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Plant biomass responses to elevated CO_2 are mediated by phosphorus uptake

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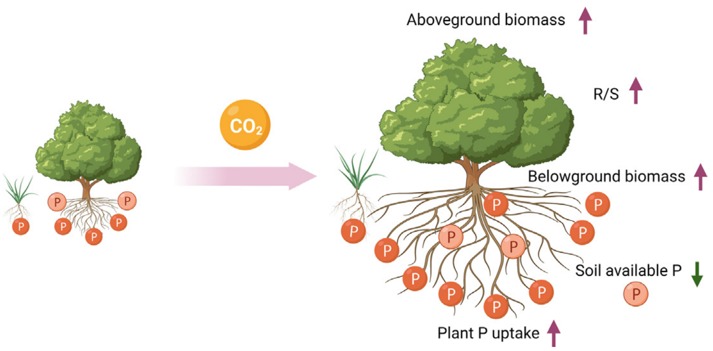
HIGHLIGHTS

- Elevated CO_2 significantly increased above- and below-ground biomass.
- Elevated CO_2 induced change in biomass was best explained by plant P uptake.
- Ecological drivers modulated elevated CO_2 effects on plant P dynamic.
- Elevated CO_2 largely decreased plant P concentration when plant P uptake was less enhanced.

GRAPHICAL ABSTRACT



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ABSTRACT

Elevated atmospheric CO_2 concentrations [CO_2] potentially alter carbon (C) and phosphorus (P) cycles in terrestrial ecosystems. Although numerous field experiments and a few meta-analyses have been conducted, it is still largely unclear how the P cycle affects plant biomass responses under elevated [CO_2] globally. Here, we conducted a global synthesis by analyzing 111 studies on the responses of above- and belowground P cycling to elevated [CO_2], to examine how changes in the P cycle affect the plant biomass response to elevated [CO_2]. Our results show that elevated [CO_2] significantly increased plant aboveground biomass (+ 13 %), stem biomass (+ 4 %), leaf biomass (+ 11 %), belowground biomass (+ 12 %), and the root: shoot ratio (+ 7 %). Effects of elevated [CO_2] on aboveground biomass, belowground biomass, and root: shoot ratio were best explained by plant P uptake. In addition, elevated [CO_2]-induced changes in the aboveground P pool, leaf P pool, and leaf P concentration were modulated by ecological drivers, such as ΔCO_2, experimental duration, and aridity index. Our findings highlight the importance of plant P uptake for both above- and belowground plant biomass responses under elevated [CO_2], which should be considered in future biosphere models to improve predictions of terrestrial carbon-climate feedbacks.

1. Introduction

Atmospheric CO_2 concentrations have risen to levels >40 % higher than pre-industrial levels, and are expected to exceed 550 ppm by 2100 (IPCC, 2021). Elevated CO_2 concentration [CO_2] could substantially impact on

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many crucial biological processes such as plant phosphorus (P) dynamics, which may modify ecosystem functions and stability (Oelkers and Cole, 2008; Akhtar, 2020; Izaguirre et al., 2021). Elevated [CO_2]-induced changes in plant biomass carbon may lead to a positive or negative feedback to climate change, which further amplifies or diminishes effects of elevated [CO_2] (Hovenden et al., 2019; Song et al., 2019; Wang and Wang, 2021).

Over the past decades, numerous studies have been conducted to quantify the response of plants to elevated [CO_2] (Deng et al., 2015; Jiang et al., 2020; Norby et al., 2022). Recent meta-analyses of these studies suggest that elevated [CO_2] generally stimulates plant biomass production (Terrer et al., 2016), but individual studies also reported decreases (Luo et al., 2004) and no changes in plant biomass (Newingham et al., 2013). More importantly, elevated [CO_2] may induce differential effects on C allocation between above- and belowground plant organs (Nie et al., 2013), resulting in changes in root: shoot ratio (R:S). However, no previous study has tested potential changes in R:S ratio globally. Several factors have been suggested as potential drivers of the response of plant biomass to elevated [CO_2], including soil nutrient availability (De Graaff et al., 2006), water content (Hovenden et al., 2014; Wang and Wang, 2021), mycorrhizal type, ecosystem type, and experimental method (Terrer et al., 2016). To evaluate the potential drivers of elevated [CO_2], a recent global study including multiple factors, such as soil C:N, demonstrated that a change in N availability induced by mycorrhizal association controls the CO_2 fertilization effect on plant biomass (Terrer et al., 2016). However, elevated [CO_2] may not have the capacity to stimulate plant growth in phosphorus (P)-limited regions of the globe, despite high levels of soil N (Chapin et al., 2002; Terrer et al., 2019). Indeed, the effects of elevated [CO_2] on the biomass of ECM plants was shown to largely depend on soil P availability (Terrer et al., 2019). In addition, elevated [CO_2] may not stimulate tree growth and ANPP in phosphorus-limited ecosystems (Ellsworth et al., 2017). These results indicate that effects of elevated [CO_2] on plant biomass may depend on P availability, but this assumption has never been tested before at the global scale.

