



# Nutrient addition and warming alter the soil phosphorus cycle in grasslands: A global meta-analysis

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## Abstract

**Purpose** Grasslands are the most extensive vegetation type in the terrestrial ecosystem and have an important role in the soil phosphorus (P) cycle. Many nutrient addition and warming experiments have been conducted in grasslands; however, the global pattern of nutrient addition and experimental warming impacts on soil P cycle is unclear.

**Methods** We conducted a meta-analysis of 68 publications to synthesize the mechanisms underlying global grassland ecosystem responses to nutrient addition and experimental warming.

**Results** Our analysis indicated that nitrogen (N) addition reduced microbial biomass P (−11.2%) but increased litter P concentration (+15.5%) and available P (+14.2%). Experimental warming reduced microbial biomass P (−10.5%) and available P (−6.7%) but increased litter P concentration (+46.2%). P addition increased available P (+222.3%) and microbial biomass P (+98.1%). The available P response to nutrient addition and experimental warming was more sensitive in temperate grasslands than in alpine grasslands. The responses of soil total and available P to nutrient addition depended on environmental conditions such as air temperature and soil pH.

**Conclusion** Our results suggest that N addition may promote P mineralization and possibly stimulate the transformation of refractory or resistant forms of soil inorganic P, whereas experimental warming accelerates the P cycle by regulating plant acquisition and enzyme activity. Environmental factors (e.g., temperature, precipitation, pH) affect the soil P response to nutrient addition by altering microbial and enzymatic activities. It is crucial to understand the dynamic changes in soil microbial and enzyme activities to predict the P cycle in grassland soils in the future.

**Keywords** Soil phosphorus cycle · Nitrogen addition · Phosphorus addition · Warming · Grassland ecosystem

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## 1 Introduction

Phosphorus (P) is a critical limiting factor for plant growth because it is indispensable for several physiological and biochemical processes (Elser et al. 2007; Zhang et al. 2019; Sharma et al. 2020). The soil P cycle and fractions have critical ecosystem roles because they affect the acquisition and utilization of P by organisms (Brucker and Spohn 2019; Siebers and Kruse 2019). Available P that can be utilized by organisms accounts for only a small part of the total soil P, and P limitation is a global issue in terrestrial ecosystems (Atere et al. 2018). Therefore, it is crucial to fully map P fractions and cycle in soil, especially within the context of continuously increasing impacts of human activities and climate change.

Human activities have become a significant factor affecting the soil P fraction and cycle (Bittman et al. 2017;

Khorshid et al. 2019). Large quantities of nitrogen (N) and P are added to agricultural lands, which greatly affect the P cycle in terrestrial ecosystems (Elser and Bennett 2011; Dietrich et al. 2017). Many studies have investigated the effects of N and P addition on the soil P cycle, but the results are inconsistent in varying grassland ecosystems. Widdig et al. (2020) reported that total soil P concentrations were not significantly affected by N and P addition in temperate grasslands, whereas other studies reported that N addition significantly reduced the total and available P in temperate grasslands (Gong et al. 2020). The response of alpine grasslands to nutrient addition differed from that of temperate grasslands (Li et al. 2020). These combined reports indicate that a global synthesis is urgently needed to define the impacts of and mechanisms underlying the effects of N and P addition on the P cycle in grassland ecosystems.

Climate change is expected to increase the global surface temperature by 1.5–2 °C by the end of the twenty-first century (IPCC 2018). Warming stimulates microbial and phosphatase activity, enhances plant P acquisition, and mineralization ability of microorganisms, ultimately accelerating the P cycle (Bell et al. 2010; Gong et al. 2020). Warming also mediates the process by which phosphatase is secreted by microorganisms and plant roots and regulates P mineralization. These actions also affect the soil P cycle (Filippelli 2008). Thus, warming alters phosphatase activity and further affects soil P cycle of terrestrial ecosystems by directly and indirectly mediating plant growth, microbial biomass, and activity (Sardans et al. 2006; Singh et al. 2010; White-Monsant et al. 2017). However, these effects may be different among varying grassland vegetations and soil types. For example, Yan et al. (2021) showed that aridity affects how roots are produced and recycled under warming and N treatments in grasslands. Gong et al. (2020) reported that experimental warming could reduce the available P content and increase the microbial biomass P and total P in temperate grasslands. By contrast, other studies reported that warming did not significantly affect the total soil P in temperate grasslands (Guo et al. 2019). Therefore, a global synthesis is needed to map the responses and mechanisms driving the soil P cycle in global grassland ecosystems under the impacts of warming.

Grasslands are among the most widespread vegetation types, accounting for approximately 26% of the terrestrial area (Obermeier et al. 2016), inhabiting all continents except Antarctica, and have a key role in the global P cycle (Rojas-Briales 2015). Grasslands cover approximately 117 million km<sup>2</sup> of vegetated lands and provide forage for more than 1800 million livestock and wildlife populations (Rojas-Briales 2015). Many grasslands are used for intense livestock production without fertilization, which results in a rapid decline in soil fertility (Shi et al. 2021). Carefully managed application of fertilizer is critical to sustain pasture

fertility and livestock production, and could double grassland yield between 2005 and 2050 (Sattari et al. 2016; Shi et al. 2021). However, this strategy is bound to affect the soil P cycle, and this effect may become exacerbated with rising temperature. Previous studies indicated that N enrichment increased acid phosphatase activity in grassland soils, which could be further strengthened under the interaction of N addition and experimental warming (Menge and Field 2007; Thakur et al. 2019). However, the underlying mechanisms and consistency among these effects were unknown. Chen et al. (2018) studied the stoichiometry of carbon, nitrogen, and phosphorus in plantation forests. Our work adds to this knowledge base in grasslands. It is necessary to investigate the comprehensive effects of warming and nutrient addition on the soil P cycle in global grassland ecosystems. This knowledge will guide the future management of grassland production.

