Plant molybdenum uptake as mediated by synergism with phosphorus but antagonism with sulfur in a fertilized and mown meadow

Yanyan Li
Ruzhen Wang (ruzhenwang@iae.ac.cn)
Institute of Applied Ecology Chinese Academy of Sciences https://orcid.org/0000-0001-8654-6677
Bin Wang
Ying Zhang
Baitao Gu
Zhirui Wang
Heyong Liu
Lijuan Yang
Yong Jiang

Research Article

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Abstract

Purpose Whether molybdenum (Mo) addition promotes Mo uptake by plants in nitrogen-fertilized ecosystems may depend on nutrient interactions. But this has rarely been paid attention to in continuously mown and nutrient-losing grassland ecosystems.

Methods We investigated Mo uptake by three dominant species and how it varied with plant phosphorus and sulfur concentrations after 6-year combined nitrogen and Mo addition and mowing management in a cold meadow.

Results Molybdenum addition increased Mo concentrations in the three plant species across all treatments due to increased soil available Mo. Without Mo addition, nitrogen addition significantly reduced Mo concentrations of *Leymus chinensis* irrespectively of mowing and of *Stipa baicalensis* with mowing. With Mo addition, the negative nitrogen-addition effect on plant Mo absorption was boosted for all plant species. This could be due to the fact that increases in plant sulfur absorption possibly induced antagonistic effects on plant Mo uptake. Additionally, reductions in plant phosphorus concentration weakened the synergistic uptake of Mo by plants with nitrogen addition, except for *Carex duriuscula*. Mowing only reduced Mo concentration of *S. baicalensis* without nitrogen addition under Mo addition.

Conclusions Our results indicated that plant Mo deficiency could occur in nitrogen-fertilized ecosystems via nutrient interplay, facilitating it a necessity to supplement Mo.

Introduction

Molybdenum (Mo) is the least abundant essential trace element in the group of biological micronutrients for sustaining the growth and metabolic cycles of higher plants (Kaiser et al. 2005; Huang et al. 2022). Mo plays vital roles in N assimilation, sulfur metabolism, plant hormone biosynthesis, and stress response (Mendel and Schwarz 2011). However, Mo deficiency is widely reported across the world (Wong et al. 2020). For instance, about 446 million hectares of Chinese farmland lack Mo (Rana et al. 2020a); the soil and plant of pastures in Jeju Island are Mo-deficit (Lee et al. 2007); and Mo deficiency in acidified soils of northeastern India severely impairs plant growth and global food security (Kumar et al. 2016).

A low Mo status commonly occurs in highly weathered acidic soils that are low in organic matter (Wójcik et al. 2020). Factors affecting soil Mo solubility mainly includes soil pH, metal oxides, clay minerals, and organic carbon content (Smith et al. 1997; Zimmer et al. 1999). Among these factors, soil pH has the strongest effect on the processes of adsorbing and releasing MoO_4^{2-}into the soil solution (Rutkowska et al. 2017). In addition to soil properties, Mo availability can also be affected by its interactions with other anions in soils, such as PO_4^{3-} and SO_4^{2-} (Gupta 1997). Consistently, it is suggested that molybdate-specific transporters from algae *Chlamydomonas reinhardtii* (Tejada-Jimenez et al. 2011) and vascular plant *Arabidopsis thaliana* (Baxter et al. 2008) belong to the same transporter family as sulfate transporters. Therefore, Mo is found to be transported across the plasma membrane via sulfate

transporters (Alhendawi et al. 2005; Fitzpatrick et al. 2008). Molybdate and sulphate share many of the same transporting routes in biological systems (McGrath et al. 2010), resulting in antagonistic interactions between the two nutrients (Tejada-Jimenez et al. 2013; Bittner 2014). Additionally, previous studies testified that there is a synergistic interaction between MoO_4^{2-} and PO_4^{3-} on their uptake by plants (Zakikhani et al. 2014; Rana et al. 2020b). For example, Mo fertilization could enhance P uptake by plants and vice versa (Liu et al. 2010; Liu et al. 2012). This could be explained by the fact that MoO_4^{2-} and PO_4^{3-} could form a complex phosphomolybdate anion to be simultaneously absorbed by plants (Barshad et al. 1951; Barrow et al. 2005; Nie et al. 2015).

In the context of global change, increased anthropogenic N inputs stimulate plant productivity and thereby altering the processes and functions of terrestrial ecosystems (Cai et al. 2017; Wang et al. 2020; Zhang et al. 2021). However, excessive N inputs cause soil acidification and sequentially alter the mobility of macro- and micronutrients (Feng et al. 2019). Plant Mo absorption can be accelerated by higher plant growth but impeded by soil acidification due to Mo binding to mineral surfaces in acidic conditions or complexing with organic matter across a wide pH range in soils (Wichard et al. 2009). Additionally, interactions between Mo and other elements could result in antagonistic or stimulative effects on plant Mo uptake under N enrichment (Maillard et al. 2016). For instance, mobilization of soil P as induced by ecosystem N enrichment (Wang et al. 2016, 2021) may synergistically enhance plant P and Mo uptake (Vistoso et al. 2012). Meanwhile, the commonly-found antagonism between Mo and sulfur (S) influences plant Mo uptake with the direction and magnitude depending on the response of S availability to N enrichment. However, there is still no consensus on how exogenous N input affects soil S availability, given by the fact that N addition was suggested to suppress soil organic S mineralization (Chen et al. 2016) but promote mobilization of insoluble S into available S due to soil acidification (Li et al. 2019). These uncertain changes in plant-soil S dynamics would largely obscure our understanding of biogeochemical Mo cycling under N deposition.

Mowing is a widely used management strategy to supply hay for dairy and livestock industries across grassland areas in the world (Han et al. 2014). Mowing can affect plant community structure and ecosystem functions through asynchronously altering the nutritional status of different plant species in semi-arid grasslands (Lü et al. 2012). Since a majority of aboveground biomass is removed from the ecosystem, mowing has significant impacts on nutrient cycling (Klumpp et al. 2011; Dee et al. 2016). Mowing changes the nutrient cycle mainly via decreasing plant carbon and thus energy supply to soil decomposers and cutting off nutrient-return route from plant litter, thereby creating a negative feedback on soil nutrient pool size and plant growth (Ilmarinen and Mikola 2009). As such, long-term mowing substantially decreases the availability of soil macro- and micronutrients (Yang et al. 2020). In addition, mowing reduces soil water content, thereby slowing down soil nutrient flow, unbalancing soil nutrient distribution and plant nutrient uptake, and eventually resulting in the formation of ecosystem patchiness (Baptist et al. 2013). Many studies have shown that combined mowing and N application accelerates nutrient losses in temperate grasslands (Wang et al. 2018; Liu et al. 2021; Li et al. 2022). Given by the widespread Mo deficiency, concerns are warranted regarding Mo application and Mo biogeochemical

cycling in continuously mown grasslands. However, previous studies about mowing effects mainly focus on macronutrients (Hu et al. 2021; Han et al. 2014) with micronutrients, especially Mo receiving less attention. To our knowledge, how mowing influences Mo uptake by dominant plant species have not been investigated under scenarios of ecosystem N enrichment.

