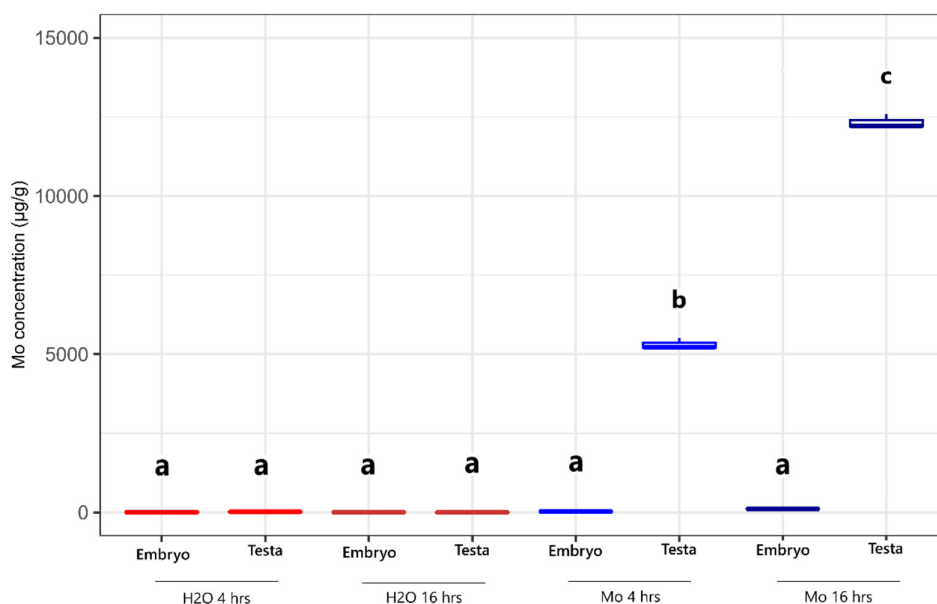


FIGURE 1 | Distribution of molybdenum (Mo) concentration ($\mu\text{g g}^{-1}$) between testa and embryo following seed priming in faba bean (*Vicia faba* L.) pooled from two independent experiments, with four replications per experiment. Different letters denote significant differences between tissues and treatments (one-way ANOVA followed by post hoc Tukey's HSD; $p < 0.05$).

experimental run as fixed factors. Treatment $\times$ run interactions were included initially and interpreted where significant. Where interactions were not significant, main effects were interpreted.

For Mo concentration and Mo content, two-way ANOVA models were fitted with seed treatment and sampling time as fixed factors. Where required, data were log-transformed to improve normality and homogeneity of variance. Assumptions of normality and homogeneity of variance were assessed visually using residual diagnostic plots (e.g., Q-Q plots and residuals-versus-fitted plots) prior to interpreting ANOVA results; data were log-transformed where these diagnostics indicated a violation of model assumptions. Post hoc comparisons were performed using Tukey's HSD. Differences were considered significant at $p < 0.05$.

3 | Results

3.1 | Mo Seed Priming Increased Seed Mo Content and Mo Accumulated Predominantly in the Testa

Preliminary seed analyses confirmed that the selected Mo priming treatments produced contrasting seed Mo contents. Water-primed seeds contained low Mo concentrations (7- to $17\text{-}\mu\text{g Mo seed}^{-1}$), whereas priming with 0.4% sodium molybdate substantially increased seed Mo content. Seeds primed with 0.4% Mo for 4 h contained approximately $395\text{-}\mu\text{g Mo seed}^{-1}$, whereas seeds primed with 0.4% Mo for 16 h contained approximately $1145\text{-}\mu\text{g Mo seed}^{-1}$.

Mo localisation differed strongly between seed tissues ($F_{7,16} = 5620$, $p < 0.001$; Figure 1). In water-primed seeds, Mo concentrations were low in both testa ($\sim 7\text{-}\mu\text{g g}^{-1}$) and embryo ($\sim 4\text{-}\mu\text{g g}^{-1}$) tissues. In Mo-primed seeds, Mo accumulated predominantly in the testa. Testa Mo concentration reached $5307\text{-}\mu\text{g g}^{-1}$ after 4-h Mo priming and $12,327\text{-}\mu\text{g g}^{-1}$ after 16-h Mo priming. Although Mo was detected in the embryo of Mo-primed

seeds, embryo Mo concentrations remained substantially lower than testa concentrations and did not differ significantly from water-primed treatments. Mo-primed testas also developed a visible dark red to burgundy colouration, indicating a clear physical change associated with Mo loading.

3.2 | Growth Medium N and Mo Concentrations Were Low

Before sowing, the sand-perlite growth medium contained low concentrations of both N and Mo. Total N concentration was $12\text{-}\mu\text{g g}^{-1}$, and Mo concentration was $3.89\text{-}\mu\text{g g}^{-1}$. After 60 days of plant growth, N concentration in the growth medium increased slightly to $78\text{-}\mu\text{g g}^{-1}$, whereas Mo concentration decreased to $0.42\text{-}\mu\text{g g}^{-1}$. These results confirmed that plants were grown under low external N and Mo availability.