We used a meta-analysis approach to integrate and analyze the available data from different field nutrient addition and warming experiments performed in global grassland ecosystems. These data can be used to better understand global grassland P dynamics under future nutrient addition and warming. In general, we hypothesized that nutrient addition directly or indirectly alters plant biomass and affect plant acquisition of soil P, or mediates the process of soil P transformation to regulate the soil P cycle. Experimental warming affects microbial and enzyme activities to participate in the regulation of soil P cycle. However, these effects may vary across grasslands due to changing environments and the interaction between nutrient addition and experimental warming. Therefore, our study had three objectives: (1) quantify the effects of N addition on the global grassland P cycle; (2) determine the mechanisms driving soil P dynamics in global grasslands under P addition; and (3) synthesize the mechanisms driving soil P dynamics in global grasslands under warming and under nutrient addition combined with warming. We also considered the impacts of environmental variables to deepen our understanding of the mechanisms driving the global grassland P cycle under future climate change.

## 2 Materials and methods

### 2.1 Data collection

We collected publications (up to July 25, 2021) that studied changes in soil P in global grassland ecosystems under warming and the addition of N/P to fields. We performed Boolean searches using the Web of Science (<http://apps.webofknowledge.com>) and China National Knowledge Infrastructure (CNKI, <https://www.cnki.net>) databases and the following keywords: (a) “N addition” or “nitrogen

addition” or “nitrogen amendment” or “nitrogen deposition”, (b) “P addition” or “phosphorus addition” or “phosphorus amendment”, (c) “warming” or “increased temperature” or “elevated temperature”, (d) “soil P” or “soil phosphorus”, (e) “microbial biomass P” and (f) “grassland” or “grassland ecosystem” or “pasture”. Seven criteria were established to select suitable publications: (1) experiments were conducted on global grassland ecosystems; (2) experiments were conducted in the field; (3) publications reported comparisons between controls (e.g., ambient temperature) and treatments (e.g., elevated temperature); (4) the publications reported means, standard deviations (SD) or standard errors (SE), and sample sizes of the selected variables; (5) the publications reported the treatment method, magnitude, and duration (at least one growing season); (6) the publications were peer-reviewed journal articles, conference collections, theses, or dissertations; and (7) if authors published in peer-reviewed journals and one or more other formats (i.e., proceedings, dissertations), only the most recent one was selected to ensure the relative independence of data. Publications that did not meet these criteria were excluded. Thus, 512 experimental comparisons were digitized from 68 studies in 55 sites across the globe (Fig. 1; supplementary material, Text 1).

We also refined the categorical variables to detect subtle patterns in response of soil P to nutrient addition and experimental warming. For example, grassland types were categorized into subgroups of temperate grassland and alpine grassland. Experimental durations were categorized into short-, intermediate-, and long-term (i.e., < 3, 3–6, and > 6 years, respectively). Yan et al. (2020) performed a similar technique to give their data set more granularity. We also explicitly considered treatment methods (e.g., fertilizer type), treatment magnitudes (e.g., nutrient addition rate), vegetation type, and soil type. We extracted site information that was related to the experiments to construct an integrated database that included geographic variables (longitude, latitude, and altitude) and climatic factors [mean annual temperature (MAT) and mean annual precipitation (MAP)]. All of these may have a subtle effect on the response pattern of soil phosphorus. GetData software (version 2.20) was used to extract data that are presented in the figures.

## 2.2 Data analysis

We conducted a meta-analysis to determine the effects of N and P addition and experimental warming on the soil P cycle in global grasslands. The natural logarithm of the response



**Fig. 1** Map of sites conducting field nitrogen and phosphorus addition and warming experiments that were included in the meta-analysis. The points with different colors represent the observations included in each study site

ratio (RR) was calculated to indicate the effect size of each treatment (Hedges et al. 1999) [Eq. (1)]:

$$RR = \ln\left(\frac{\bar{X}_T}{\bar{X}_C}\right) = \ln\bar{X}_T - \ln\bar{X}_C \quad (1)$$

where  $\bar{X}_T$  and  $\bar{X}_C$  are the mean treatment and control values, respectively.

The variance ( $v$ ) of each RR was calculated using Eq. (2):

$$v = \frac{S_T^2}{n_T \bar{X}_T^2} + \frac{S_C^2}{n_C \bar{X}_C^2} \quad (2)$$

where  $n_T$  and  $n_C$  are the sample sizes, and  $S_T$  and  $S_C$  are the standard deviations of means for each treatment and control, respectively. Most of the included studies reported SE, which was transformed to SD according to Eq. (3):

$$SD = SE \times \sqrt{n} \quad (3)$$

where  $n$  was the sample size.

