A meta-analysis highlights globally widespread potassium limitation in terrestrial ecosystems

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Summary

- Potassium (K^+) is the most abundant inorganic cation in plant cells, playing a critical role in various plant functions. However, the impacts of K on natural terrestrial ecosystems have been less studied compared with nitrogen (N) and phosphorus (P).
- Here, we present a global meta-analysis aimed at quantifying the response of aboveground production to K addition. This analysis is based on 144 field K fertilization experiments. We also investigate the influences of climate, soil properties, ecosystem types, and fertilizer regimes on the responses of aboveground production.
- We find that: K addition significantly increases aboveground production by 12.3% (95% CI: 7.4–17.5%), suggesting a widespread occurrence of K limitation across terrestrial ecosystems; K limitation is more prominent in regions with humid climates, acidic soils, or weathered soils; the effect size of K addition varies among climate zones/regions, and is influenced by multiple factors; and previous N : K and K : P thresholds utilized to detect K limitation in wetlands cannot be applied to other biomes.
- Our findings emphasize the role of K in limiting terrestrial productivity, which should be integrated into future terrestrial ecosystems models.

Introduction

Vegetation carbon sinks may help to mitigate global climate warming (Norby *et al.*, 2005; Ciais *et al.*, 2014) because plant production currently exceeds the total loss from decomposition and disturbance such as fire and diseases/pests. Although photosynthesis responds positively to elevated CO_2, nutrient availability constrains CO_2 fertilization of global plant biomass in terrestrial ecosystems (Fleischer *et al.*, 2019; Terrer *et al.*, 2019). N and P are considered to be the two major limiting nutrients (Elser *et al.*, 2007; LeBauer & Treseder, 2008; Vitousek *et al.*, 2010), while potassium (K) has been frequently neglected (Sardans & Peñuelas, 2015), even though it is the second most abundant nutrient in leaves and plays an important role in plant physiology (Leigh & Wyn Jones, 1984; Sardans & Peñuelas, 2021). At the individual level, K is crucial for water economy (Sardans & Peñuelas, 2015; Yang *et al.*, 2023). When ecosystems face drought stress, guard cell potassium ions (K^+) help mitigate water losses by maintaining cellular turgor and osmotic pressure, thereby governing water conductance and transpiration (Andrés *et al.*, 2014; Battie-Laclau *et al.*, 2014). Additionally, K directly influences photosynthesis (Tränkner *et al.*, 2018). It has been reported that K deficiency would reduce leaf area and subsequently resulted in a reduction of gross primary productivity (GPP; Hu *et al.*, 2020), and K addition increased leaf photosynthetic rates where K is limited (Hou *et al.*, 2019). Furthermore, K affects leaf life span and carbon allocation (Laclau *et al.*, 2009; Epron *et al.*, 2012) and is considered as a critical component for the transfer of other nutrients (such as inorganic P) to plants (Garcia & Zimmermann, 2014). However, how K affects plant production at the ecosystem level remains unclear.

Some fertilization experiments have examined K effects on plant production, but their results show divergence. Plant production reportedly increases (Ouimet & Moore, 2015; Wright *et al.*, 2018), decreases (Cleve & Oliver, 1982; Kidd *et al.*, 2017), or shows no change in response to K addition (Chadwick *et al.*, 1999). Different responses may be attributed to different ecosystem types, climate, soil properties, K application rates, and

fertilizer forms. Complex interconnections and interactions among these factors result in great variation in K effects. It has been reported that parent material is one of the most important factors driving soil K availability and K fertilization response and that the presence of K-bearing minerals, even in small amounts, can significantly affect soil K availability (Darunsontaya et al., 2012). However, almost none of the studies in the literature reported parent material information, which limited our analysis. A long-held notion is that K limitation is more likely to exist in the humid tropics (Baribault et al., 2012; Schlesinger, 2020; Cornut et al., 2021). The reasons given are that these regions: are generally older and have more weathered soils relative to temperate regions (Aerts & Chapin, 1999); have relatively small quantities of K-bearing minerals (Darunsontaya et al., 2012); have a higher leaching rate due to high precipitation (Huston, 2012); and have lower foliar potassium concentrations (X. Li et al., 2021). Consequently, atmospheric K deposition (with a mean value of $4.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$) may play an important role in these forests (Sardans & Peñuelas, 2015; Van Langenhove et al., 2020). However, these facts only suggest the likelihood of K limitation. It is better to determine the actual K limitation magnitude by field fertilization experiments (Chapin et al., 1986). A previous meta-analysis showed an overall limiting effect of K on tree growth, with 22 of 32 studies (69%) showing some degree of K limitation in forest ecosystem (Tripler et al., 2006). Of these growth studies, however, only eight studies were exclusively fertilized with K in the field. When analyses are based on limited data, obtaining a quantitative measure of K effects on plant growth in forest becomes difficult. Furthermore, nearly none of synthesized results have evaluated K effects in wetlands and tundra, which provide important services (Schuur et al., 2009; Salimi et al., 2021). Although previous syntheses and nutrient addition experiments have emphasized the importance of K for forest and grassland (Tripler et al., 2006; Fay et al., 2015), no global meta-analysis has been conducted so far to reveal generalizable patterns of K limitation across terrestrial ecosystems.