Grassland ecosystems in northern China are an integral part of Eurasian steppe, which serve as important national ecological barrier and production base of green animal husbandry (Shao et al. 2006). Therefore, grasslands in this area play important roles in maintaining national ecological security, food security, and even global ecological balance (Luo et al. 2021). The main utilization of these grasslands is for grazing and mowing (Li et al. 2020). A large amount of micronutrients is thereby taken away via frequent biomass removal, which would potentially deplete soil nutrient pool and affect plant growth (Mladkova et al. 2015). Additionally, soil acidification as induced by N deposition reduces the availability of Mo via mineral binding in the grassland ecosystems (Brennan 2002; Lehoczky et al. 2005; Brennan 2006). Therefore, fertilization is urgently needed to supply nutrients for the sustainable development of the grasslands. We established an experimental platform with combined fertilization of urea and Mo with and without mowing treatments since 2014 in this meadow. The study investigated Mo content in three dominant plant species (*Leymus chinensis*, *Carex duriuscula*, and *Stipa baicalensis*) and available Mo concentration in the soil under different fertilization and mowing regimes. We hypothesized that (i) soil acidification as induced by N addition reduces soil Mo availability and thus plant Mo uptake, and this reduction can be strengthened by soil S mobilization but weakened by P mobilization due to elemental interactions (ii) mowing further reduces soil Mo availability and plant Mo concentration; (iii) Mo fertilization reverses the negative effects of N and mowing treatments on Mo dynamics in plant and soil system.

Materials And Methods

Study site and experimental design

The experiment was conducted at the Erguna Forest-Steppe Ecotone Research Station (50°10'46" N, 119°22'56" E, 523 m a.s.l.) of Chinese Academy of Sciences, which locates near Heishantou town, Erguna City, Inner Mongolia Autonomous Region. The area is characterized by a transitional zone between a cold-temperate and a mid-temperate climate with mean annual precipitation and temperature of 363 mm and − 2.45°C, respectively (Wang et al. 2021). The plant community is dominated by *L. chinensis*, *C. duriuscula* and *S. baicalensis* accounting for approximately 86.96% of community biomass. The annual plant growth season is mainly from May to September. The soil type is a Haplic Chernozem (IUSS Working Group WRB 2015), and the proportions of sand, silt, and clay in the soil are 37%, 40%, and 23%, respectively.

In May 2013, a randomized block design was set up with eight treatments including control and Mo addition intersected with two N-addition treatments (no addition vs. addition) and two mowing treatments (no mowing vs. mowing), *i.e.*, 2 Mo treatments × 2 N treatments × 2 mowing treatments. Each

treatment plot was 8 × 8 m in size and replicated six times within six field blocks as separated by a 1-m buffer zone between any two adjacent plots and blocks. Ammonium molybdate was added at 0.4 kg Mo ha^{-1} yr^{-1}, which was dissolved in 10 L deionized water and evenly spread on the surface soil of each plot. The plots without Mo addition received the same amount of deionized water, which is approximately 0.16 mm precipitation. Nitrogen was applied manually as urea pellets at 100 kg N ha^{-1} yr^{-1}. Fertilizers were applied in the middle of May every year since 2014. Mowing was conducted once a year in late August since 2013.

Sampling and chemical analysis

Soil and plant samples were collected in mid-August 2020. Aboveground biomass was clipped from the soil surface and sorted into species from three 0.4 × 0.4 m quadrats in each plot. Plant samples were dried at 65°C for 48 h to constant weight in a drying oven to determine biomass of each species. In August 2020 (*i.e.*, after six years of treatment), samples of topsoil (0–10 cm depth) were collected. For each plot, five soil cores were randomly collected using a 5-cm diameter auger and then homogenized into one composite sample. Fresh soil samples were sieved through a 2-mm sieve to remove visible roots, plant residues, and stones.

Soil samples were air dried and sieved through a 2-mm screen to remove roots and stones for subsequent analyses. Soil pH was determined on the 2-mm sieved soils in a 1:2.5 (w/v) soil to deionized water suspension with a pH meter (S210 SevenCompact™, Mettler, Germany). Soil volumetric moisture was measured continuously with a soil temperature and moisture sensor of TMS-4 datalogger (TOMST s.r.o, Michelská, Czech Republic). The TMS-4 datalogger recorded soil moisture every 10 min. Soil available Mo was determined by inductively coupled plasma mass spectrometry after extraction with oxalic acid-ammonium oxalate. Briefly, 5.00g of the air-dried soil was extracted with 50 mL of oxalic acid-ammonium oxalate solution with a pH of 3.3, and placed in a 100 mL plastic bottle. The plastic bottles were placed on the shaker and shaken for 8 hours. After filtration, soil available Mo was analyzed using inductively coupled plasma mass spectrometry (5100 ICP-OES, Perkin Elmer, America). Soil available Mo as measured contained water-soluble Mo and a proportion of adsorbed Mo. For soil available S, 10.0 g of the air-dried soil was extracted with 0.25 M ammonium acetate and then measured with the turbidimetry method using 0.5 g of $BaCl_2$ crystal (Bardsley and Lancaster 1960). The Olsen P of soil was quantified by colorimetric analysis following extraction of soil with $NaHCO_3$ solution (Olsen et al. 1954). Briefly, 2.5 g of the air-dried soil was mixed with 50 ml 0.5 M $NaHCO_3$ (pH 8.5) into a 150 ml Erlenmeyer flask. The flasks were shaken at 150 rpm for 30 min. After filtration, the extracts were analyzed for P concentration by the molybdenum blue colorimetric method (Murphy and Riley 1962).

Individuals of the dominant plant species (*L. chinensis*, *C. duriuscula*, and *S. baicalensis*) in similar sizes were subsampled from the clipped biomass and ball-milled for homogenization before chemical analysis. Plant Mo and P concentrations were measured by digesting 0.3 g of dried and ground plant samples with 8 mL HNO_3 + 4 mL $HClO_4$ and analyzed by inductively coupled plasma mass spectrometry (5100 ICP-OES, Perkin Elmer, America). We digested 0.3 g of dried and ground plant samples with a

mixture of 4 mL HNO_3 + 2 mL $HClO_4$ + 1 mL HCl to determine plant S concentration with turbidimetry method using $BaCl_2$ crystal.