Phosphorus (P) generally limits plant growth, especially in tropical regions (Elser et al., 2007; Hou et al., 2020). Increased plant P uptake caused by human activities (e.g., afforestation) may further induce P limitation for plant growth in plantations under elevated [CO_2], since plants are repeatedly harvested and the biomass and nutrients are removed from the site (Deng et al., 2017). Meanwhile, increased soil P availability and plant P uptake by elevated [CO_2] may maintain plant growth in P-limited forests (Hoosbeek, 2016). Moreover, elevated [CO_2] may induce the unbalanced availability and uptake of plant C, N, and P, resulting in significant shifts in nutrient cycles and subsequently P limitation (Wang et al., 2010; Goll et al., 2012; Peñuelas et al., 2013). Thus, we hypothesized that plant P uptake is the key factor determining plant growth responses to elevated [CO_2], explaining more variation than any of the previously suggested determinants.

To test our hypothesis, we synthesized 1487 observations from 111 studies conducted in the field (Fig. 1, Supplementary Text. S1), separating aboveground biomass, belowground biomass, and root: shoot ratio (R:S), to evaluate the key drivers determining elevated [CO_2] responses of plant biomass. We used random-forest models to identify the underlying factors that best explain variation in the plant biomass response.

2. Materials and methods

2.1. Data source

We searched for peer-reviewed journal articles published between January 1950 and August 2021 on the impact of elevated [CO_2] on the phosphorus cycle using Web of Science and China National Knowledge Infrastructure (CNKI). The search term was ("phosphorus" OR "phosphatase" OR "phosphor") AND ("elevated CO_2" OR "increasing CO_2" OR "increased CO_2") and ("plant biomass" OR "plant production" OR "total biomass" OR "aboveground biomass" OR "belowground biomass"). Studies were selected based on the following five criteria: (i) At least one independent variable in the experiment was used to examine the effects of elevated [CO_2] on P cycling in terrestrial ecosystems. (ii) At least one of the selected variables related to P cycling (e.g. plant phosphorus, soil phosphorus, phosphorus uptake) was examined in all treatment and control groups at same temporal and spatial scales. (iii) Control and treatment plots had the same initial environmental conditions, species composition, and soil parameters. (iv) The treatment method of elevated [CO_2] (e.g. FACE (Free-Air CO_2 Enrichment) or OTC (Open Top Chambers) should be specified clearly. Meanwhile, the experimental duration should be longer than one growing season. (v) The mean value, sample size (n), and standard error (SE) or standard deviation (SD) of the selected variables in the control and treatment were extracted directly from the tables, graphs, or text. Values from graphs were extracted using the software Getdata. In total for our analysis, we selected 111 published papers with 1487 observations distributed around the world (Fig. 1, PRISMA in Fig. S1, Text S1).

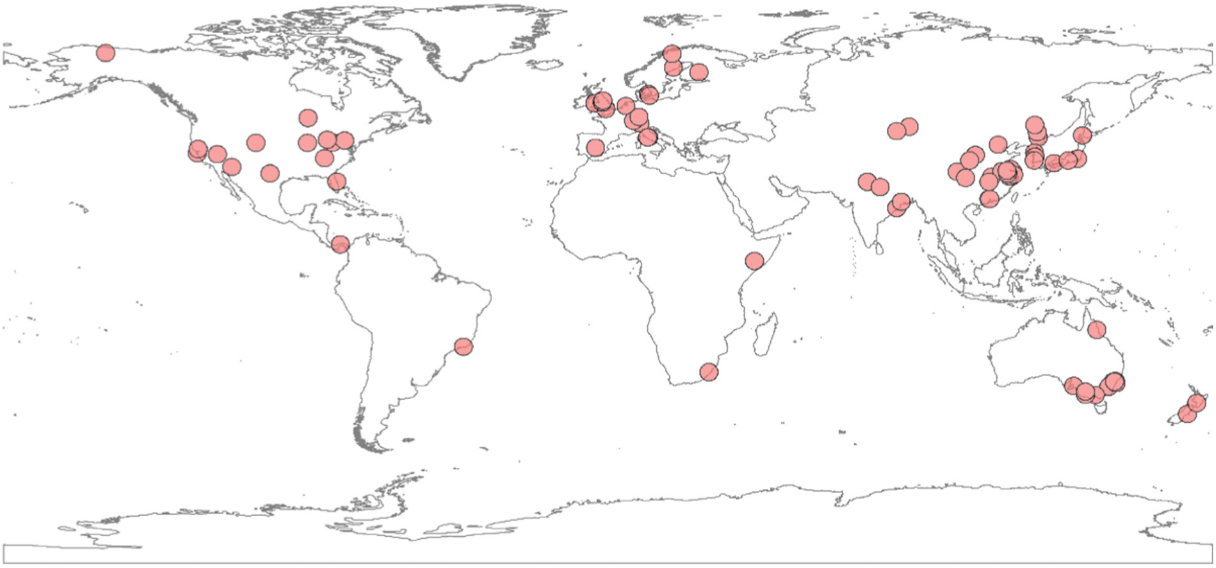

Fig. 1. Global distribution of the 92 experimental sites (covered in 111 studies) included in the meta-analysis. We could include 38 studies reporting aboveground biomass, 29 on belowground biomass, 21 on aboveground phosphorus (P), 9 on belowground P pool, 56 on aboveground P concentration, and 28 on belowground P concentration. Altogether, 1487 observations were considered in this study.