The weighted value of response ratio ( $RR_{++}$ ) and standard error [ $s(RR_{++})$ ] of each class were calculated (Hedges et al. 1999). The natural logarithm transformed  $RR_{++}$  ( $\ln RR_{++}$ ) was determined by specifying studies as a random factor using the *rma* model in the “*metafor*” package version 3.0–2 of R version 4.1.2 (The R Project for Statistical Computing, <https://www.r-project.org/>) (Yuan and Chen 2015). The effects of treatments on selected variables were considered statistically significant if the 95% CI did not overlap zero. As well the effects between groups and tests under different environmental conditions differed if their 95% CIs did not overlap. We also used Egger’s regression to examine the effects of publication bias on the effect size of each variable (Egger et al. 1997). If the test results were subject to publication bias (Egger’s  $P < 0.05$ ), we used two methods (trim-and-fill method and PET-PEESE method) to rectify the effect size (Duval and Tweedie 2000; Moreno et al. 2009; Stanley and Doucouliagos 2014). We finally adopted the results corrected by the trim-and-fill method when the effect size modified by the two methods have the same significance. On the contrary, we considered the effect size of the variable was unclear due to the different significance of corrected effect size between two methods (see specific results in supplementary material, Table S1).

Besides, the percent change (%) was calculated based on response ratios using the equation  $[\exp(RR) - 1] \times 100$  (Yan et al. 2020) to clarify data interpretation. We computed multiple comparisons to examine differences in treatment effects on different groups or under different conditions. We applied a continuous randomized-effects model to test the linear relationships between  $\ln RR$  of variables, geographic variables, and climate factors. Statistical results were reported

as differences among group cumulative effect size (QM) and residual error (QE). We conducted a regression analysis to further examine nonlinear relationships between the  $\ln RR$  of variables, geographic variables, and climate factors. Statistical differences were considered as significant when  $P < 0.05$ . All statistical analyses were performed in R version 4.1.2.

## 3 Results

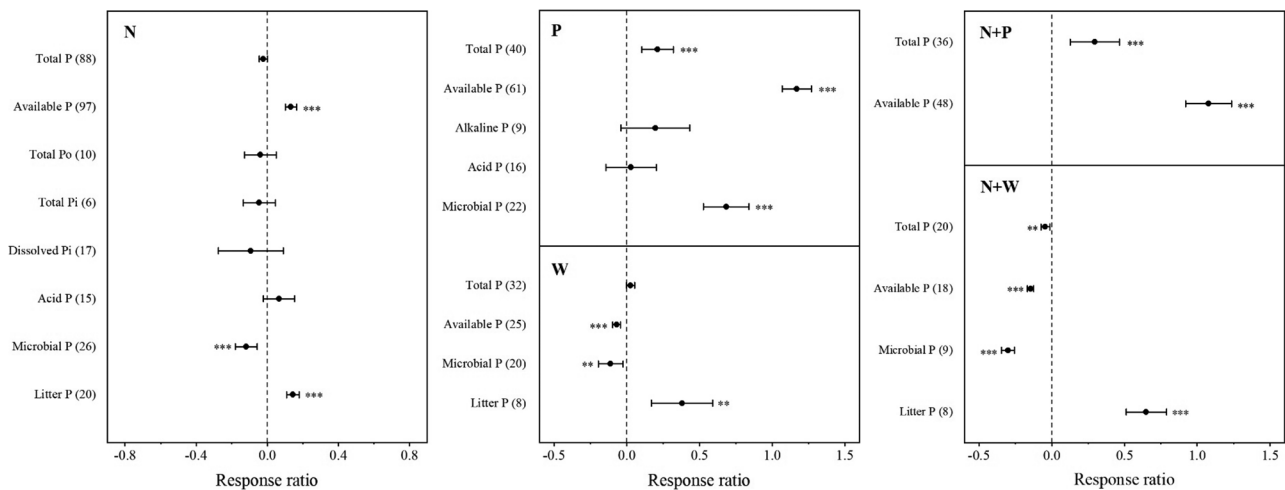
### 3.1 Effects of N addition on soil P

Nitrogen addition reduced soil microbial biomass phosphorus (MBP) by 11.2% ( $P < 0.001$ , Fig. 2). By contrast, N addition enhanced the soil available phosphorus (AP, i.e., phosphorus that is readily acquired by plants, including phosphate ions, dissolved inorganic P, and adsorbed P) and litter phosphorus concentration (litter P) by 14.2% ( $P < 0.001$ ) and 15.5% ( $P < 0.001$ ), respectively (Fig. 2). N addition did not significantly affect the soil total phosphorus (TP), soil total organic phosphorus (TOP), soil total inorganic phosphorus (TIP), soil dissolved inorganic phosphorus (DIP, i.e., inorganic P dissolved in water), or acid phosphatase activity (acid P) ( $P > 0.05$ , Fig. 2). The relationships between TP or AP and N addition rates revealed that TP decreased with increasing N addition rate. However, AP was not significantly altered by N addition (Fig. 3).

Subgroup analysis under N addition indicated that vegetations dominated by *Leymus chinensis* and *Stipa krylovii* (vegetation type), Mollic Gleysols (soil type), temperate grassland (grassland type),  $\text{NH}_4\text{NO}_3$  (fertilizer type), and intermediate experiments (3–6 years) all showed a decrease in TP and an increase in AP in response to N addition (Figs. 4 and 5). N addition unexpectedly reduced AP in soils of Calcic Chernozems and TP in soils of Luvic Kastanozems, but it did not significantly affect AP in soils of Luvic Kastanozems or TP and AP in alpine grassland (Fig. 5). Long-term experiments ( $> 6$  years) and using urea as fertilizer did not significantly affect TP but significantly increased AP (Fig. 5). The regression analysis of geographic variables and climate factors, and response ratios of TP and AP indicated that pH, altitude, MAT, and MAP all significantly affected changes in TP and AP under N addition (Fig. 4).