Statistical analyses

Prior to statistical analyses, all data were tested for normality using the Kolmogorov-Smirnov test. Three-way ANOVAs were performed to test the main and interactive effects of N addition, Mo addition and mowing treatments on soil pH, plant biomass and concentrations of Mo, P, and S in soils and plants, with block as a random factor. Student's *t*-test was used to determine the differences in Mo, P, S concentration and plant biomass in soils and plants between plots without and with Mo addition for each mowing and N addition treatments. Duncan's multiple range tests were used to compare significant differences for all soil parameters across N addition and mowing treatments without and with Mo addition separately. All analyses above were performed in SPSS16.0 (SPSS Inc., Chicago, IL, USA) with significance accepted at $p < 0.05$.

Structural equation modeling (SEM) was performed across the three plant species from Mo-addition plots to determine the direct and indirect effects of Mo and N addition on plant Mo uptake via affecting plant P and S uptake using AMOS 24.0 (Amos Development, Spring House, Pennsylvania, USA). The SEM analysis used data from plots with Mo addition, because the synergism and antagonism of plant Mo with P and S were only detected when Mo was added. The maximum likelihood estimation method was used to fit the data to the model. The fit was considered adequate when there was a non-significant χ^2 test ($p > 0.05$), low Akaike information criterion (AIC) value, and low root mean square error of approximation (RMSEA) value.

Results

Soil pH, soil moisture, and concentrations of soil available Mo, S, and P

Molybdenum and N addition significantly reduced soil pH ($p < 0.001$; Fig. 1a). Mowing reduced soil volumetric moisture (Fig. 1b, p = 0.01). Molybdenum addition significantly increased the soil available Mo concentration across all N addition and mowing treatments with the highest concentration in combined N and mowing plots (Fig. 2a, p < 0.001). Nitrogen addition increased soil available S concentration (Fig. 2b, p = 0.01) but decreased soil available P as averaged across Mo-addition and mowing treatments (Fig. 2c, p = 0.01).

Biomass of plant species

Without mowing treatments, N addition significantly increased the biomass of *L. chinensis*, but reduced that of *C. duriuscula* both with and without Mo addition (Fig. S1a, b; both $p < 0.05$). With mowing, N addition increased biomass of *L. chinensis* and *S. baicalensis* irrespective of Mo addition (Fig. S1a, c; $p <$

0.05). Mowing treatments significantly reduced the biomass of *L. chinensis* independent of N addition, while it increased biomass of *S. baicalensis* with N addition (Fig. S1a, c; $p < 0.05$).

Concentrations of Mo, S and P in dominant plant species

Mo concentration

Molybdenum addition significantly increased the Mo concentration of three dominant plant species across all N addition and mowing treatments (Fig. 3a-c, $p < 0.05$, $p < 0.001$). Without Mo addition, N addition decreased Mo concentration of *L. chinensis* without mowing by 33.07% (Fig. 3a) and that of *S. baicalensis* with mowing by 40.16% (Fig. 3c). With Mo addition, N addition reduced the Mo concentration of three species irrespective of mowing treatments by 74.25%, 66.99% and 84.71%, respectively (Fig. 3a-c; $p < 0.001$). Mowing only decreased Mo concentration of *S. baicalensis* in plots with Mo addition but without N addition.

S concentration

Without Mo addition, combined N addition and mowing treatment increased the S concentration of *L. chinensis* (Fig. 4a, $p < 0.001$). With Mo addition, N addition only increased the S concentration of *L. chinensis* without mowing treatments (Fig. 4a, $p < 0.01$). Molybdenum addition reduced the S concentration of *C. duriuscula* under combined N addition and mowing treatment (Fig. 4b, $p < 0.01$). Nitrogen addition increased the S concentration of *C. duriuscula* both with and without Mo addition (Fig. 4b, $p = 0.01$). Mowing increased the S concentration of *C. duriuscula* irrespective of N addition without Mo addition (Fig. 4b, $p < 0.001$), but the increase was only found in plots without N addition under Mo addition ($p < 0.05$). Overall positive N-addition effect was found on the S concentration of *S. baicalensis* ($p = 0.01$) with the significance mainly in the plot without mowing but with Mo addition (Fig. 4c).

P concentration

Nitrogen decrease P concentration of *L. chinensis* averaging across mowing and Mo-addition treatments (Fig. 5a, $p = 0.01$). Mowing showed opposite effects on P concentration of *L. chinensis* between treatments without and with N addition (Fig. 5a, interactive N×M effect: $p = 0.01$). Nitrogen addition increased P concentration of *C. duriuscula* averaging across Mo-addition and mowing treatments (Fig. 5b, $p = 0.01$). Nitrogen addition overall reduced the P concentration of *S. baicalensis* across Mo-addition and mowing treatments ($p = 0.02$), with the significance mainly detected under mowing with Mo addition (Fig. 5c).

Correlation analyses of Mo, S and P in dominant plant species

Without Mo addition, there was a significant negative correlation between Mo and S in *L. chinensis*, the most dominant species (Fig. 6a, $p < 0.01$). With Mo addition, significant negative correlations between Mo and S were found in three dominant species (Fig. 6b, d, f, $p < 0.01$). However, there were significant positive correlations between Mo and P for *L. chinensis* and *S. baicalensis* only with Mo addition (Fig. 7b, f, $p < 0.01$).

Structural equation modelling

Structural equation modelling explained 60% of the variation for plant Mo uptake (Fig. 8). The decrease of soil pH with N addition directly decreased plant Mo uptake of three plant species. Soil pH drop enhanced plant S uptake, thereby inducing negative effects on plant Mo uptake and plant biomass. Mainly for *L. chinensis* and *S. baicalensis*, a N-induced decrease in plant P uptake marginally weaken downregulated plant Mo uptake.

Discussion

Nitrogen addition reduced Mo concentration in dominant plant species

Partially consistent with the first hypothesis, N addition significantly reduced the Mo concentration of *L. chinensis* and *S. baicalensis* (Fig. 3a,c). This could be due to the dilution effect caused by N-induced increases in plant biomass (Marschner et al. 2012; Cai et al. 2017). Decreased soil pH (Fig. 1a) might also enhance the adsorption of molybdate anions onto positively charged Fe-, Mn-, and Al-oxides in the soil after N addition (Geng et al. 2013; Jiang et al. 2015; Rosado et al. 2021). However, soil available Mo concentration increased with N addition showing an opposite trend with that of plant Mo, especially under Mo addition (Fig. 2a). It might be due to the act that soil available Mo as measured in this study included both water-soluble Mo and adsorbed Mo (Xu et al. 2013). Soil water-soluble Mo is readily available for plants but adsorbed Mo should be desorbed before taken up by plants (Lian et al. 2013; Alrashidi et al. 2020). With N addition, Mo addition possibly increased the concentration of soil adsorbed Mo instead of water-soluble Mo, thus resulting in higher soil available Mo concentration but lower plant Mo concentrations (Rosado et al. 2021).