The selected studies had at least one of 18 variables related to P cycling to be included in the database. The database included plant biomass (i.e., biomass of aboveground parts, stem, leaf, root, litter, as well as root: shoot ratio (R/S), P pool (P stocks in aboveground biomass, stem, leaf, root, and litter), P concentration (P concentration in aboveground biomass, stem, leaf, root, and litter), and plant P use (i.e., P uptake and P use efficiencies). Meanwhile, we also extracted soil total P, soil available P, microbial biomass P, and phosphatase activity from the selected studies if available. Environmental and geographic variables including mean annual temperature (MAT), mean annual precipitation (MAP), longitude, and latitude were recorded directly from papers or cited papers, or in case that the MAT and MAP were not reported, extracted from the global climate database (http://www.worldclim.org/) using information on site geographical coordinates. Because plant N acquisition strategies depend on mycorrhizal association of the host plant (Terrer et al., 2016), we also compiled information on the mycorrhizal association of the dominant species at each experimental site, using the database of Wang and Qiu (2006). Soil C:N data were obtained from the reference, from other studies conducted at the same experimental site, or from the SoilGrids database (https://www.isric.org/explore/soilgrids), if the respective data were not reported. This approach was proven useful in global syntheses (Zhou et al., 2022). For each experiment in our dataset, we calculated the aridity index (AI) as the ratio of annual precipitation over potential evaporation; the latter term was obtained from the Global Aridity Index and Potential Evapotranspiration Climate Database v2 (www.worldclim.org/data/bioclim.html).

2.2. Meta-analysis

We quantified the effect of elevated [CO_2] on the focal response variables by calculating the natural log of the response ratio (LnR), a metric commonly used in meta-analysis (Hedges and Gurevitch, 1999). We weighted LnR by the inverse of its variance and estimated missing variances using the average coefficient of variation across our dataset. The meta-analysis was conducted using the 'rma.mv' function in the 'metafor' package in R software (R Development Core Team). The meta-analysis model included the variable "study" as a random factor to account for non-independence of observations derived from the same study. The effects of elevated [CO_2] were considered significant, if the 95 % confidence interval did not overlap with zero. The results of LnR were back-transformed and reported as the percentage change under elevated [CO_2] (i.e. $100 \times (e^{LnR} - 1)$) to ease interpretation. We included plant P uptake, aridity index, experimental duration, latitude, MAT, MAP, soil C:N, mycorrhizal type, plant type, ΔCO_2, and ecosystem type as moderators to predict the effect of elevated [CO_2] on the dependent variables (e.g., aboveground biomass) and