3.3 | Mo Seed Priming Did Not Increase Early Nodulation

All nodules observed at 30 days after sowing were visually classified as effective. Seed treatment had no significant effect on effective nodule number, total nodule dry weight or mean nodule dry weight (Table 1). Effective nodule number ranged from 62 to 85 nodules plant^{-1} across treatments. Total nodule dry weight ranged from 28.8 to 42.0 mg plant^{-1} . Although nodule biomass was numerically higher in some Mo-primed treatments, these differences were not statistically significant.

Experimental run had a significant effect on all nodulation variables, including effective nodule number ($p < 0.001$), total nodule dry weight ($p < 0.001$) and mean nodule dry weight ($p < 0.001$). However, no treatment $\times$ run interactions were detected for any nodulation parameter. Therefore, although nodulation differed

between runs, the lack of a Mo priming effect was consistent across both runs.

3.4 | Mo Seed Priming Did Not Increase Biomass, C or N Accumulation

At 60 days after sowing, seed treatment had no significant effect on shoot dry weight, root dry weight, total plant dry weight, shoot height, shoot N content, root N content, total plant N

content, shoot C content, root C content or total plant C content (Tables 1 and 2). Total plant dry weight ranged from 7.35 to 8.59 g plant⁻¹ across treatments, whereas total plant N ranged from 0.198 to 0.219 g plant⁻¹. Shoot N content ranged from 0.100 to 0.109 g plant⁻¹, and root N content ranged from 0.095 to 0.112 g plant⁻¹.

Experimental run significantly affected root dry weight, total plant dry weight and root N content but did not significantly affect shoot dry weight, shoot height, shoot N content or total

TABLE 1 | Summary of two-way ANOVA results for nodulation, biomass, nitrogen and carbon parameters in faba bean following seed priming treatments. *F* values and *p* values are shown. Significance is indicated as *p* < 0.05 (*), *p* < 0.01 (**) and *p* < 0.001 (***). n.s. denotes non-significant effects. Treatment and treatment × run effects have degrees of freedom *F*_{4,30}; run effects have degrees of freedom *F*_{1,30}.

Harvest	Response variable	Treatment	Run	Treatment × run
30 days	Effective nodule number	<i>F</i> = 1.14, <i>p</i> = 0.36 n.s.	<i>F</i> = 13.70, <i>p</i> < 0.001***	<i>F</i> = 0.26, <i>p</i> = 0.90 n.s.
30 days	Total nodule dry weight	<i>F</i> = 2.01, <i>p</i> = 0.12 n.s.	<i>F</i> = 7.70, <i>p</i> < 0.001**	<i>F</i> = 0.13, <i>p</i> = 0.97 n.s.
30 days	Average nodule dry weight	<i>F</i> = 1.19, <i>p</i> = 0.34 n.s.	<i>F</i> = 21.03, <i>p</i> < 0.001***	<i>F</i> = 0.58, <i>p</i> = 0.68 n.s.
60 days	Shoot dry weight	<i>F</i> = 0.29, <i>p</i> = 0.88 n.s.	<i>F</i> = 1.29, <i>p</i> = 0.27 n.s.	<i>F</i> = 0.15, <i>p</i> = 0.96 n.s.
60 days	Root dry weight	<i>F</i> = 0.84, <i>p</i> = 0.51 n.s.	<i>F</i> = 17.11, <i>p</i> < 0.001***	<i>F</i> = 0.07, <i>p</i> = 0.99 n.s.
60 days	Total plant dry weight	<i>F</i> = 0.52, <i>p</i> = 0.73 n.s.	<i>F</i> = 9.28, <i>p</i> < 0.001***	<i>F</i> = 0.11, <i>p</i> = 0.98 n.s.
60 days	Shoot height	<i>F</i> = 0.31, <i>p</i> = 0.87 n.s.	<i>F</i> = 0.21, <i>p</i> = 0.65 n.s.	<i>F</i> = 0.98, <i>p</i> = 0.44 n.s.
60 days	Shoot N	<i>F</i> = 0.26, <i>p</i> = 0.90 n.s.	<i>F</i> = 2.21, <i>p</i> = 0.15 n.s.	<i>F</i> = 0.56, <i>p</i> = 0.70 n.s.
60 days	Root N	<i>F</i> = 0.59, <i>p</i> = 0.67 n.s.	<i>F</i> = 6.45, <i>p</i> < 0.05*	<i>F</i> = 0.22, <i>p</i> = 0.93 n.s.
60 days	Total N	<i>F</i> = 0.27, <i>p</i> = 0.90 n.s.	<i>F</i> = 0.86, <i>p</i> = 0.36 n.s.	<i>F</i> = 0.41, <i>p</i> = 0.80 n.s.
60 days	Shoot C	<i>F</i> = 0.31, <i>p</i> = 0.87 n.s.	<i>F</i> = 0.64, <i>p</i> = 0.43 n.s.	<i>F</i> = 0.13, <i>p</i> = 0.97 n.s.
60 days	Root C	<i>F</i> = 0.42, <i>p</i> = 0.80 n.s.	<i>F</i> = 2.87, <i>p</i> = 0.10 n.s.	<i>F</i> = 1.45, <i>p</i> = 0.24 n.s.
60 days	Total C	<i>F</i> = 0.29, <i>p</i> = 0.88 n.s.	<i>F</i> = 1.35, <i>p</i> = 0.26 n.s.	<i>F</i> = 0.26, <i>p</i> = 0.90 n.s.