Synergistic interactions between P and Mo uptake in plants might explain the asymmetric changes in soil and plant Mo (Barrow et al. 2005; Liu et al. 2010), where decreases in P concentrations of *L. chinensis* and *S. baicalensis* with N addition contributed to declines in plant Mo uptake therein (Fig. 5a,c; Fig. 8) This synergistic interactions between plant P and Mo uptake were further supported by the significant positive correlation between Mo and P concentrations for *L. chinensis* and *S. baicalensis* (Fig. 7b,f). However, we realized that the positive correlations were only detected in Mo-addition plots instead of treatments without Mo addition. This could be due to Mo, as a micronutrient, only significantly interacting with soil PO_4^{3-} ions when it was relatively abundant in soils. We propose that the dosage threshold for

the facilitation of P effect on plant Mo uptake could provide valuable insights in fertilization practices to manage P and Mo simultaneously. Consistently, previous P and Mo fertilization experiments have found that an increase in availability of soil Mo would cause a significant increase in soil available P fractions (e.g., H_2O- and $NaHCO_3$-extractable P fractions), and vice versa (Zakikhani et al. 2014; Nie et al. 2015; Rana et al. 2020b). The formation of a complex phosphomolybdate anion might be the reason for coordinated P and Mo uptake by plants (Rana et al. 2020a). Also, relatively excessive soil PO_4^{3-} in plots without N addition could compete with Mo for adsorption sites and then release exchangeable MoO_4^{2-} to soil solution for plant uptake (Sun and Selim 2017).

Consistent with our first hypothesis, significant increases in soil available S and the S concentration in the three plant species were concurrent with decreases in plant Mo uptake (Fig. 4a,b,c; Fig. 8). Significant negative correlations between Mo and S concentrations of three plant species under Mo addition (Fig. 6b,d,f) further suggested that there might be an antagonistic effect between Mo and S (Pasricha et al. 1977; Zimmer and Mendel 1999). In line with this, some studies found that under S-deficient conditions, high levels of Mo accumulate in plant tissues (Schiavon et al. 2012); however, the supply of S would lead to plant Mo deficiency (Macleod et al. 1997). Indeed, sulfate transporters from plants have been described as potentially involving in root uptake of Mo (Yoshimoto et al. 2002). Because MoO_4^{2-} and SO_4^{2-} are chemical analogues with similarities in terms of net charge, structure and hydrogen binding characteristics (Dudev 2004; Bittner 2014), and thus they might compete for binding sites from the same transporters. Moreover, a high-affinity sulfate transporter (SHST1) and its homologs (SULTR1.1 and SULTR1.2) were responsible for the uptake of available sulfate and molybdate from soils (Smith et al. 1995; Fitzpatrick et al. 2008). In summary, the decrease in Mo uptake in the three plant species might be due to the decrease in the coordinated uptake of Mo with P and the enhancement in antagonistic interactions between Mo and S uptake in presence of higher plant available S under N addition.

Mowing conditionally reduced plant Mo concentration

Partially consistent with our expectations, mowing only reduced the Mo concentration of *S. baicalensis* under Mo addition without N fertilization (Fig. 3c). However, mowing showed no impact on Mo uptake of the other two species with higher dominance, so the decrease in Mo concentration of *S. baicalensis* might be due to the competitive or luxury absorption of Mo by the other two species. For *L. chinensis* and *C. duriuscula*, higher biomass dominance and biomass recover after mowing facilitate higher competitiveness and Mo demand to offset negative mowing effects (Liu et al. 2020; Li et al. 2022).

Additionally, the decrease in Mo concentration of *S. baicalensis* might be related to the decrease in soil moisture (Fig. 1b) and consequently lower nutrient mobility caused by mowing. A previous study showed that mowing increased water evaporation of surface soil, concurrent with reduction in vegetation coverage (Bao et al. 2019). Moisture deficiency could limit the diffusion and mass flow of soil nutrients to lower plant Mo uptake, especially for the less competitive species (Meisser et al. 2019). Under water-deficient conditions, lower plant transpiration further slows down the transportation of nutrient ions from soil to root surface (Tadayyon et al. 2018), thereby reducing the Mo uptake by plant roots (Gunes et al.

2008). Such drought stress could also inhibit plant Mo uptake via deteriorating root traits (e.g., specific root length and root volume size) and root development (Barkaoui et al. 2016).

Molybdenum addition exaggerated the negative effects of N addition and mowing on plant Mo concentration

Contrary to the third hypothesis, negative N-addition effect was exaggerated for Mo concentration of *L. chinensis* and *S. baicalensis* and it turned from non-significant to significant for *C. duriuscula* after Mo addition (Fig. 3a,b,c). Moreover, negative mowing effect was only detected on Mo concentration of *S. baicalensis* with Mo addition. Significantly negative correlations between Mo and S were found in all the three plant species under Mo addition, as compared with the only case in the most dominant species of *L. chinensis* across treatments without Mo addition. Similarly, positive correlations between plant Mo and P were also mainly found in plots with Mo addition. This suggested that the relationships between Mo and S (antagonism) and between Mo and P (synergism) were strengthened by Mo addition. These nutrient interactions could further explain the decoupling relationships between soil available Mo and plant Mo concentration.

Strongly constrained by temperature, plant productivity is generally low in cold meadow grasslands as a result of relatively short growing season (Li et al. 2020). To elevate plant productivity and compensate nutrient losses from mowing and grazing, exogenous nutrient supply is increasingly recognized as an efficient approach to support the human population in these marginal land areas (Egan et al. 2019). In this context, interplay between macro- and micronutrients, such as Mo with P and S in this study, must be taken into account for policy-makers when initiating fertilization management practices in these continuously-mown cold meadows. Therefore, knowledge of nutrient interactions as obtained in the current study shed lights on providing guidelines for fertilization trials, alleviating Mo deficiency, and optimizing fertilization regimes for high forage yields and high nutrient use efficiencies.

Conclusion

Molybdenum addition increased soil available Mo concentration, thereby significantly promoting plant Mo uptake across all treatments. Nitrogen addition alone reduced the Mo concentration of *L. chinensis* by lowering soil pH and increasing plant biomass. Irrespectively of mowing treatment, combined addition of Mo and N reduced the Mo concentration in the three plant species as compared with plots with only Mo addition. This was mainly caused by antagonism with S and synergism with P in the context of S enhancement but P reduction in the soils and plants under N addition. Mowing treatments reduced the Mo concentration of *S. baicalensis* through the removal of plant biomass and the reduction of soil moisture. Our results suggest that long-term mowing and N addition would eventually decrease ecosystem Mo stock, thus threatening the sustainable development of the grassland ecosystems and facilitating the necessity of Mo fertilization. More importantly, changes in macronutrient availabilities as induced by mowing and N fertilization should be fully considered when initiating Mo-supply policies due to their strong interplay.