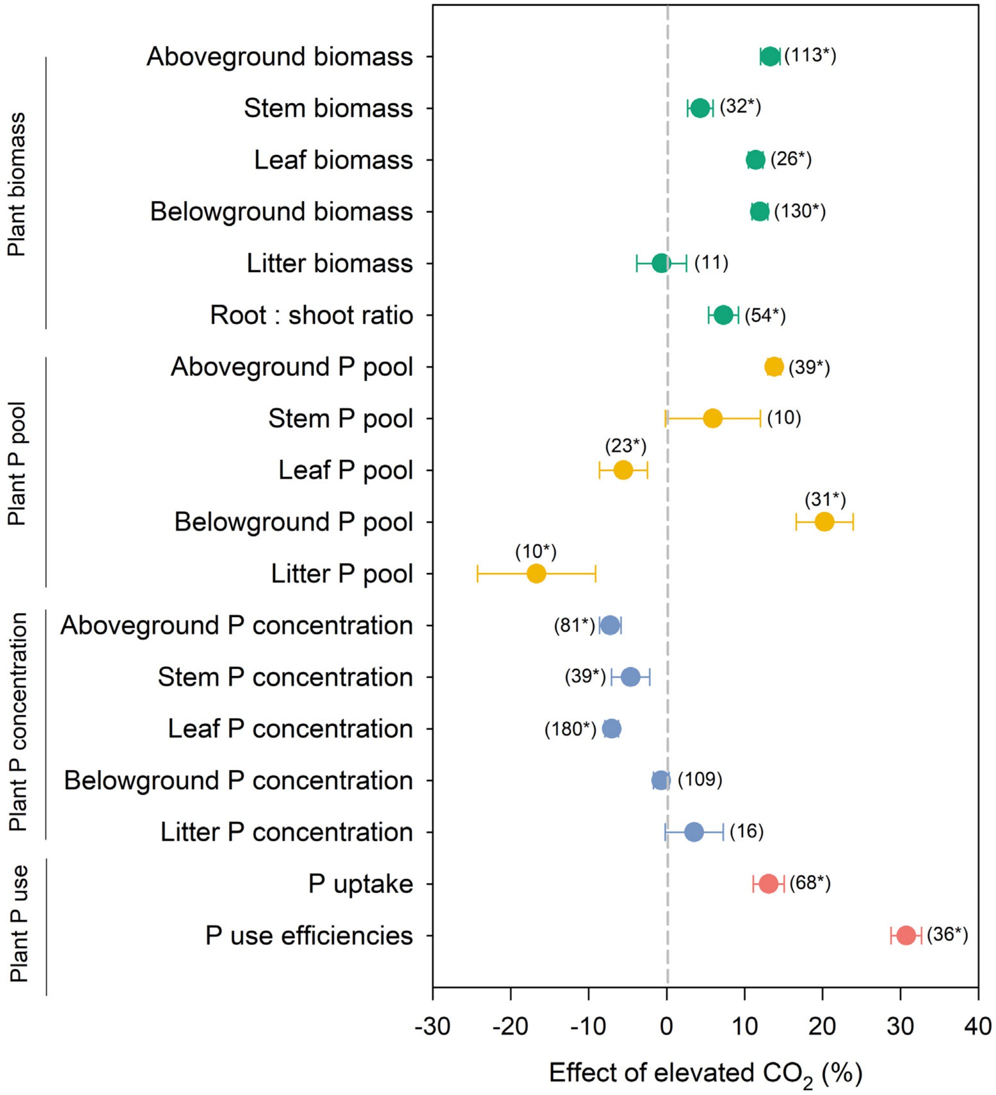

Fig. 2. Meta-analysis of the effect of elevated [CO_2] on biomass, phosphorus pool, and phosphorus concentration of different parts of the plant, P uptake, and P use efficiencies. Error bars represent 95 % confidence intervals. Numbers in brackets refer to the number of observations. Statistically significant effects ($P < 0.05$) are indicated by an asterisk.

identify the most important factors. Random forest analysis was conducted using R package 'randomForest'. We then evaluated the impacts of the most important factors on elevated [CO_2]-induced changes in the dependent variables (e.g., aboveground biomass) using linear regression analysis in R.

3. Results

3.1. Effect of elevated [CO_2] on above- and belowground P process

Elevated [CO_2] has significantly affected above- and belowground P process (Fig. 2). Specifically, elevated [CO_2] significantly increased aboveground biomass, stem biomass, leaf biomass, belowground biomass, and root: shoot ratio by 13 %, 4 %, 11 %, 12 %, and 7 %, respectively, while litter biomass was not significantly affected (Fig. 2). The enhanced biomass coincided with significantly increased aboveground P pool and belowground P pool by 14 % and 20 %, respectively, in response to elevated [CO_2]. In contrast, elevated [CO_2] significantly decreased P concentration in aboveground, stem, and leaf biomass by 7 %, 5 %, and 7 %, respectively, while no significant effects on belowground P concentration and litter P concentration were found (Fig. 2). Elevated [CO_2] significantly enhanced plant P uptake and P use efficiency by 13 % and 31 %, respectively (Fig. 2). In addition, our results showed that elevated [CO_2] significantly