TABLE 2 | Mean nodulation, biomass, nitrogen and carbon parameters in faba bean following seed priming treatments. Values are means ± standard deviation (*n* = 8 plants per treatment). Mo 4 h and Mo 16 h refer to seeds primed with 0.4% sodium molybdate for 4 or 16 h, respectively.

Harvest	Parameter	Unprimed	H ₂ O 4h	Mo 4h	H ₂ O 16h	Mo 16h
30 days	Effective nodule number	62 ± 32	85 ± 29	75 ± 28	83 ± 25	85 ± 34
30 days	Total nodule dry weight (mg)	28.8 ± 12.8	31.9 ± 11.3	42.0 ± 8.9	39.8 ± 17.2	41.0 ± 10.4
30 days	Average nodule dry weight (mg)	554 ± 211	411 ± 197	684 ± 387	551 ± 413	565 ± 272
60 days	Shoot dry weight (g)	3.75 ± 1.17	3.98 ± 0.84	3.76 ± 0.72	4.18 ± 0.94	3.78 ± 0.95
60 days	Root dry weight (g)	3.74 ± 1.94	3.48 ± 0.83	4.10 ± 1.12	4.41 ± 1.39	3.56 ± 1.47
60 days	Total plant dry weight (g)	7.49 ± 3.02	7.46 ± 1.42	7.86 ± 1.56	8.59 ± 2.09	7.35 ± 2.18
60 days	Shoot height (cm)	60.0 ± 12.4	61.8 ± 11.5	58.1 ± 7.2	63.5 ± 10.2	62.5 ± 10.8
60 days	Shoot N (g)	0.100 ± 0.024	0.109 ± 0.018	0.103 ± 0.013	0.106 ± 0.023	0.104 ± 0.025
60 days	Root N (g)	0.097 ± 0.034	0.095 ± 0.018	0.109 ± 0.023	0.112 ± 0.033	0.097 ± 0.035
60 days	Total N (g)	0.198 ± 0.052	0.204 ± 0.027	0.209 ± 0.024	0.219 ± 0.051	0.201 ± 0.051
60 days	Shoot C (g)	1.57 ± 0.51	1.66 ± 0.35	1.56 ± 0.28	1.75 ± 0.41	1.57 ± 0.40
60 days	Root C (g)	0.71 ± 0.16	0.78 ± 0.22	0.69 ± 0.14	0.70 ± 0.16	0.69 ± 0.18
60 days	Total C (g)	2.28 ± 0.65	2.44 ± 0.50	2.24 ± 0.28	2.45 ± 0.50	2.26 ± 0.54

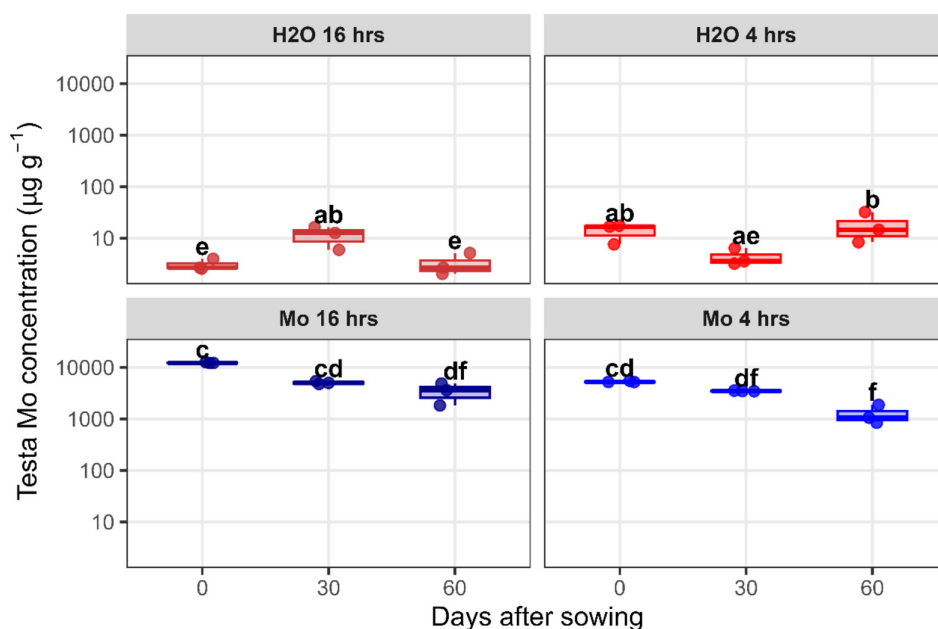


FIGURE 2 | Changes in testa molybdenum (Mo) concentration ($\mu\text{g g}^{-1}$) over time following seed priming treatments in faba bean (*Vicia faba* L.) pooled from two independent experiments, with four replications per experiment. Different letters indicate significant differences among treatments based on two-way ANOVA followed by Tukey's HSD test ($p < 0.05$).

plant N content. No treatment $\times$ run interactions were detected for biomass, C or N parameters. Therefore, Mo seed priming did not alter plant growth or N accumulation despite differences in overall growth between experimental runs.