Declarations

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Author contributions

Conceptualization: RW, YL. Data curation: YL, BW, YZ, BG, ZW, HL. Formal analysis: YL. Funding acquisition: RW, YJ, HL. Project administration: YJ, LY. Supervision: RW, YJ, LY. Writing-original draft: YL, RW.

Conflict of interest

The authors declare no competing interests.

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Data Availability

The data supporting the findings of this study are available from the corresponding author, (Ruzhen Wang), upon request.

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Figures

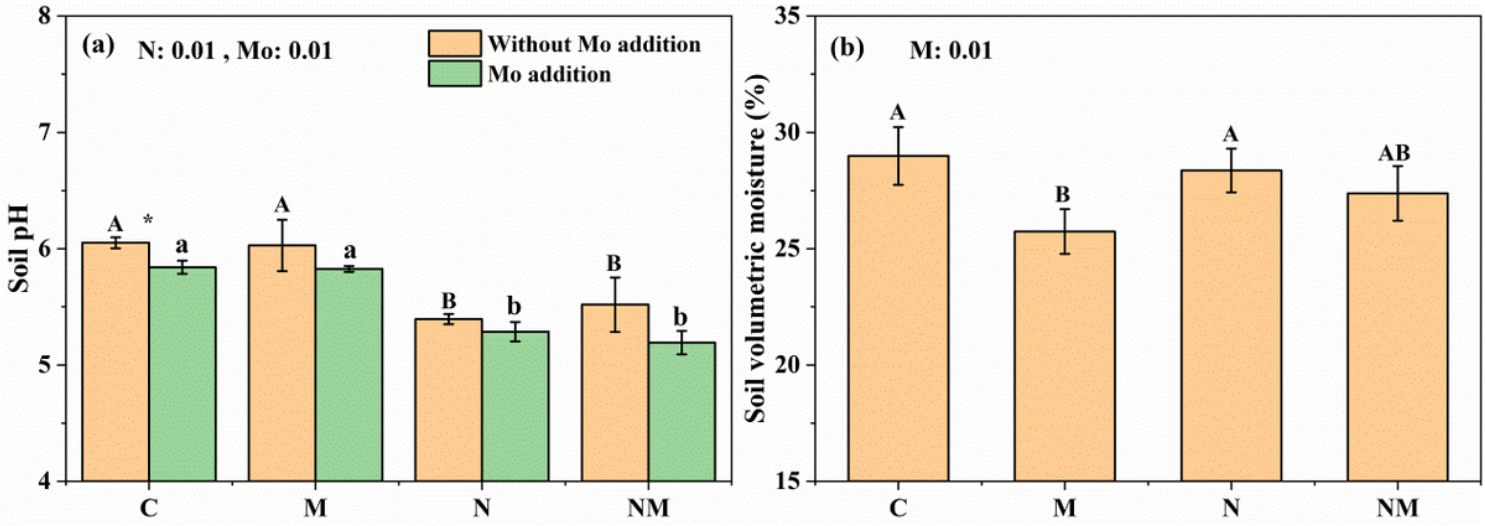

Figure 1

Response of (a) soil pH and (b) soil volumetric moisture to molybdenum (Mo) and nitrogen (N) addition and mowing. Values are means of six replicates (± SE). Double asterisks indicate the significance at $p < 0.01$. Different letters indicate significant differences across N addition and mowing treatments without (capital letters) and with Mo addition (lowercase letters) separately. *P*-values of the three-way ANOVAs are labelled when significant ($p < 0.05$). C, control; M, mowing; N, N addition; NM, N and mowing combination.

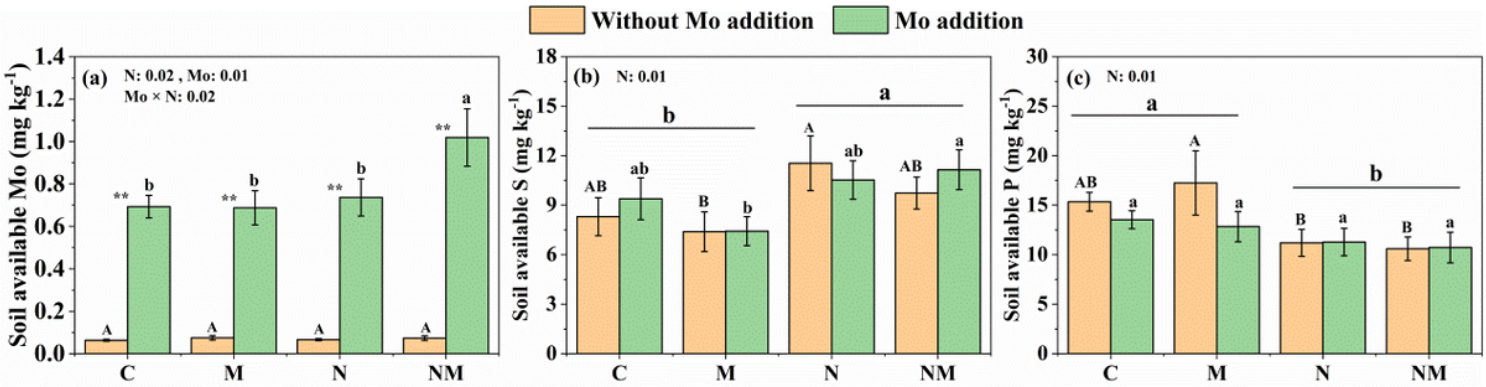

Figure 2

Concentrations of (a) soil available molybdenum (Mo), (b) soil available sulfur (S), and (c) soil available phosphorus (P) in response to Mo and nitrogen (N) addition and mowing. Values are means of six replicates (± SE). Double asterisks indicate the significance between treatments without and with Mo addition at $p < 0.01$ level. Different letters are labelled to indicate significant differences across N addition and mowing treatments without (capital letters) and with Mo addition (lowercase letters) separately. Lowercase letters above the short lines represent significant N-addition effects as averaged across Mo-addition and mowing treatments. *P*-values of the three-way ANOVAs are labelled when significant ($p < 0.05$). C, control; M, mowing; N, N addition; NM, N and mowing combination.