Olde Venterink et al. (2003) performed a synthesis of 44 fertilization experiments conducted in European wetlands and showed that plants at $N : K > 2.1$ and $K : P < 3.4$ were K or N + K limited. These N : K and K : P thresholds were proposed based on the relationship between plant N : K and K : P ratios in unfertilized control plots, and nutrient limitation type determined through fertilization experiments in wetland. Although these N : K and K : P thresholds have universally been used to detect plant terrestrial ecosystem K limitation (including wetland, grassland, tundra, and forest; Du et al., 2011; Gong et al., 2011; Müllerová et al., 2014; Vourlitis et al., 2014; Wang & Moore, 2014; Beermann et al., 2015; Luo et al., 2020; Yang et al., 2020; Mansur et al., 2021; Marler, 2021; Wassen et al., 2021), the validity of this threshold, and whether it applies to other ecosystems, remains unclear.

The lack of knowledge regarding the importance of K for terrestrial ecosystem production limits our ability to predict land carbon sink trends in response to elevated CO_2. Therefore, we conducted a global meta-analysis based on 95 papers, covering most ecosystem types and regions (Supporting Information

Table S1). The objectives were: (1) to systematically assess the response of aboveground production to K addition alone; (2) to examine which factors affect the response of aboveground production to K fertilization, and how; and (3) to evaluate the applicability of previous N : K and K : P thresholds in detecting K limitation.

Materials and Methods

Data collection and preparation

We compiled a database that included all papers and data associated with K addition responses of plant biomass production. We searched peer-reviewed articles using the Web of Science (https://www.webofscience.com), Dimensions (https://www.dimensions.ai), and China National Knowledge Infrastructure (https://www.cnki.net) up to January 2022. The search terms were combinations of keywords such as (potass* OR potash) AND (fertili* OR enrich* OR limit* OR add* OR applicat*). We also included articles used in previously published synthesis related to K addition (Wright et al., 2018). The papers included in our database were then filtered to satisfy the following criteria: (1) The K addition experiment was conducted in ecosystems with permanent vegetation (not croplands), which had not been fertilized before the K application trial; (2) each fertilization trial must include solely K addition and control treatments (K fertilization must not be combined with N and P fertilization in one treatment to avoid the effects of N and P) with the same ecosystems in the same environment; (3) the studies must contain the measures of plant biomass production at a community level; (4) the means and sample sizes for K addition and control treatments can be obtained directly; (5) when more than one paper reported the same experiments, we selected the data from the latest paper; and (6) if an experiment had different fertilization rates, we chose the highest amount of K addition.

Finally, 95 papers were selected for this study based on a PRISMA flow diagram for meta-analysis (Fig. S1; Notes S1, S2). From the literature, three data groups were extracted: (1) aboveground production; (2) belowground production (fine root and total root biomass); and (3) plant tissue (including leaf and aboveground biomass) N : K and K : P ratios. As outlined in Table S2, when the response was not assessed on aboveground production, we also considered other variables related to plant growth. In forest, apart from aboveground production (10), we also accepted height (11), basal area (4), diameter (6), and stem volume (10). In tundra, we also included leaf mass (2) alongside aboveground production (1). Notably, no significant difference was observed among the various variables (Table S2). Measurements from different study sites in the same article were regarded as independent experiments. When data were presented in figures, we extracted the values using the digitizing software GetData Graph Digitizer 2.26 (http://www.getdata-graph-digitizer.com). Furthermore, basic background information, such as location (latitude and longitude), elevation, mean annual precipitation (MAP), mean annual temperature (MAT), soil pH, soil exchangeable K, and ecosystem type, was recorded and collected

from each study site. If a paper did not report the location, a similar latitude and longitude were extracted by retrieving site names in Google Earth 7.1. Additionally, when studies did not report MAP and MAT, then these data were obtained from WorldClim2.0 (Fick & Hijmans, 2017), and the missing elevations were extracted from Google Earth 7.1 using geographic coordinates (latitude and longitude). The aridity index (AI) for each study site was derived from Global-AI_PET (Antonio & Robert, 2019); lower AI values indicate a higher degree of aridity. Soil organic carbon concentration, clay, and sand content, as well as unreported soil pH values of the 0–15-cm layer, were extracted from SoilGrids2.0 (Poggio *et al.*, 2021). Soil type classification refers to the US Department of Agriculture soil classification system (Nachtergaele, 2001). Soil types were grouped based on their weathering degrees (Augusto *et al.*, 2017). Andisols, Histosols, Entisols, and Inceptisols were slightly weathered soils; Aridisols, Vertisols, Mollisols, and Alfisols were intermediately weathered soils; and Spodosols, Ultisols, and Oxisols were strongly weathered soils.