3.5 | Seed-Derived Mo Was Mobilised From the Testa During Plant Development

Testa Mo concentration was strongly affected by seed treatment, sampling time and their interaction (two-way ANOVA on log-transformed data: treatment, $F_{3,24} = 829.0$, $p < 0.001$; day, $F_{2,24} = 8.80$, $p = 0.001$; treatment $\times$ day, $F_{6,24} = 11.13$, $p < 0.001$; Figure 2). Water-primed seeds had low testa Mo concentrations at all sampling dates. Testa Mo concentration started high and then declined over time in both Mo-primed treatments. In the Mo 16-h treatment, testa Mo concentration decreased from $12,327 \pm 133 \mu\text{g g}^{-1}$ at Day 0 to $5058 \pm 190 \mu\text{g g}^{-1}$ at Day 30 and $3440 \pm 884 \mu\text{g g}^{-1}$ at Day 60. In the Mo 4-h treatment, testa Mo concentration decreased from $5307 \pm 104 \mu\text{g g}^{-1}$ at Day 0 to $3486 \pm 28 \mu\text{g g}^{-1}$ at Day 30 and $1258 \pm 313 \mu\text{g g}^{-1}$ at Day 60. Despite this decline, Mo concentrations in Mo-primed testas remained much higher than those of water-primed controls at all sampling dates.

3.6 | Mo Was Redistributed to Roots and Shoots, Particularly After 16-h Mo Priming

The proportional distribution of recovered Mo among testa, root and shoot tissues changed over time (Figure 3). At Day 0, all measured Mo was located in the testa. By 30 days after sowing, Mo had been redistributed into vegetative tissues in all treatments, although redistribution patterns differed between water- and Mo-primed plants.

In water-primed plants, most recovered Mo was located in the shoot by Day 30. In the water 16-h treatment, 65.0% of recovered Mo was in the shoot, 25.8% in the root and 9.23% in the testa. In the water 4-h treatment, 80.2% was in the shoot, 15.1% in the root and 4.75% in the testa. In contrast, Mo-primed plants retained a larger proportion of recovered Mo in the testa. At Day 30, 73.3% of recovered Mo remained in the testa in the Mo 16-h treatment, whereas 86.2% remained in the testa in the Mo 4-h treatment.

By 60 days after sowing, water-primed plants showed predominantly shoot-associated Mo. In the water 16-h treatment, 95.6% of recovered Mo was located in the shoot. In Mo-primed plants, a substantial proportion of Mo remained in the testa, although redistribution was more pronounced in the Mo 16-h treatment. In the Mo 16-h treatment, recovered Mo was distributed among testa (36.0%), root (33.8%) and shoot (30.2%). In the Mo 4-h treatment, most recovered Mo remained in the testa (71.0%), with smaller proportions in root (16.0%) and shoot (13.0%).

Root Mo content was significantly affected by seed treatment ($F_{3,16} = 7.74$, $p = 0.002$), but not by sampling time, and there was no significant treatment $\times$ time interaction (Figure 4). Root Mo content was low in water-primed treatments. The greatest root Mo content was observed in the Mo 16-h treatment, increasing numerically from $106.7 \pm 77.5 \mu\text{g plant}^{-1}$ at Day 30 to $335.0 \pm 115.5 \mu\text{g plant}^{-1}$ at Day 60. Across harvest dates, the Mo 16-h treatment had significantly greater root Mo content than the water-primed treatments, whereas the Mo 4-h treatment was intermediate.

Shoot Mo content was significantly affected by seed treatment, sampling time and their interaction ($p < 0.001$ for all effects; Figure 5). Shoot Mo content remained low in water-primed

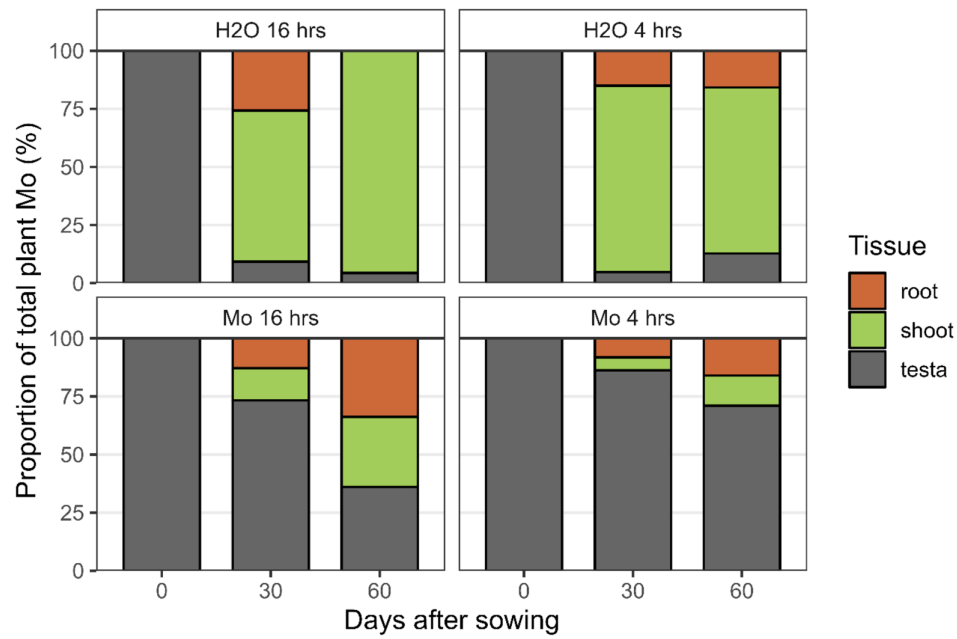


FIGURE 3 | Proportional distribution of total plant molybdenum (Mo) among testa, root, and shoot tissues over time following seed priming treatments in faba bean (*Vicia faba* L.) pooled from two independent experiments, with four replications per experiment.