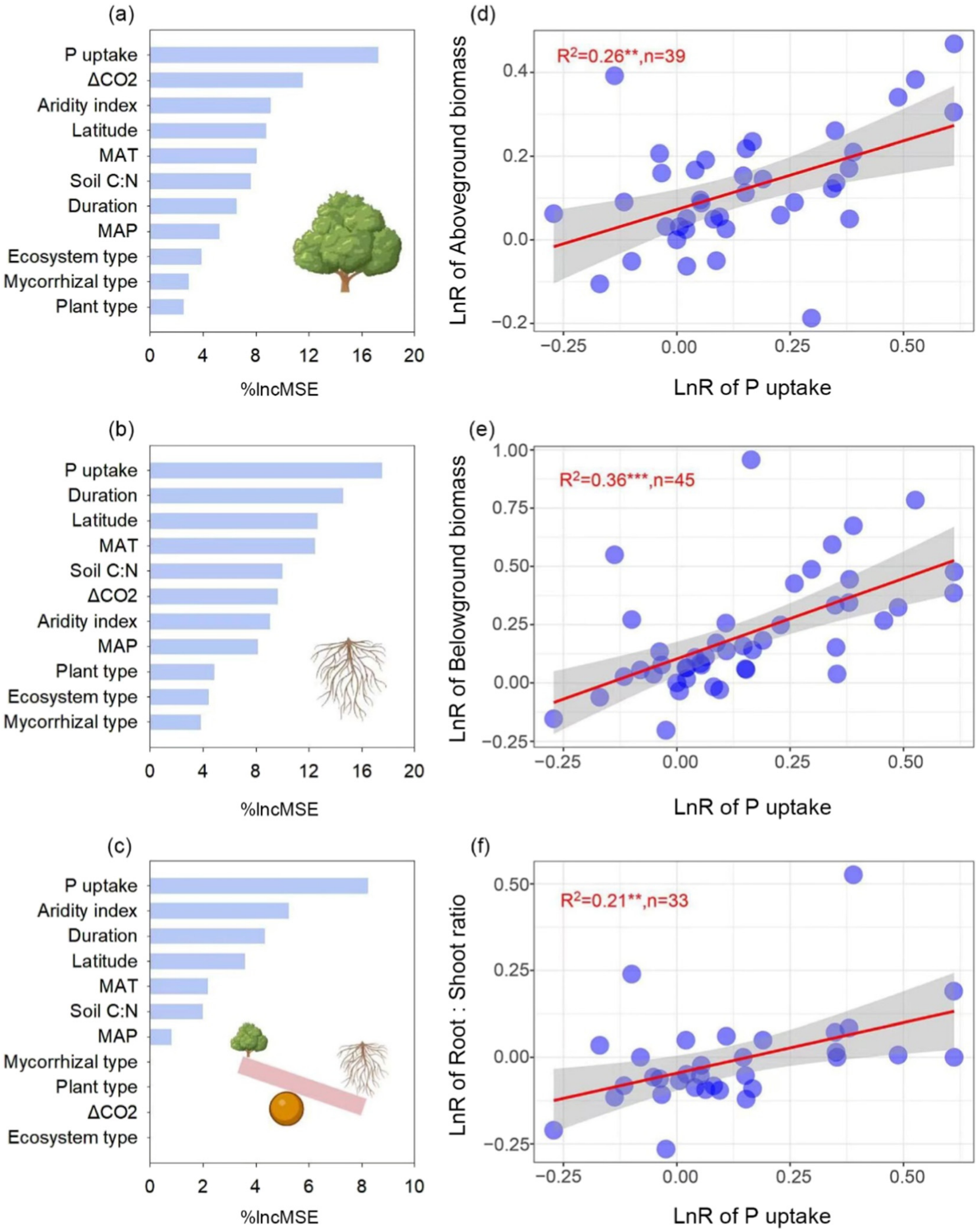

Fig. 3. Results of random forest analyses showing the relative importance of predicting factors in driving plant aboveground biomass (a), belowground biomass (b), and root: shoot ratio (c) under elevated [CO_2]. Relationships between the most important factors and the response ratio (LnR) of aboveground biomass (d), belowground biomass (e), and root: shoot ratio (f) under elevated [CO_2]. The importance of predictors is determined using %IncMSE from random forest models; negative relative importance values are not shown, indicating a lack of importance. Significance levels: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

increased soil microbial P and phosphatase activity by 20 % and 9 %, respectively, but decreased soil available P by 3 % (Fig. S2).

3.2. Effect of elevated [CO_2] on plant biomass mediated by plant P uptake

Random forest analysis showed that changes in aboveground biomass, belowground biomass, and root: shoot ratio induced by elevated [CO_2] were best explained by plant P uptake (Fig. 3). More specifically, the change in P uptake caused by elevated [CO_2] was significantly positively correlated with aboveground biomass ($R^2 = 0.26$, $P < 0.01$), belowground biomass ($R^2 = 0.36$, $P < 0.001$), and root: shoot ratio ($R^2 = 0.21$, $P < 0.01$) (Fig. 3). Moreover, we further found that plant P uptake could also best explain the changes in both aboveground and belowground P concentration induced by elevated [CO_2] (Fig. S3). The elevated [CO_2]-induced decreases in aboveground P concentration and belowground P concentration both became stronger when plant P uptake was less enhanced (Fig. S3). In addition, the enhanced plant P uptake induced by elevated [CO_2] tended to be stronger when soil phosphatase activity was more strongly affected (Fig. S4).

3.3. Ecological and environmental drivers

The effect of elevated [CO_2] on plant biomass largely depended on the part of the P cycle (Fig. 4). More specifically, we found that the LnR of aboveground biomass exhibited a positive correlation with the LnR of aboveground P concentration. The same relationships were also observed between the LnR of leaf biomass and the LnR of leaf P concentration, as well as between the LnR of belowground biomass and the LnR of belowground P pool. Meanwhile, our results also showed that elevated [CO_2] synchronously increased above- and belowground biomass. Moreover, significant positive correlations were found between the LnR of stem biomass and the LnR of leaf biomass, between the LnR