### 3.2 Effects of P addition on soil P

P addition increased TP, AP, and MBP by 23.6, 222.3, and 98.1%, respectively ( $P < 0.001$ ), but did not significantly affect alkaline P or acid P activity ( $P > 0.05$ ) (Fig. 2). AP was altered by increasing P addition (Fig. 3). Subgroup analysis indicated that TP significantly increased in response to

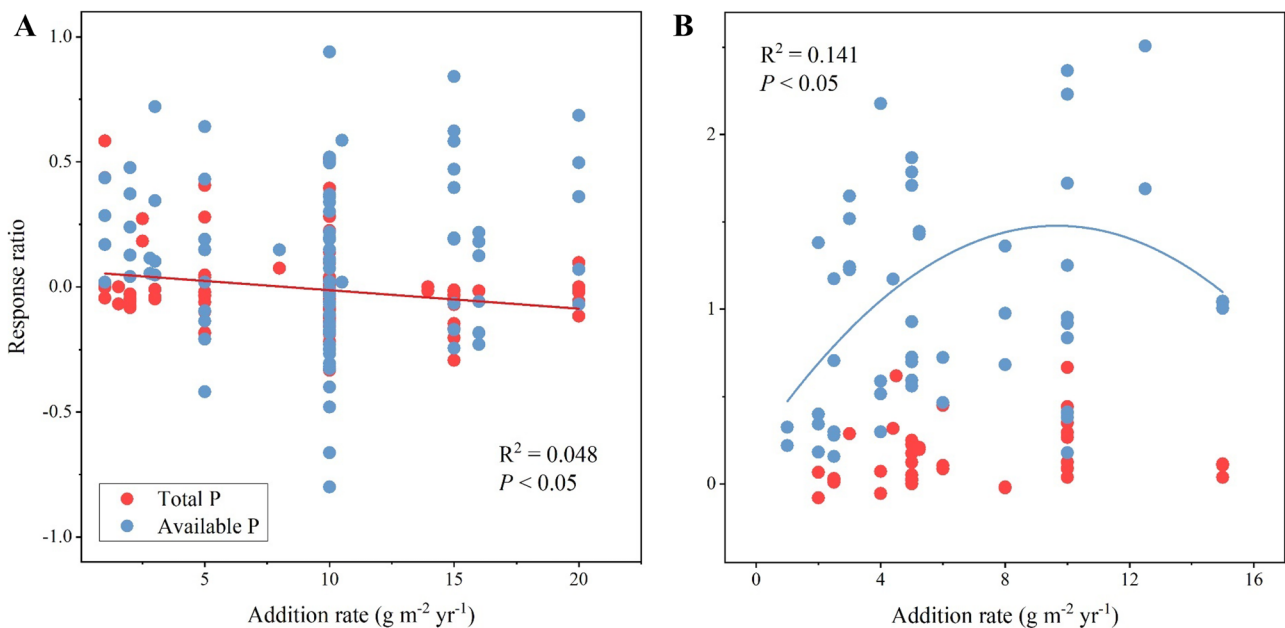


**Fig. 2** Responses of soil phosphorus variables to experimental variables in global grassland ecosystems: N addition (N), P addition (P), experimental warming (W), N combined with P addition (N+P), and N addition combined with experimental warming (N+W). Total P, soil total phosphorus; available P, soil available phosphorus; total Po, soil total organic phosphorus; total Pi, soil total inorganic phosphorus; dissolved Pi, soil dissolved inorganic phosphorus; alkaline P, alkaline phosphatase; acid P, acid phosphatase; microbial P, soil