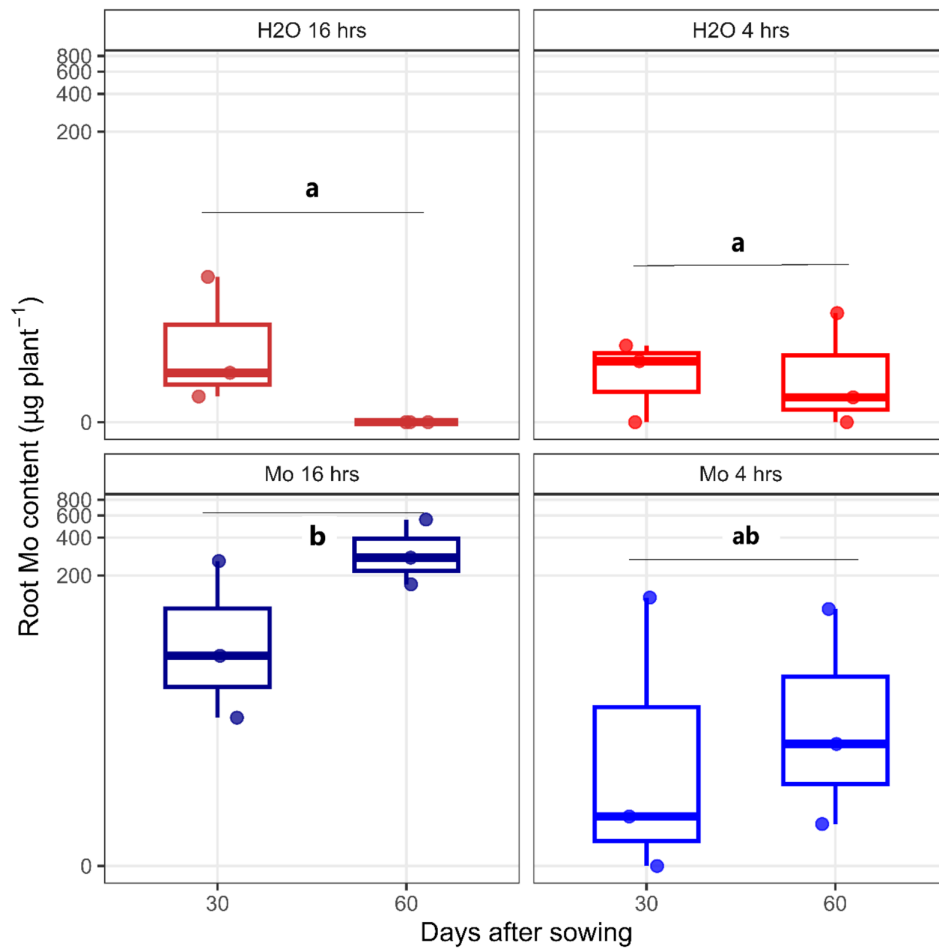


FIGURE 4 | Effect of seed priming treatment and harvest time on root molybdenum (Mo) content (µg plant⁻¹) in faba bean (*Vicia faba* L.) pooled from two independent experiments, with four replications per experiment. Different letters denote significant differences among seed priming treatments based on Tukey's HSD following a two-way ANOVA ($p < 0.05$). Main effects only are interpreted as the treatment × day interaction was not significant.