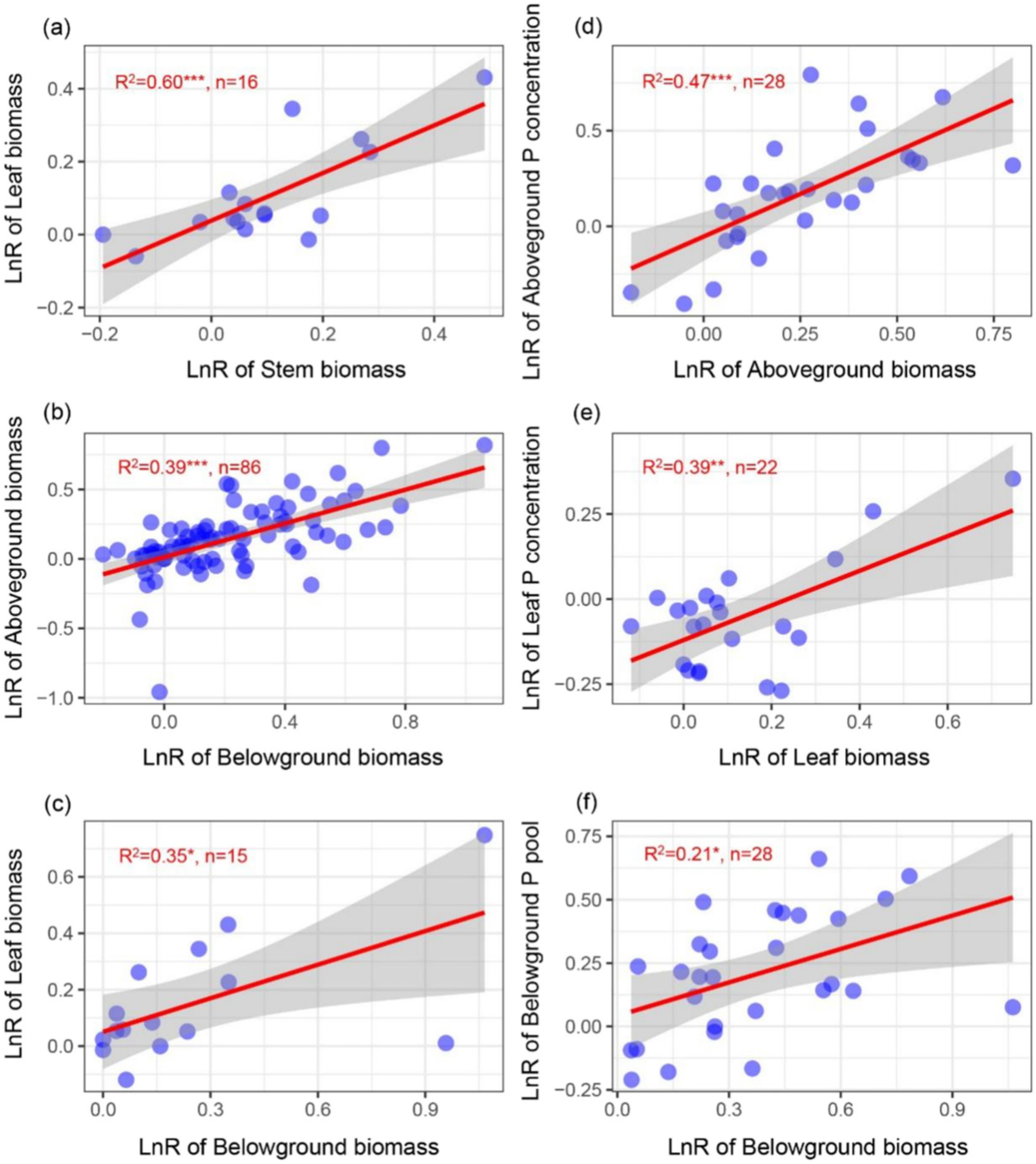

Fig. 4. Relationships between the response ratio (LnR) of different variables under elevated [CO_2]. Relationship between the LnR of stem biomass and leaf biomass (a), belowground biomass and aboveground biomass (b), belowground biomass and leaf biomass (c), aboveground biomass and aboveground P concentration (d), leaf biomass and leaf P concentration (e), as well as belowground biomass and belowground P pool (f) under elevated [CO_2]. Significance levels: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

of belowground biomass and the LnR of aboveground biomass, as well as between the LnR of belowground biomass and leaf biomass. In addition, the elevated [CO_2]-induced change in the aboveground P pool was positively related to aboveground P concentration (Fig. S5).

We also found that environmental and experimental factors affected plant P dynamics (Fig. 5). The effect of elevated [CO_2] on the aboveground P pool was significantly negatively related to the magnitude of the elevated CO_2 manipulation. Moreover, the response of the leaf P pool was affected by experimental duration, with larger increase for long-term experiments with elevated [CO_2]. Furthermore, the effects of elevated [CO_2] on leaf P concentration was best predicted by aridity index. More specifically, aridity index positively correlated with elevated [CO_2]-induced changes in leaf P concentration.

4. Discussion

4.1. Plant phosphorus uptake mediates biomass responses to elevated [CO_2]

Understanding the effects of elevated [CO_2] on plant biomass is crucial to better predict future feedback between C cycle and climate change (Reich et al., 2014; Terrer et al., 2021; Walker et al., 2021). We analyzed 111 published papers with 1487 observations and found that elevated