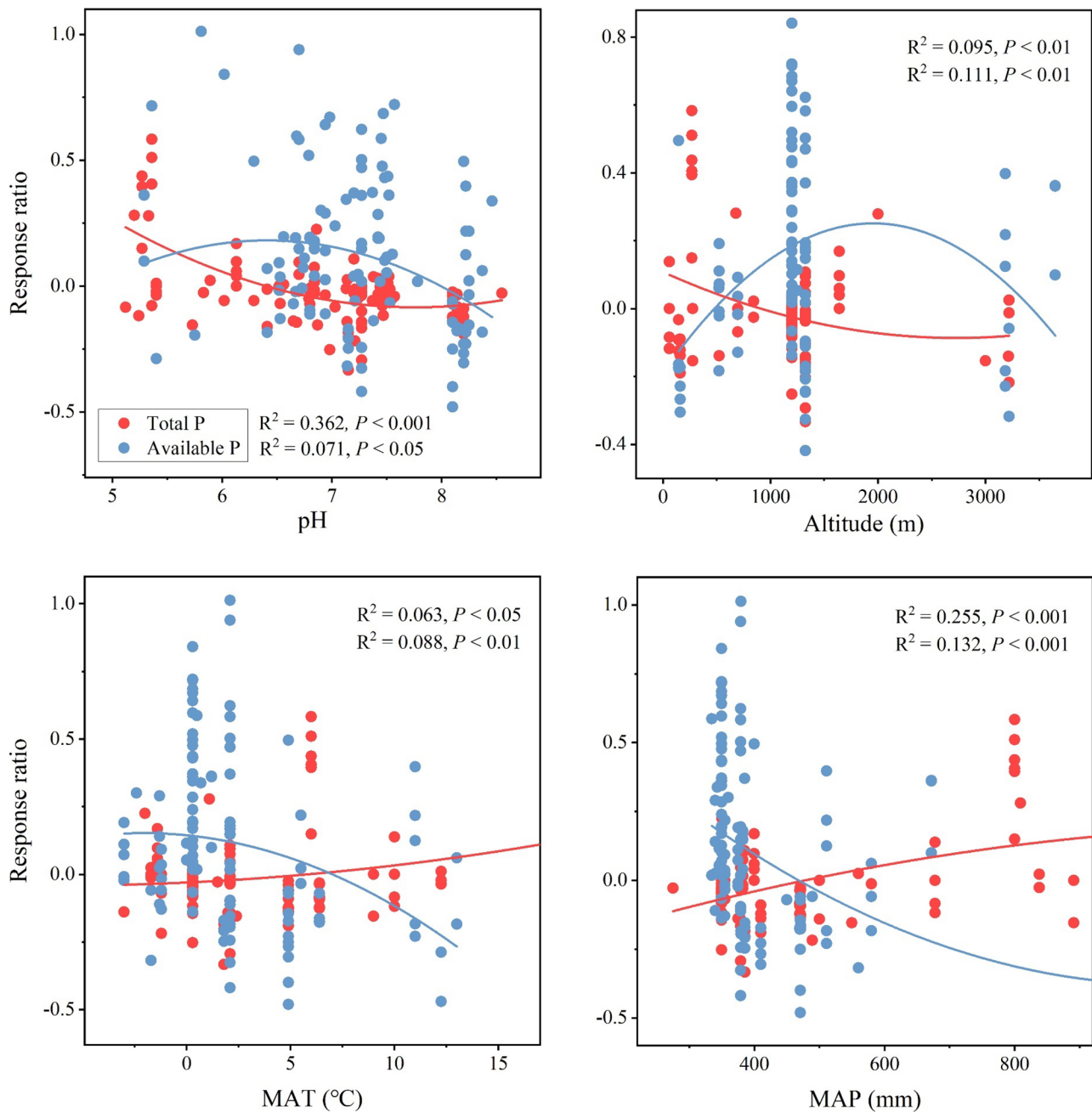
microbial biomass phosphorus; litter P, litter phosphorus concentration. Error bars represent 95% confidence intervals (CI). Vertical dashed line represents response ratio=0. The effect of treatment was statistically significant (denoted by \*) if 95% CI did not overlap zero. \*, \*\*, and \*\*\* indicate significant correlations at  $p < 0.05$ ,  $p < 0.01$ , and  $p < 0.001$ , respectively. The sample size for each variable is given in parentheses

P addition but depended on experimental durations, vegetation types, soil types, grassland types, and fertilizer types (Fig. S1). P addition significantly increased P availability under all conditions (Fig. S1). Regression analysis showed

that MAT significantly affected TP. However, AP responded differently to MAT, depending on latitudes and altitudes ( $P < 0.05$ , Fig S3).



**Fig. 3** Relationships of the response ratio of soil total phosphorus (total P) and soil available phosphorus (available P) with **A** N addition and **B** P addition rate. Regression lines indicates a significant correlation ( $p < 0.05$ )



**Fig. 4** Relationships of the response ratio of soil total phosphorus (total P) and soil available phosphorus (available P) with environmental and experimental variables under N addition. MAT mean annual tempera-

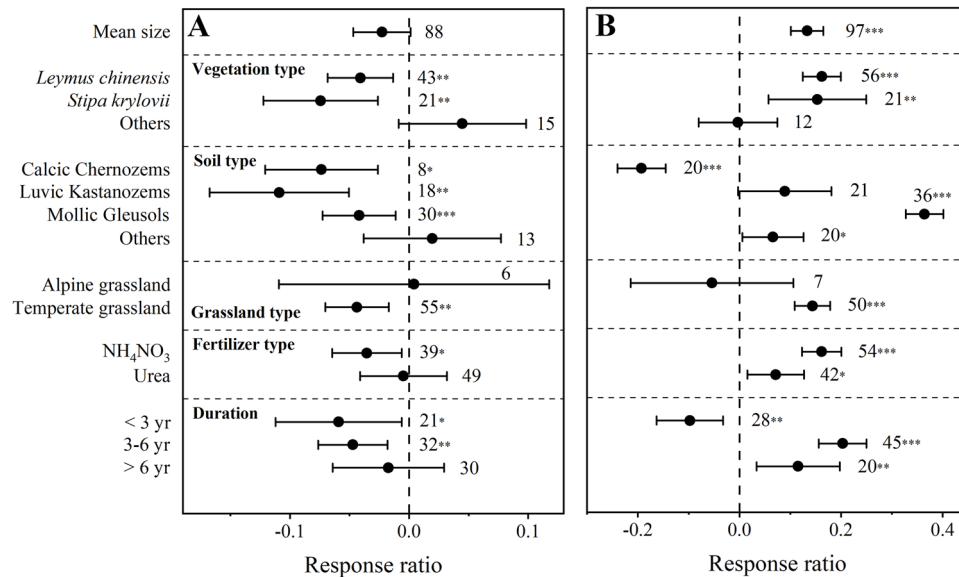
ture, MAP mean annual precipitation. Regression lines indicates a significant correlation ( $p < 0.05$ )

### 3.3 Effects of experimental warming, warming combined with N addition, and N combined with P addition on soil P

Experimental warming reduced AP and MBP by 6.7% ( $P < 0.001$ ) and 10.5% ( $P < 0.01$ ), respectively, whereas it increased litter P concentration by 46.2% ( $P < 0.01$ ) (Fig. 2). N addition combined with warming reduced AP and MBP

by 13.6% ( $P < 0.001$ ) and 26.0% ( $P < 0.001$ ), respectively, whereas it increased litter P concentration by 91.5% ( $P < 0.001$ ) (Fig. 2). The combination of N and P addition increased TP and AP by 34.5% and 194.0%, respectively ( $P < 0.001$ , Fig. 2).