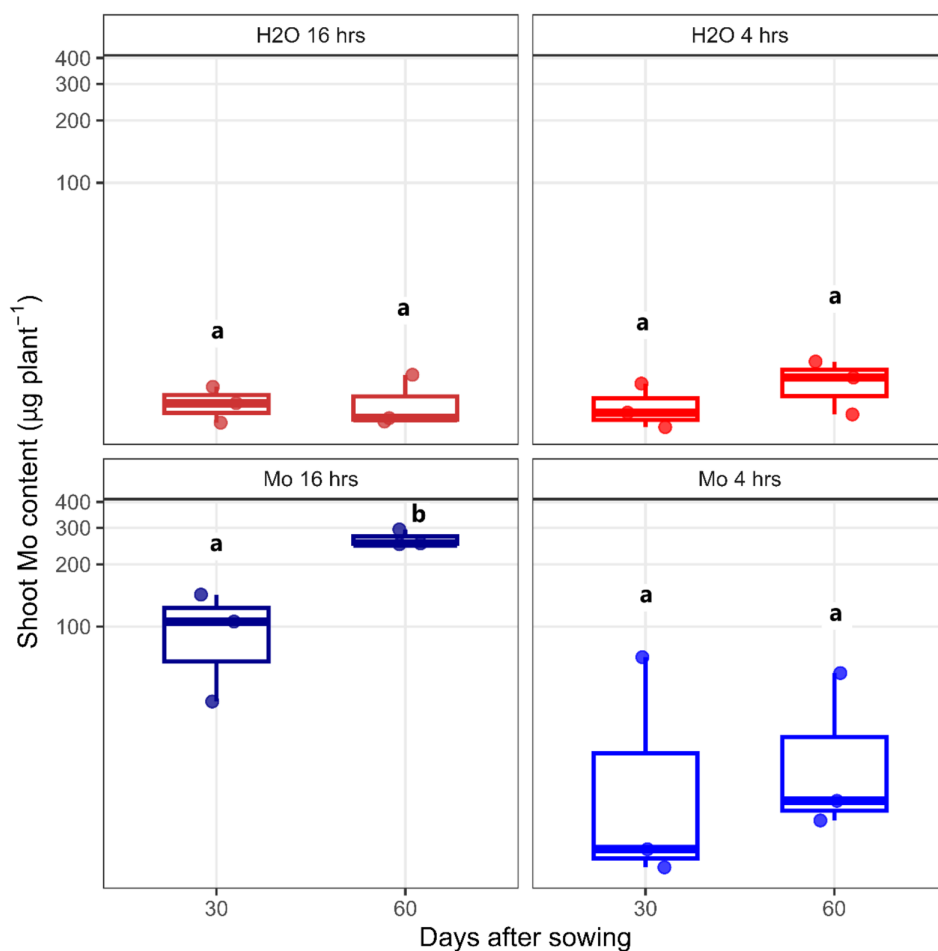


FIGURE 5 | Effect of seed priming treatment and sampling time on shoot molybdenum (Mo) content ($\mu\text{g plant}^{-1}$) in faba bean (*Vicia faba* L.) pooled from two independent experiments, with four replications per experiment. Different letters indicate significant differences across treatments (Tukey's HSD following two-way ANOVA; $p < 0.05$).

treatments at both sampling dates ($1.3\text{--}9.5 \mu\text{g plant}^{-1}$). In the Mo 16-h treatment, shoot Mo content increased from $97.2 \pm 29.1 \mu\text{g plant}^{-1}$ at day 30 to $265.7 \pm 14.5 \mu\text{g plant}^{-1}$ at day 60. The Mo 16-h treatment at day 60 had significantly greater shoot Mo content than all other treatment $\times$ day combinations. In contrast, shoot Mo content in the Mo 4-h treatment remained lower and did not increase between Days 30 and 60.

4 | Discussion

This study tested whether Mo supplied through seed priming is mobilised during early faba bean development and whether this improves nodulation or plant N accumulation under controlled N-free and Mo-limited conditions. The results show that Mo priming was successful in increasing seed Mo content and suggest that Mo in the testa was later redistributed to roots and shoots. However, this increase in plant Mo pools did not result in measurable improvements in nodulation, biomass, C accumulation or N accumulation. The key finding is therefore not that Mo priming failed as a delivery method but that successful Mo delivery did not translate into improved symbiotic performance under the conditions tested. The key finding is that Mo increased tissue Mo content, but this did not translate into improved symbiotic performance under the conditions tested.

4.1 | The Testa Is the Main Initial Reservoir for Primed Mo

Mo priming substantially increased faba bean seed Mo content, particularly after 16-h priming. However, most of this Mo was initially located in the testa rather than the embryo. This suggests that seed Mo content alone may be a poor indicator of immediately available Mo for the developing seedling. In faba bean, Mo seed priming appears to create a large testa-associated Mo reservoir from which only part of the accumulated Mo is subsequently mobilised during early plant development.

This localisation pattern is important for interpreting the biological effect of Mo priming. If a large proportion of primed Mo remains associated with the testa, then the timing and extent of Mo release from the seed coat may determine whether primed Mo is available during the period of nodule initiation and early symbiotic N acquisition.

The strong retention of Mo within the testa suggests that molybdate may interact with seed-coat constituents rather than remaining freely mobile. Faba bean testas contain abundant phenolic compounds, tannins and structural proteins (Zhong et al. 2018) that could potentially provide binding sites for

molybdate, thereby slowing its release during germination and early growth. Although the chemical form of retained Mo was not determined in the present study, such interactions provide a plausible explanation for the delayed and incomplete mobilisation observed. Determining the molecular associations responsible for Mo retention represents an important direction for future research.

4.2 | Seed-Derived Mo Was Mobilised but Not Completely Released From the Testa

Mo concentrations in the testa declined between sowing and 60 days after sowing, whereas root and shoot Mo contents increased, particularly in the Mo 16-h treatment. This demonstrates that Mo accumulated during priming was not permanently immobilised in the seed coat. Instead, a proportion of seed-derived Mo became available to the growing seedling and was transported into vegetative tissues.

However, mobilisation was incomplete. Even at 60 days after sowing, substantial Mo remained in the testa of Mo-primed plants. This was especially clear in the Mo 4-h treatment, where most recovered Mo was still located in the testa. In contrast, the Mo 16-h treatment showed greater redistribution, inferred from mass balance patterns, with recovered Mo distributed more evenly among testa, root and shoot by 60 days. Therefore, increasing priming duration increased both total Mo loading and later Mo transfer to vegetative tissues.