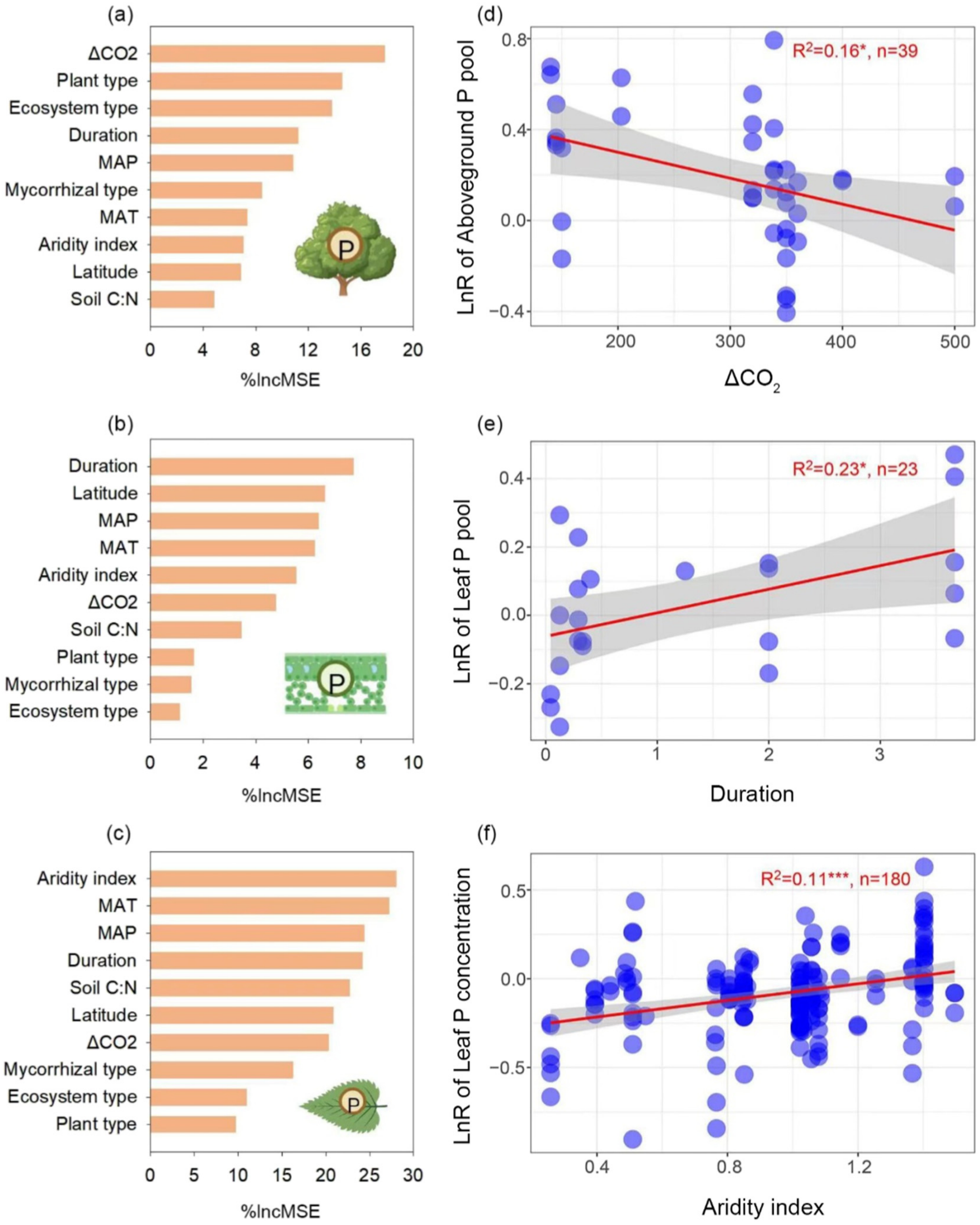

Fig. 5. Results of random forest analyses showing the relative importance of predicting factors in driving the plant aboveground P pool (a), leaf P pool (b), and leaf P concentration (c) under elevated [CO_2]. Relationships between the most important factors and the response ratio (LnR) of aboveground P pool (d), leaf P pool (e), and leaf P concentration (f) under elevated [CO_2]. The importance of predictor is determined using %IncMSE from random forests. Significance levels: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$.

$[CO_2]$ significantly increased above- and belowground plant biomass globally. A slightly asynchronous increase of above- versus belowground biomass resulted in an increased root: shoot ratio in response to elevated $[CO_2]$. Most importantly, our study identified that plant P uptake is strongly related to changes in above- and belowground biomass in response to elevated $[CO_2]$, while nitrogen availability was identified as an important driver before (Terrer et al., 2016). We further found that elevated $[CO_2]$-induced changes in aboveground biomass, belowground biomass, and root: shoot ratio were all positively correlated with plant P uptake at the global scale. Taken together, our study highlights the important role of P dynamics in driving the carbon cycle under elevated $[CO_2]$, and provides solid empirical evidence calling to incorporate P dynamics into next generation models for better predicting climate change feedbacks of carbon.

We found that elevated $[CO_2]$ significantly promoted aboveground and belowground biomass (Fig. 2), consistent with several previous studies (Jiang et al., 2020; Wang and Wang, 2021). Such increased plant biomass may be attributed to enhanced photosynthesis as well as water-use efficiency, which further increased the C input and then biomass accumulation (Kimball and Idso, 1983; Morison, 1985; Kimball et al., 2007). Meanwhile, elevated $[CO_2]$ is also likely to stimulate root growth in deeper soils to absorb additional nutrients (e.g., nitrogen) to meet the demands of plant growth, thereby increasing root biomass and belowground C inputs (Luo et al., 2006; Iversen, 2010; Jin et al., 2015). Moreover, we found that elevated $[CO_2]$ significantly increased the root: shoot ratio, suggesting belowground biomass accumulation is greater than aboveground biomass accumulation. It has been shown that elevated $[CO_2]$ promoted C allocation to the roots to increase P uptake (Van Vuuren et al., 1997), resulting in higher root: shoot ratio. More importantly, our results show for the first time at the global scale that the effect of elevated $[CO_2]$ on aboveground biomass, belowground biomass, and root: shoot ratio is best explained by plant P uptake (represented by the elevated $[CO_2]$-induced increase in these three variables that are positively correlated with plant P uptake). Elevated $[CO_2]$ has been shown to stimulate root exudation and possibly the decomposition of root litter and organic matter, thereby promoting plant uptake of P bound to soil organic matter (Song et al., 2019). The increased soil P availability via enhancing soil phosphatase activity by elevated $[CO_2]$ may thus result in higher plant P uptake and, subsequently, an increase in plant biomass (Bhattacharyya et al., 2014; Deng et al., 2015). In addition, elevated $[CO_2]$ may also stimulate the activity of the root epidermis and root hairs, which may enhance plant P uptake and biomass production (Smith et al., 2003, 2011). Moreover, elevated $[CO_2]$ has been shown to increase C inputs to the soil, supporting a higher abundance and activity of soil microorganisms (Chapin et al., 2002; Hungate et al., 2006), including arbuscular mycorrhizal fungi (Terrer et al., 2019), which play a key role in plant P uptake (Smith and Read, 2010).