Subgroup analysis showed that experimental warming increased TP and reduced AP in temperate grasslands, and these effects were more significant in grasslands dominated



**Fig. 5** Responses of **A** soil total phosphorus (total P) and **B** soil available phosphorus (available P) to N addition in global grassland ecosystems. Soil types (FAO classifications) were obtained from the Harmonized World Soil Database v 1.2 (HWSD Viewer) based on the longitude and latitude of the study site. Error bars represent 95%

confidence intervals (CI). Vertical dashed line represents response ratio=0. The effect of N addition was statistically significant (denoted by \*) if 95% CI did not overlap zero. \*, \*\*, and \*\*\* indicate significant correlation at  $p < 0.05$ ,  $p < 0.01$ , and  $p < 0.001$ , respectively. Corresponding sample size is given at the back of each variable

by *L. chinensis* and in Calcic Chernozem soil ( $P < 0.01$ ) (Fig. S2). By contrast, warming did not significantly affect TP and AP in alpine grassland ( $P > 0.05$ ) (Fig. S2). Warming induced by infrared radiators and open-top chambers (OTC) did not significantly affect TP ( $P > 0.05$ ) (Fig. S2). Infrared radiators significantly affected AP ( $P < 0.001$ ), whereas OTC did not significantly affect AP ( $P > 0.05$ ) (Fig. S2). None of the tested warming magnitudes, irrespective of the temperature range, affected TP ( $P > 0.05$ ), but significantly reduced AP ( $P < 0.001$ ). Short-term warming experiments increased TP ( $P < 0.001$ ) and reduced AP ( $P < 0.001$ ). Long-term warming experiments did not significantly affect TP or AP ( $P > 0.05$ , Fig. S2). Regression analysis showed that pH, altitude, MAT, and MAP all significantly affected TP responses to combined N and P addition ( $P < 0.05$ , Fig. S4). Only altitude and MAT significantly affected AP ( $P < 0.05$ ), whereas other environmental factors did not significantly affect AP ( $P > 0.05$ , Fig. S4).

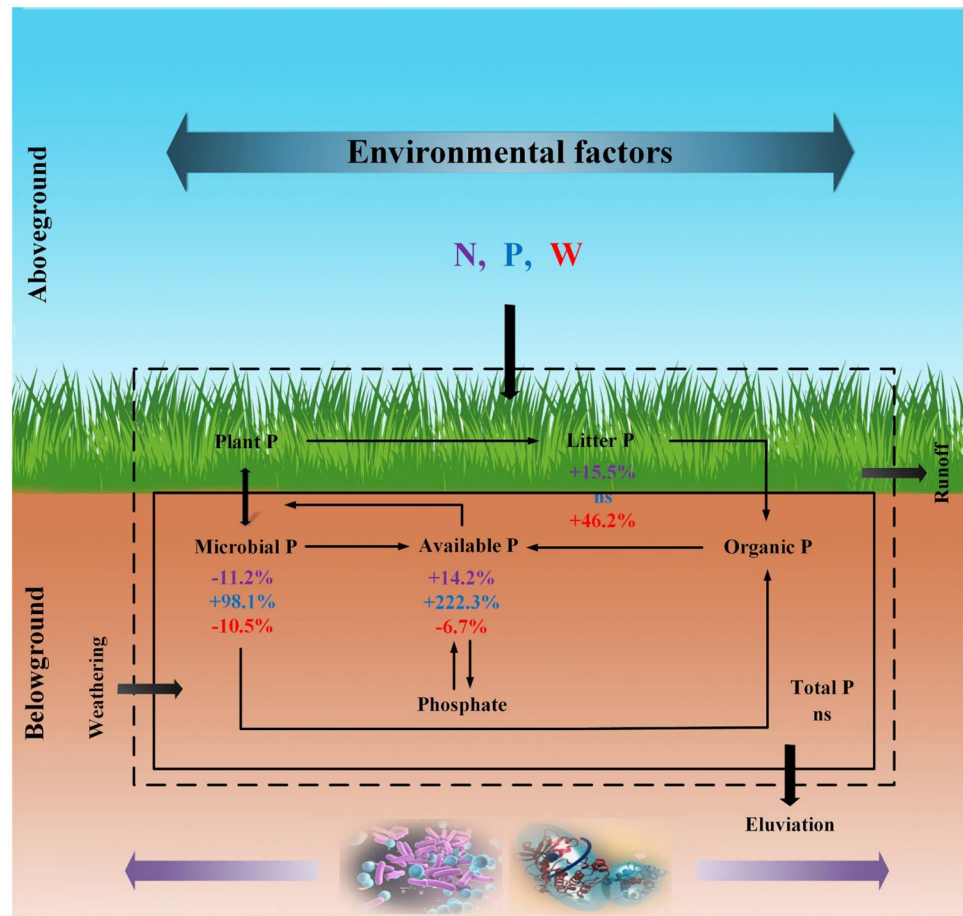
## 4 Discussion

This meta-analysis showed that N addition and experimental warming increased litter P concentration but reduced microbial biomass P. The increased P availability in soils under N addition could be attributed to enhanced mineralization of P and conversion of refractory, or forms of inorganic P typically resistant to change. Experimental warming maintained