Together, these observations indicate that total seed Mo loading and functional Mo availability are not equivalent. Although Mo priming substantially increased total seed Mo, much of the additional Mo remained associated with the testa throughout early development. Consequently, total seed Mo concentration alone is unlikely to predict the amount of Mo immediately available to developing tissues or to support early symbiotic N acquisition. The present results further demonstrate that increased Mo accumulation within the seed does not necessarily result in greater nodulation or N accumulation. This observation reinforces that the physiological benefits of seed-applied Mo depend on the interaction between micronutrient availability, seed quality and subsequent regulation of N metabolism rather than simply increasing seed Mo concentration (Carmo-Filho et al. 2025).

4.3 | Increased Mo Availability Did Not Improve Nodulation or Plant N Accumulation

Despite clear evidence of increased plant Mo pools, Mo priming had no significant effect on effective nodule number, nodule dry weight or mean nodule size. It also had no significant effect on shoot biomass, root biomass, total plant biomass, shoot N, root N or total plant N. As an N-free growth medium was used, the latter measurements serve as a proxy for BNF, although we acknowledge that plant N accumulation also integrates seed N remobilisation and any residual mineral N uptake, in addition to symbiotically fixed N; background mineral N in the growth medium was very low throughout (Section 3.2), minimising the latter contribution, but a contribution from seed N remobilisation, particularly during very early growth, cannot be excluded.

This lack of response was consistent across two independent experimental runs.

These findings contrast with studies in other legumes in which Mo seed treatments increased BNF, N accumulation or yield (Majda et al. 2019; Umair et al. 2011). However, they are consistent with evidence that seed Mo treatments do not always increase %N derived from the atmosphere or plant growth (Chagas et al. 2010). It should be noted that Chagas et al. (2010) achieved seed Mo enrichment through foliar Mo application to the mother plant rather than through direct seed priming, and the two enrichment routes are not necessarily equivalent in terms of Mo dose, timing or seed tissue localisation; nonetheless, this study similarly demonstrates that elevated seed Mo content does not guarantee improved BNF outcomes. The effectiveness of Mo seed enrichment therefore appears to be context-dependent rather than universal.

One likely explanation is that Mo was not functionally limiting for symbiotic N acquisition in the present system. The growth medium contained a total Mo concentration of $3.89 \mu\text{g g}^{-1}$ before sowing, which declined further to $0.42 \mu\text{g g}^{-1}$ over 60 days of plant growth. Although this total Mo concentration is low relative to some agricultural soils, it is not equivalent to plant-available Mo, and we cannot exclude the possibility that this background Mo, in combination with seed-derived Mo, was sufficient to meet plant Mo demand. Indeed, unprimed faba bean seeds contained approximately $5 \mu\text{g Mo seed}^{-1}$. This is higher than values reported for common bean seeds, which can range from 0.007 to $3.639 \mu\text{g seed}^{-1}$ (Vieira et al. 2011). Although direct comparison between species is complicated by differences in seed size and seedling demand, the endogenous Mo reserve in faba bean seed may have been sufficient to support early nodulation and symbiotic N acquisition.

A second possibility is that Mo was mobilised to roots and shoots but was not delivered to nodules in a way that increased nitrogenase activity. It is important to distinguish here between Mo concentration or content in a tissue and metabolically active Mo that has been incorporated into the FeMo cofactor of nitrogenase: an increase in the former does not necessarily imply an increase in the latter, because seed-derived Mo may be stored, sequestered or allocated to other Mo-dependent enzymes before (or instead of) being incorporated into functional nitrogenase. Root Mo content increased following Mo priming, but nodule Mo concentration was not measured directly, and no attempt was made to distinguish nodule Mo pools from Mo specifically incorporated into the FeMo cofactor. Therefore, increased root Mo cannot be assumed to mean increased Mo availability at the precise site of N fixation. Future studies should quantify Mo specifically in nodules and, ideally, distinguish between total nodule Mo and Mo incorporated into functional nitrogenase, alongside direct functional measurements such as nitrogenase activity (e.g., the acetylene reduction assay), nitrate reductase activity, *nifH* gene expression and ^{15}N natural abundance or ^{15}N isotope dilution, all of which would provide more direct evidence of BNF than the nodulation and N accumulation proxies used here. The use of isotopic methods may also be justified to trace the exact path of micronutrients introduced via seed priming. The present findings further demonstrate that increasing Mo availability within the seed does not necessarily translate into greater nodulation

or biological N fixation, emphasising that Mo supply represents only one component regulating the establishment of an effective legume-rhizobium symbiosis. Recent evidence also highlights that the physiological response to micronutrient availability depends on multiple interacting factors governing rhizosphere functioning and symbiotic efficiency (Moreira et al. 2026).

4.4 | Implications for Mo Seed Priming in Faba Bean

These results indicate that, under the specific experimental conditions adopted here, Mo seed priming did not increase nodulation or plant N accumulation in faba bean, most likely because baseline seed and background Mo reserves were already sufficient to meet plant Mo demand. This should not be generalised to conclude that Mo seed priming is inherently ineffective as a strategy across all faba bean production contexts; rather, it shows that increasing Mo supply through seed priming did not improve nodulation or plant N accumulation under the Mo- and N-replete conditions tested here, even though Mo was successfully loaded into seeds and mobilised into the plant.