4.2. Links between above- and belowground P processes to elevated $[CO_2]$

Our results also show that elevated atmospheric $[CO_2]$ has an impact on the relationships between the biomass, P pool, and P concentration of/in different plant organs. More specifically, we found that the LnR of belowground biomass was positively correlated with the LnR of aboveground biomass and leaf biomass. Since plants have a high ability to coordinate the growth of organs, an elevated $[CO_2]$-induced change in aboveground biomass would positively associate with belowground responses (Poorter and Nagel, 2000). The "fertilization effect" induced by elevated $[CO_2]$ may thus promote leaf biomass accumulation, while stem biomass and belowground biomass also increase to meet the growth balance and support the leaves. Conversely, an increase in root biomass will promote plants to absorb more soil nutrients, which in turn is beneficial for aboveground biomass production. The positive relationship between the LnR of biomass and LnR of P concentration in our study (Fig. 4d, e) indicates that with an increase in plant biomass, plant P concentration may also increase under elevated $[CO_2]$. Our result is consistent with a global meta-analysis (Li et al., 2016), suggesting that plant P concentration is a good indicator for P limitation. We also found that the LnR of belowground biomass was positively correlated with the LnR of the belowground P pool (Fig. 4f), which may be due to an elevated $[CO_2]$-induced increase in the allocation of plant biomass to roots to increase P uptake, thereby enhance root P pool (Xiao et al., 2016).

4.3. Environmental and experimental drivers of plant P processes

Environmental and experimental factors have been shown to modulate the effect of elevated $[CO_2]$ on plant P pool or concentration (Sardans et al., 2017). In this study, we found that the effects of elevated $[CO_2]$ on the aboveground P pool was best explained by ΔCO_2; and ΔCO_2 exhibited a negative correlation with the LnR of the aboveground P pool. It has been shown that excessive $[CO_2]$ may lower the photosynthesis as well as plant P uptake, which may be an explanation for reduced biomass accumulation and plant C pool (Chapin et al., 2002). Moreover, the effect of elevated $[CO_2]$ on the leaf P pool was best explained by experimental duration, with a positive correlation between LnR of the leaf P pool and experimental duration. It has been shown that long-term elevated $[CO_2]$ exposure may significantly stimulate photosynthesis as well as plant P uptake, which could further increase leaf biomass and then the leaf P pool (Chapin et al., 2002). Furthermore, we found that the LnR of leaf P concentration was increased by the aridity index. These changes may result from the fact that plant productivity and microbial activity in wetter regions are usually greater than the drier ones, and the actual responses of leaf P concentration to elevated $[CO_2]$ may have been masked, causing the leaf P concentration to increase with increasing water availability (Chapin et al., 2002; He and Dijkstra, 2014).

4.4. Implications for future modeling development and experimental design

Understanding the effects of elevated $[CO_2]$ on plant biomass production as well as identifying key driving factors are crucial to advance climate change biology (Yuan and Chen, 2015; Terrer et al., 2016). In this study, we identified that plant P uptake was a key driver regulating the above- and belowground plant biomass responses to elevated $[CO_2]$ globally. However, most current Earth System Models usually do not fully consider the role of plant P uptake in regulating plant biomass production under elevated $[CO_2]$, which may create a challenge to predict the potential effect of global change on ecosystem functions (Wieder et al., 2015; Reed et al., 2015). Therefore, it is necessary to consider plant P uptake and dynamics in next generation Earth System Models to develop more precise process-based mechanisms for better forecasting the global carbon cycle (Ziehn et al., 2021). Moreover, our results also show that the elevated $[CO_2]$-induced change in plant biomass was positively correlated with experimental duration. However, the duration of the majority of the selected studies in our database was <5 years, which may prevent us from obtaining the true long-term response, since the effect of elevated $[CO_2]$ may decrease with time due to progressive nitrogen limitation (Luo et al., 2004). More long-term experiments are thus urgently needed to develop a more comprehensive understanding of the ecosystem responses to elevated $[CO_2]$. Furthermore, most studies in this meta-analysis were distributed in temperate regions, especially in North America, eastern Asia, and Europe (Fig. 1). Thus, more research needs to be conducted in other regions (especially in tropical areas, Africa, and South America) to examine how elevated $[CO_2]$ may influence terrestrial C and P cycles.

CRediT authorship contribution statement

G.Y.Z and X.H.Z designed the study. Q.L and X.M.H collected the data, and analyzed data. X.M.H and G.Y.Z wrote the manuscript. All authors contributed to the revision of the paper.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declared no conflict of interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.160775.

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