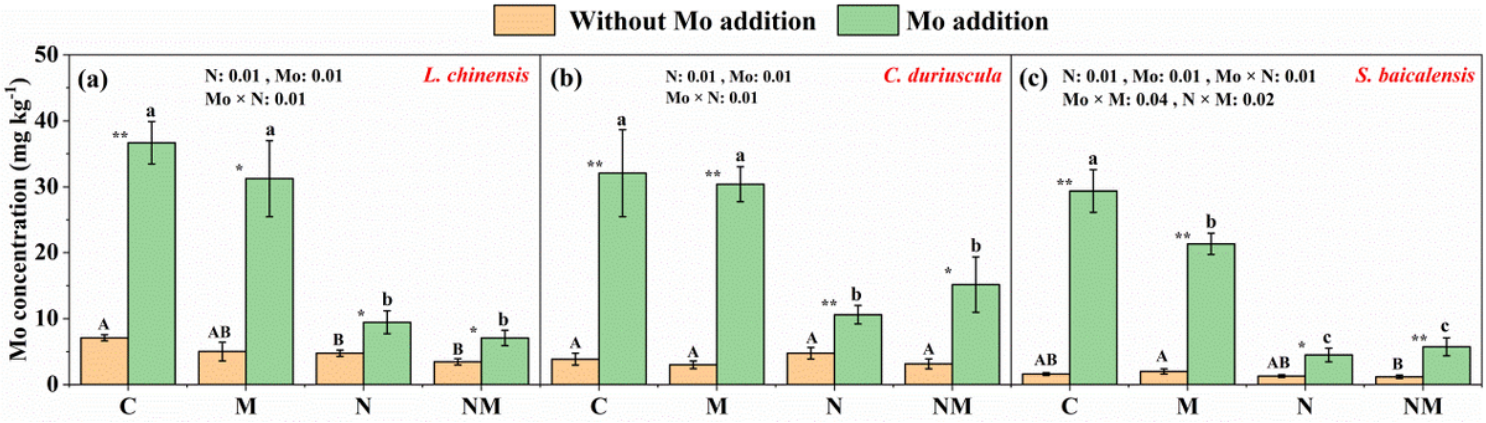

Figure 3

Response of molybdenum (Mo) concentrations in plant species of (a) *Leymus chinensis*, (b) *Carex duriuscula*, and (c) *Stipa baicalensis* to Mo and nitrogen (N) addition and mowing. Values are means of six replicates (± SE). Single and double asterisks indicate the significance between treatments without and with Mo addition at $p < 0.05$ and 0.01 levels, respectively. Different letters are labelled to indicate significant differences across N addition and mowing treatments without (capital letters) and with Mo addition (lowercase letters) separately. *P*-values of the three-way ANOVAs are labelled when significant ($p < 0.05$). C, control; M, mowing; N, N addition; NM, N and mowing combination.

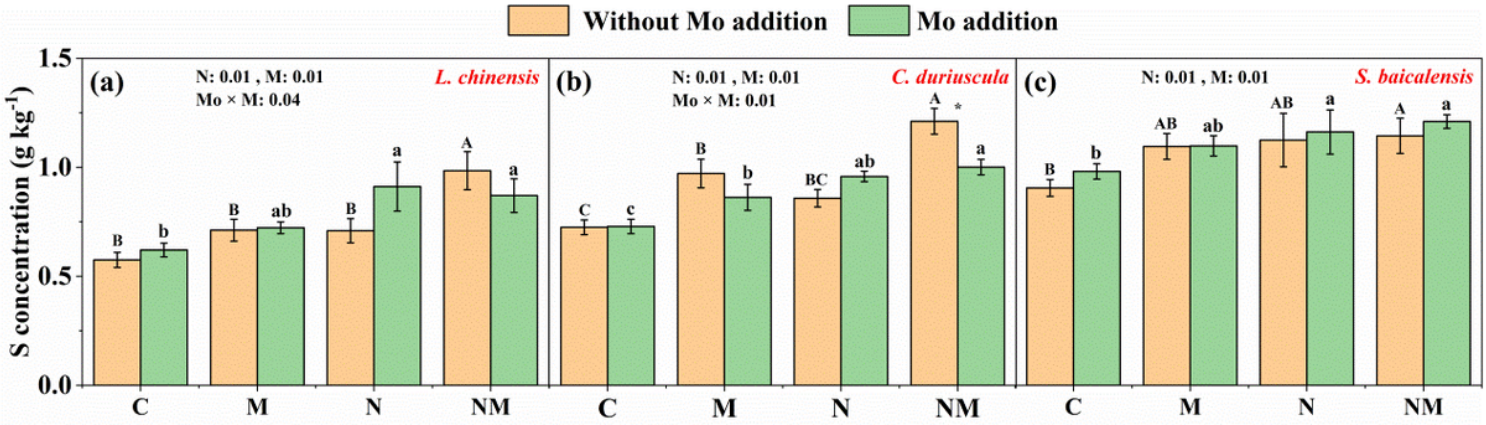

Figure 4

Response of sulfur (S) concentrations in plant species of (a) *Leymus chinensis*, (b) *Carex duriuscula*, and (c) *Stipa baicalensis* to molybdenum (Mo) and nitrogen (N) addition and mowing. Values are means of six replicates (± SE). Asterisks indicate the significance between treatments without and with Mo addition at $p < 0.05$ level. Different letters indicate significant differences across N addition and mowing treatments without (capital letters) and with Mo addition (lowercase letters) separately. *P*-values of the three-way ANOVAs are labelled when significant ($p < 0.05$). C, control; M, mowing; N, N addition; NM, N and mowing combination.

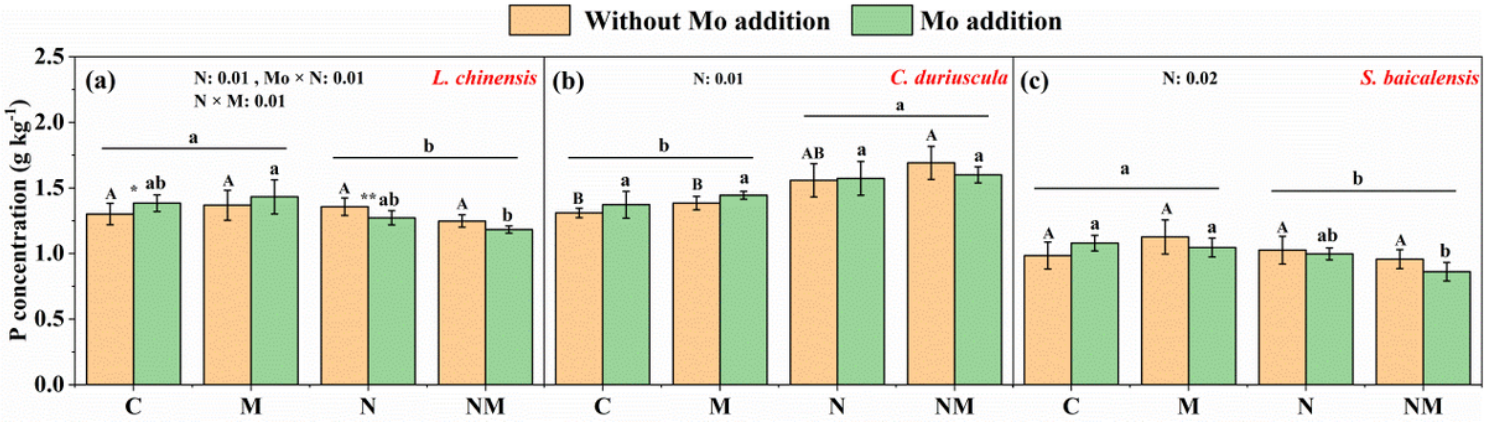

Figure 5

Response of phosphorus (P) concentrations in plant species of (a) *Leymus chinensis*, (b) *Carex duriuscula*, and (c) *Stipa baicalensis* to molybdenum (Mo) and nitrogen (N) addition and mowing. Values are means of six replicates (± SE). Single and double asterisks indicate the significance between treatments without and with Mo addition at $p < 0.05$ and 0.01 levels, respectively. Different letters are labelled to indicate significant differences across N addition and mowing treatments without (capital letters) and with Mo addition (lowercase letters) separately. Lowercase letters above the short lines represent significant N-addition effects averaged across Mo-addition and mowing treatments. *P*-values of the three-way ANOVAs are labelled when significant ($p < 0.05$). C, control; M, mowing; N, N addition; NM, N and mowing combination.