the balance of soil total P, likely by regulating plant acquisition and enzyme activity. P addition accelerated the immobilization of microbial P and the solubilization of inorganic P, leading to an increase in available P, and microbial biomass P. N addition combined with warming increased litter P concentration but decreased available P, and microbial biomass P, suggesting that soil P might continue to be consumed and P limitation could be intensified under the scenario of increasing N deposition and rising temperature in grassland ecosystems. This was particularly evident in Calcic Chernozems grassland. Soil available P in *L. chinensis* and *S. krylovii* grassland had a strong response to nutrient addition and experimental warming (i.e., increased under nutrient addition and decreased under experimental warming).

The combination of N and P addition masked their individual effects on soil available P. Available P was more sensitive to nutrient addition and experimental warming in temperate grasslands than in alpine grasslands, which might lead to drastic changes in the soil P cycle in temperate grasslands under future climate change. Soil available P responses to nutrient addition depended on environmental factors such as altitude and pH. The results indicated that environmental factors might alter the P cycle response to nutrient addition by affecting microbial and enzyme activities (Fig. 6). Therefore, it is important to accurately determine the dynamic changes in soil microbial and enzyme activities to accurately predict the P cycle in grassland soils in the future.

**Fig. 6** Response of soil phosphorus cycle to nitrogen addition (N), phosphorus addition (P), and warming (W) in global grassland ecosystems. Total P, soil total phosphorus; available P, soil available phosphorus; organic P, soil organic phosphorus; litter P, litter phosphorus concentration; microbial P, microbial biomass phosphorus; Plant P, phosphorus absorbed and utilized by plants. Dashed arrows indicate phosphorus competition between plants and microorganisms. Numerical percentages of different colors represent changes under treatment with the corresponding color (+ and – indicate increase and decrease, respectively). Numerical percentages shown in the figure are significant ( $p < 0.05$ ), ns indicates insignificant ( $p > 0.05$ ) or not observed



#### 4.1 N addition significantly affected soil P in grasslands

The observed increase in P availability may result from the N-induced enhancement of soil organic P mineralization. N enrichment promotes plant growth and leads to increase soil organic matter from leaf litter, which accelerates soil organic P mineralized into available P (Widdig et al. 2019). Thus, N addition increased organic P mineralization while maintaining the balance of soil organic P. The observed increase in available P also might be attributed to the N-induced transformation of refractory form of soil inorganic P to less available soil inorganic P and then to available P, which was reported in previous studies (De Schrijver et al. 2012; Wang et al. 2020). N addition reduced microbial biomass P in grassland ecosystems. This result could have two explanations. (1) N fertilization caused microbial growth limited by C restriction, and thereby reduced microbial biomass and activity and inhibiting microbial immobilization of P (Demoling et al. 2008; Gong et al. 2020). (2) An increase in plant biomass increased P acquisition by plants, which might reduce the microbial immobilization of P (Alster et al. 2013; Gong et al. 2020). The increase of litter P concentration

response to N addition in our analysis also likely reflected this phenomenon that N addition generally promotes plant growth, which has relatively high demands for P (Yuan and Chen 2015; Möhl et al. 2019).

N addition inhibited microbial growth and activity, which could stimulate a decrease in immobilization of P by microorganisms and increasing P acquisition by plants, and thereby soil total P gradually decreased (García-Velázquez et al. 2020; Liu et al. 2021). A recent study showed that N addition rate at  $4 \text{ g N m}^{-2} \text{ year}^{-1}$  was the critical N loading level for alpine grassland microorganisms (Chen et al. 2021). This addition rate also seems to be the critical turning point for soil total P responses to N addition. At this inflection, soil total P changed from increasing to decreasing in our analysis. The microbial turnover or mineralization of P in the soil may not be significantly affected by N addition despite the decreased microbial immobilization of soil P (Liu et al. 2021). Therefore, available P was not significantly affected by N addition.

Subgroup analysis showed that grasslands dominated by *L. chinensis* and *S. krylovii* generally had the same responses to N addition (i.e., reduced total P and increased available P), likely due to the fact that *L. chinensis* and *S. krylovii*



produce extensive root networks that could display more sensitive responses to N addition (Wang et al. 2019). Besides, the decreased available P in response to N addition in soil dominated by Calcic Chernozems might be attributed to the stronger P adsorption and fixation capacity of this soil type, which reduced AP (Eckmeier et al. 2007). Moreover, the results indicated that N addition induced higher available P in temperate grasslands than in alpine grasslands. This outcome might owe to low phosphatase activity and microbial activity under extreme conditions in alpine grasslands (Chen et al. 2019; Li et al. 2020). Experiments testing different fertilizer types and durations had similar effects in increasing the available P in soil, but varied effects on total P.

Regression analysis between pH and soil total or available P revealed that grasslands with different soil pH showed varied responses to N addition, which may owe to the changes in enzyme and microbial activities. The habitats of enzyme and microorganisms could be altered dramatically due to N addition-induced acidification in alkaline grasslands, and result in more severe depression in microbial and enzyme activities than in acidic or neutral grassland. Others previously attributed changes in microbial and enzyme activities as the cause for variable responses in soil TP and AP (Buttler et al. 2019; D'Alo et al. 2021). They also assigned that environmental factors were largely responsible for the changes in microbial and enzyme activity.