Mo availability for BNF is also unlikely to act in isolation from other nutrients. In particular, Mo and P interact both directly and indirectly in the regulation of BNF: P supports the energetic demands of nodule formation and nitrogenase activity, whereas Mo uptake and transport can itself be influenced by plant P status, such that P deficiency could mask or exacerbate the physiological consequences of variation in Mo supply. Because P was supplied in nonlimiting amounts throughout the present study, potential Mo $\times$ P interactions could not be evaluated here, but they represent an important consideration for interpreting Mo priming responses in field soils where P availability is more variable. It is also possible that the absence of a treatment effect reflects the specific developmental window examined.

BNF demand typically increases as nodules mature and canopy N demand rises; if Mo requirements scale with BNF activity, any benefit of additional seed-derived Mo may only become apparent at later developmental stages than those assessed here (30 and 60 days after sowing), particularly under conditions of greater symbiotic N demand than in the present N-free, controlled system.

Mo seed priming may prove more effective under conditions where BNF demand exceeds baseline seed Mo supply, for example, in soils with severe Mo deficiency, in acidic soils where Mo availability is chemically restricted or in legume species or genotypes with lower endogenous seed Mo reserves or higher BNF demand than the faba bean cultivar used here. Future studies testing Mo seed priming across a gradient of soil Mo availability and pH, as well as in genotypes with lower baseline seed Mo content, would help establish the conditions under which this delivery method is agronomically beneficial. Different Mo delivery strategies have been proposed to improve crop nutrition, including fertiliser enrichment and seed treatments. Recent work has demonstrated that incorporation of Mo into urea modifies fertiliser physicochemical properties and may interact with urease inhibitors, illustrating that the agronomic performance of Mo depends not only on plant physiology but also on

the characteristics of the fertiliser source (Moreira et al. 2025). Seed priming therefore represents one of several complementary Mo delivery strategies, alongside soil and foliar application and seed coating (see Section 1), whose relative effectiveness is likely to depend on soil Mo status, crop growth stage and fertiliser formulation.

The strong retention of Mo within the testa may also have broader implications for legume species differing in seed coat composition. If molybdate binding is influenced by testa polyphenols, tannins or other seed coat constituents, cultivars or species with more phenolic-rich testas could differ in the rate at which primed Mo becomes available during germination. Whether this enhances long-term Mo storage or instead delays Mo availability sufficiently to limit early symbiotic N acquisition remains unknown and warrants further investigation.

Several limitations should be acknowledged. Nodule Mo concentration was not measured, so the study cannot determine whether seed-derived Mo reached the nodule in sufficient quantity or at the correct developmental stage. Only one faba bean cultivar and one rhizobial strain were used, so genotype- or strain-specific responses cannot be excluded. Strain JHI24 was previously validated as effective with this cultivar under N-free conditions in a sand-vermiculite medium (Maluk et al. 2022), but its effectiveness had not previously been tested under the combined N- and Mo-free conditions used here, so we cannot fully exclude the possibility that rhizobial performance itself was influenced by Mo availability in this system. The experiment was conducted under controlled glasshouse conditions in an autoclaved sand-perlite medium. This was useful for isolating seed-derived Mo effects but does not capture the complexity of field soils, including variation in soil pH, native Mo availability and its chemical form, indigenous soil microbial and rhizobial community composition and variable climatic conditions, all of which could modify both baseline Mo sufficiency and the response to Mo seed priming under field conditions. Conclusions drawn here should therefore be understood as applying specifically to the controlled, Mo- and N-limited system tested, with field validation needed before extrapolating to agronomic practice. Finally, sodium molybdate was used to avoid adding N during priming; responses may differ with ammonium molybdate or with other nutrient delivery methods.

5 | Conclusions

Mo seed priming substantially increased faba bean seed Mo content, with most Mo initially retained in the testa. During early plant development, Mo was progressively mobilised from the testa and redistributed to roots and shoots, particularly following 16-h Mo priming. However, Mo priming did not increase effective nodule number, nodule biomass, plant biomass, C accumulation or N accumulation under the conditions tested, in a system where baseline seed and background Mo reserves were most likely already sufficient to meet plant Mo demand.

This study provides, to our knowledge, the first systematic characterisation of seed-derived Mo dynamics in faba bean, demonstrating that Mo seed priming creates a large testa-associated Mo reservoir from which Mo is progressively mobilised to root and

shoot tissues during early plant development. This physiological finding represents the principal contribution of this study. Under the conditions tested, endogenous seed Mo and/or background Mo availability were apparently sufficient to support early symbiotic N acquisition, and the additional seed-derived Mo did not increase nodulation or plant N accumulation. The study therefore shows that successful micronutrient loading and redistribution do not necessarily translate into measurable physiological benefits under conditions in which Mo was apparently nonlimiting while providing new evidence that the testa is the principal storage compartment for primed Mo in faba bean.

Author Contributions

Tamanna Kasakaitis: conceptualization, methodology, investigation, formal analysis, writing – original draft. **Euan K. James:** supervision, writing – review and editing. **Pietro P. M. Iannetta:** supervision, writing – review and editing. **Becky Howard:** supervision. **Edward Dickin:** supervision. **James M. Monaghan:** conceptualization, methodology, funding acquisition, writing – review and editing, supervision.

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Ethics Statement

No human participants, human tissue, animals or regulated animal procedures were involved in this study.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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