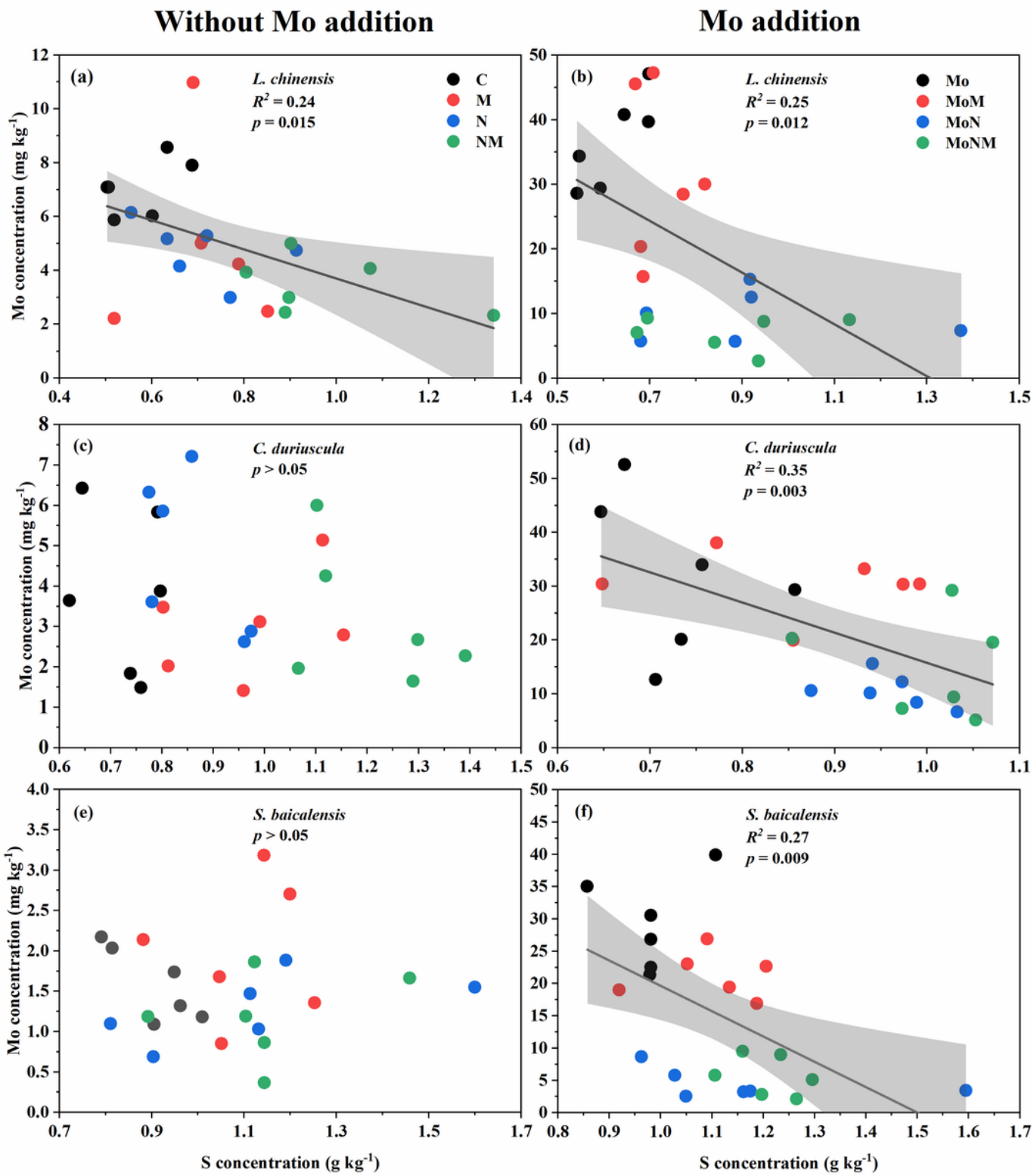

Figure 6

Correlation analyses between molybdenum (Mo) and sulfur (S) in three plant species without and with Mo addition separately. C, control; M, mowing; N, N addition; NM, N and mowing combination.