## 4.2 P addition significantly affected soil P in grasslands

P addition increased microbial immobilization of P and solubilization of inorganic P, thereby increasing soil available P and microbial biomass P (Olander and Vitousek 2000; Widdig et al. 2019; DeForest and Moorhead 2020). By contrast, P addition did not significantly affect phosphatase activity, possibly because microbial phosphatase activity also is regulated by availability of C, N, and other elements (Liu et al. 2019). Therefore, increased inorganic P solubilization and insignificant change in phosphatase activity under P addition, possibly induced a switch in the dominant P mobilization processes from organic P mineralization to inorganic P solubilization. The response of TP to P addition was unclear in our analysis because of publication bias (Table S1). Grassland ecosystems are generally limited by P availability, and thus low P addition can alleviate such limitation (Seabloom et al. 2021; Vogl et al. 2021). However, high P addition may cause microorganisms to be restricted by the availability of other elements such as C or N, thus inhibiting the increase of soil P availability (Liu et al. 2019).

Subgroup analysis indicated that temperate grasslands displayed stronger responses in soil available P to P addition than alpine grasslands (i.e., the greater change of response ratio). These stronger responses could be attributed to low

microbial and enzyme activity in alpine grasslands, similar to the response to N addition. The total P response ratio increased with increasing MAT. However, we postulated that this response ratio could reach maximum at a critical threshold MAT. Enzyme and microbial activities declined at high and low temperatures, and thereby inhibited the responses of total P (Ghiloufi and Chaieb 2021; Fanin et al. 2022). The fact that P addition significantly altered the available P response ratios at varying latitude and altitude could also be attributed to temperature-related changes induced by latitude and altitude effects on enzyme and microbial activities (Zhao et al. 2021).

## 4.3 Warming, warming combined with N addition, and N combined with P addition significantly affect soil P in grasslands

Consistent with previous results, experimental warming promoted the acquisition of P by plants, and thereby increased litter P concentration and decreased soil available P (Olander and Vitousek 2000; Wang et al. 2008). Inconsistent with previous reports (Rinnan et al. 2008; Rui et al. 2012), we found that warming did not significantly affect soil total P in grassland ecosystems. This may be the result that warming promoted phosphatase and microbial activity, accelerated litter decomposition, and returned P to the soil to maintain the balance of total soil P (Chen et al. 2003; Guo et al. 2019). Besides, we suggest that warming reduced microbial biomass P for similar reasons as those under N addition. Growing plants acquire a large quantity of P, which disadvantages microorganisms in competition for P. The quantity of microbially immobilized P declines, thereby reducing microbial biomass P (Dalling et al. 2016). These results indicate that experimental warming regulates the P cycle in grassland soil by promoting phosphatase activity and phosphorus acquisition by plants.

The combined addition of N and P showed a lower increase in the percentage of available P than the addition of P alone. This may be the result that N addition promoted plant growth and growing plants acquired higher levels of available P. By contrast, the increase of percentage available P was higher under combined addition of N and P than that resulting from N addition alone. This likely owes to the combined addition of N with P accelerated the conversion of soil inorganic P into soil available P (Liu et al. 2019). Therefore, the effects on available P in grassland soil were masked when N was added in combination with P. Warming combined with N addition reduced available P and microbial biomass P, but increased litter P concentration. These results indicate that future warming combined with increased N fertilization will accelerate soil organic P mineralization in grassland ecosystems, and plants will acquire more P. This will exacerbate the imbalance in soil N and P, which will

further aggravate P limitation and disrupt the sustainable supply of P in grassland ecosystems (Gong et al. 2020).

The total P response ratio displayed nonlinear relationships with altitude, and MAT under the addition of N combined with P, which could be related to changes in microbial and enzyme activities. Variations in pH could be explained by changes in enzyme and microbial activities, whereas variations in MAP could be attributed to P acquisition by plants. Extremely low or high precipitation inhibits plant growth, thereby reducing plant P acquisition and leading to an increase in total P accumulation. The available P response ratio significantly altered only with changes in altitude and MAT. We postulated that MAT-induced changes in the available P response ratio should display a maximum value.

## 5 Conclusions

Our meta-analysis synthesized grassland soil P cycle responses to nutrient addition and warming. The results suggested that (1) nutrient addition altered the soil P cycle by promoting P mineralization and solubilization of inorganic P, (2) experimental warming regulated plant acquisition and enzyme activity to accelerate soil P cycle, and (3) environmental factors mediated the responses of soil P cycle to nutrient addition by affecting enzyme and microbial activities. These findings revealed critical information regarding the potential effects of warming and nutrient addition on the global grassland ecosystem soil P cycle. However, most of the data in our analysis were derived from the eastern and northern hemispheres, and do not include grasslands in other global zones. Our analysis primarily evaluated changes in different soil P fractions in grassland ecosystems. Future work will verify these results by including data on changes in P fractions of plants and microorganisms. The effects of future global climate changes on the soil P cycle in grassland ecosystems should be investigated using extensive data networks for long-term, real-time monitoring, and data sharing.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11368-022-03276-y>.

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## Declarations

**Conflict of interest** The authors declare no conflict of interest.

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