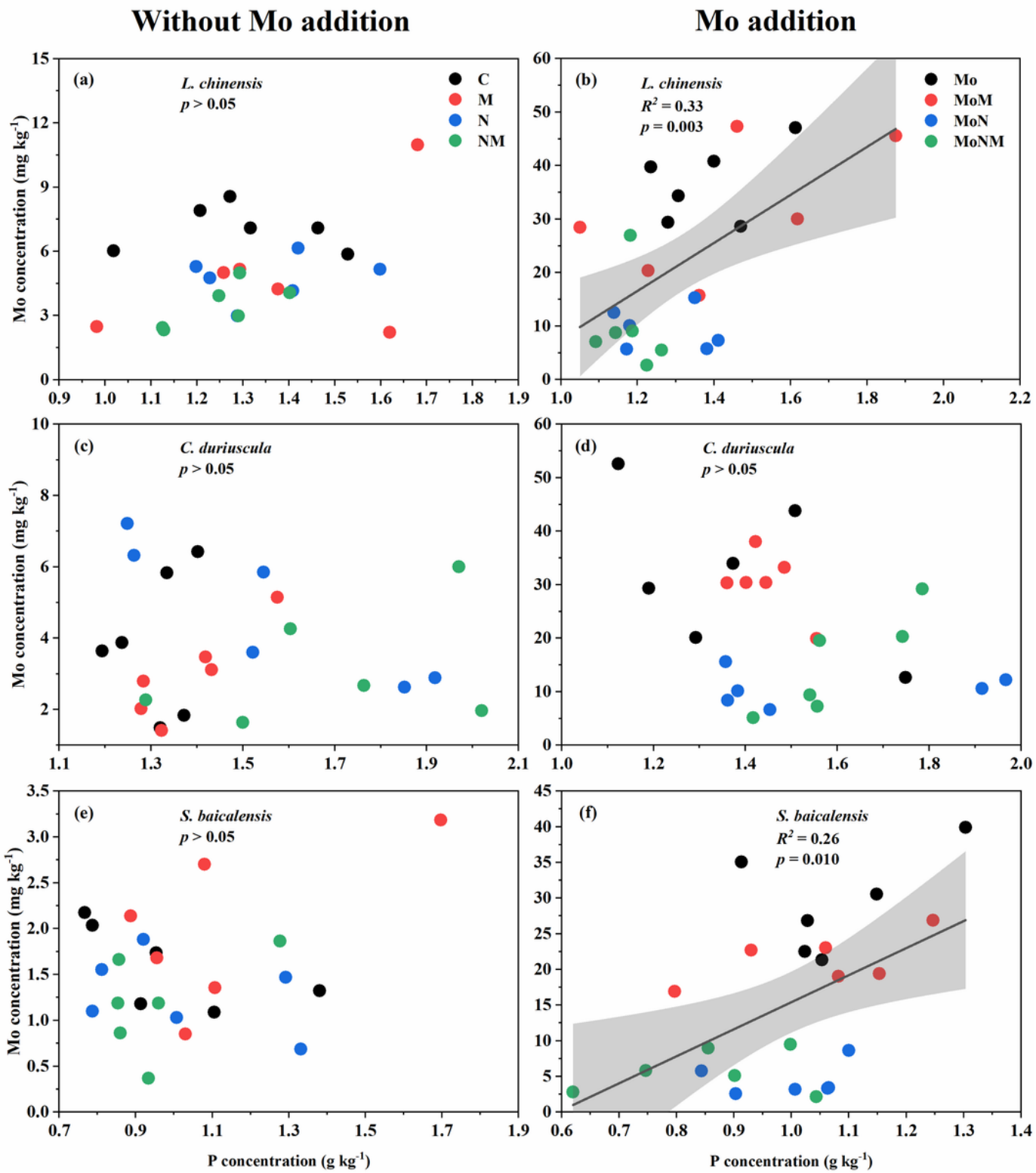

Figure 7

Correlation analyses between molybdenum (Mo) and phosphorus (P) in three plants without and with Mo addition separately. C, control; M, mowing; N, N addition; NM, N and mowing combination.

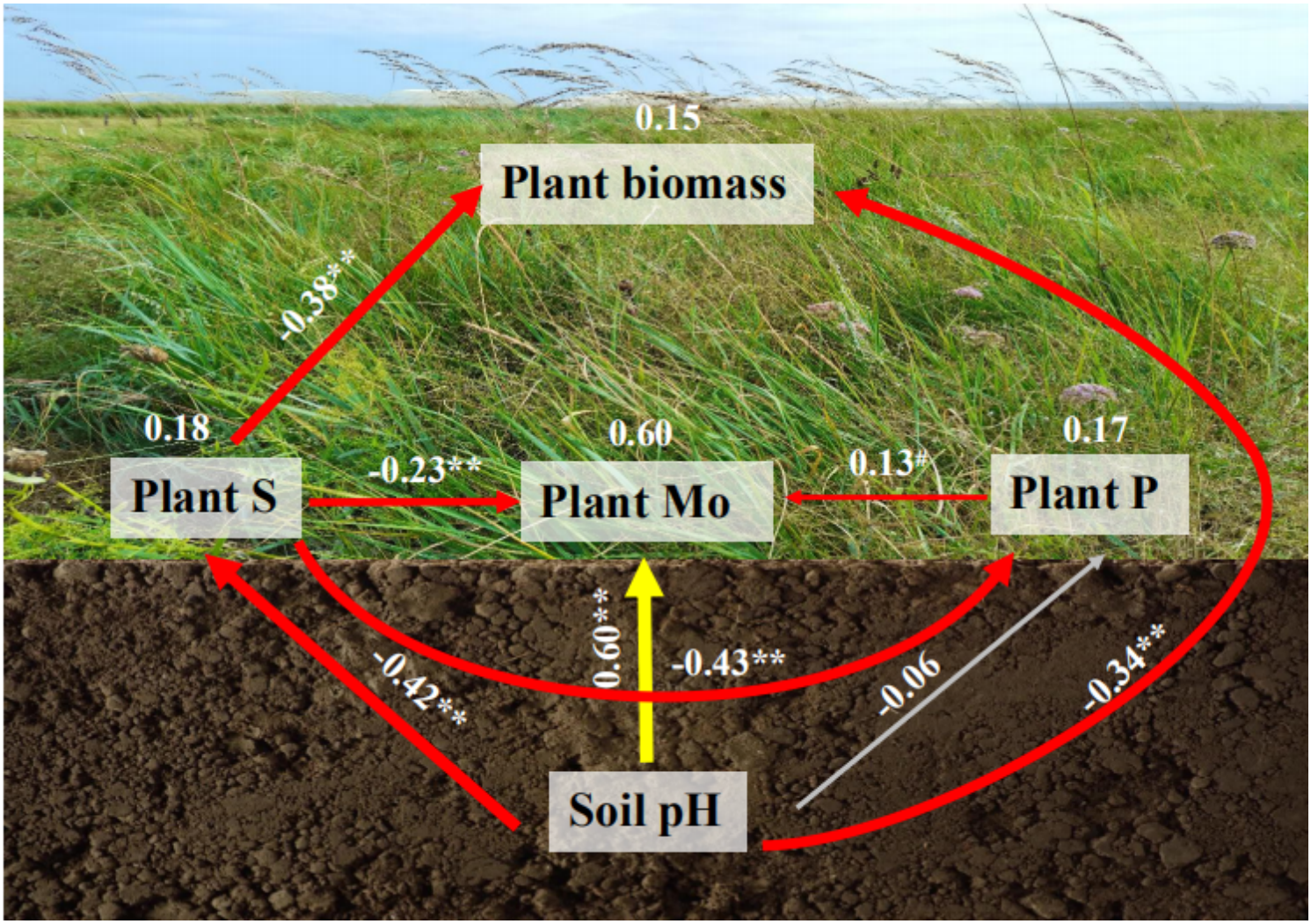

Figure 8

Structural equation modelling showing the direct and indirect pathways of the mechanisms underlying the impacts of molybdenum (Mo) and nitrogen (N) addition on plant Mo uptake. The results of model fitting for dominant plant species c = 0.317, df = 2, p = 0.853, RMSEA = 0.001, AIC = 26.317. Yellow and red arrows represent significantly positive and negative pathways, respectively, and grey arrows indicate nonsignificant pathways. Numbers at arrows are standardized path coefficients and arrow width is proportional to the strength of the relationship. The number next to each response variable indicates the proportion of variance (R^2) explained by the model. $^{\#}$ p < 0.1, * P < 0.05, ** P < 0.01.

Supplementary Files

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