In total, our database consisted of 144 experiments for aboveground production (from 89 papers; Note S1), 42 experiments for belowground production (from 15 papers; Note S2). To compare K effects among ecosystems, regions, and experiments, we divided the database into different groups following a previous workflow (Hou *et al.*, 2020). First, data were grouped according to ecosystem types: forest, grassland, wetland, and tundra (plantations, shrublands, and savannas were regarded as forest). Second, data were divided based on absolute latitude into four regions: tropics (23.4°S–23.4°N), subtropics (23.4°S–35°S or 23.4°N–35°N), temperate (35°S–66°S or 35°N–66°N), and arctic (> 66°S or > 66°N). Third, data were grouped according to the geographic scope of each continent: Asia, Africa, Europe, North America, Oceania, and South America. Fourth, data were grouped based on AI into five groups: arid (AI ≤ 0.20), semiarid (0.2 < AI ≤ 0.50), dry subhumid (0.5 < AI ≤ 0.65), subhumid (0.65 < AI ≤ 1), and humid (1 < AI). Finally, data were grouped according to the length of experimental duration (≤ 3, and > 3 yr), fertilization type (Sulfate of Potash (K$_2$SO$_4$), Muriate of Potash (KCl), and others), K application rate (≤ 50, 50–100, and > 100 kg ha^{-1} yr^{-1}), elevation (≤ 1000 and > 1000 m), and soil pH (acidic: pH < 6.6, neutral: 6.6 ≤ pH ≤ 7.3, and alkaline: 7.3 < pH (Soil Science Division Staff, 2017)). The distribution of study sites in this meta-analysis is shown in Fig. 1a.

Meta-analysis

In our meta-analysis, we used log-transformed response ratio (LNRR) to evaluate the effects of the K addition treatment (Hedges *et al.*, 1999):

$$LNRR = \log_e\left(\frac{\overline{X}_t}{\overline{X}_c}\right) = \log_e(\overline{X}_t) - \log_e(\overline{X}_c) \qquad \text{Eqn 1}$$

where $\overline{X}_t$ and $\overline{X}_c$ are the mean values in the K treatment and control groups, respectively.

The variance (v) of each log$_e$RR was calculated as:

$$v = \frac{S_t^2}{n_t \overline{X}_t^2} + \frac{S_c^2}{n_c \overline{X}_c^2} \qquad \text{Eqn 2}$$

where n_t and n_c are the sample sizes for the K treatment and control groups, respectively; S_t and S_c are the standard deviations for the K treatment and control groups, respectively. If the studies reported standard error (SE) rather than standard deviation (SD), SE was transformed to SD based on the following equation:

$$SD = SE\sqrt{n} \qquad \text{Eqn 3}$$

where n is the sample size. If the studies did not include SD or SE, we estimated the missing SD by multiplying the mean by the average coefficient of variation across all studies with nonmissing data (Follmann *et al.*, 1992). There was no significant difference in the results with or without those experiments that lacked variance (Table 1).

The weighting factor (w) of each experiment was calculated as:

$$w = \frac{1}{v} \qquad \text{Eqn 4}$$

The weighted mean response ratios for all experiments were calculated as:

$$\log_e(RR_+) = \frac{\sum_i w_i \times \log_e RR_i}{\sum_i w_i} \qquad \text{Eqn 5}$$

where $\log_e RR_i$ and w_i are log$_e$ RR and w of the ith experiments, respectively.

The standard error of $\log_e(RR_+)$ was calculated as:

$$s(\log_e(RR_+)) = \sqrt{\frac{1}{\sum_i w_i}} \qquad \text{Eqn 6}$$

The 95% confidence interval (CI) for $\log_e(RR_+)$ was calculated as:

$$95\%CI = \log_e(RR_+) \pm 1.96\, s(\log_e(RR_+)) \qquad \text{Eqn 7}$$

We used a random-effect model to calculate the weighted mean response ratios and the 95% confidence interval (95% CI) with the 'meta' package in R v.4.0.3 (https://www.r-project.org/). If the 95% CI values did not overlap with zero, the effects were considered significant. To better demonstrate the effects of K addition, we transformed $\log_e(RR_+)$ and the 95% CI to percentage change as follows:

$$\text{Effect size (\%)} = \left(e^{\log_e(RR_+)} - 1\right) \times 100\% \qquad \text{Eqn 8}$$

Funnel plots (Fig. S2) and the fail-safe number (N; Rosenberg, 2005) were used to assess possible publication bias. If the data
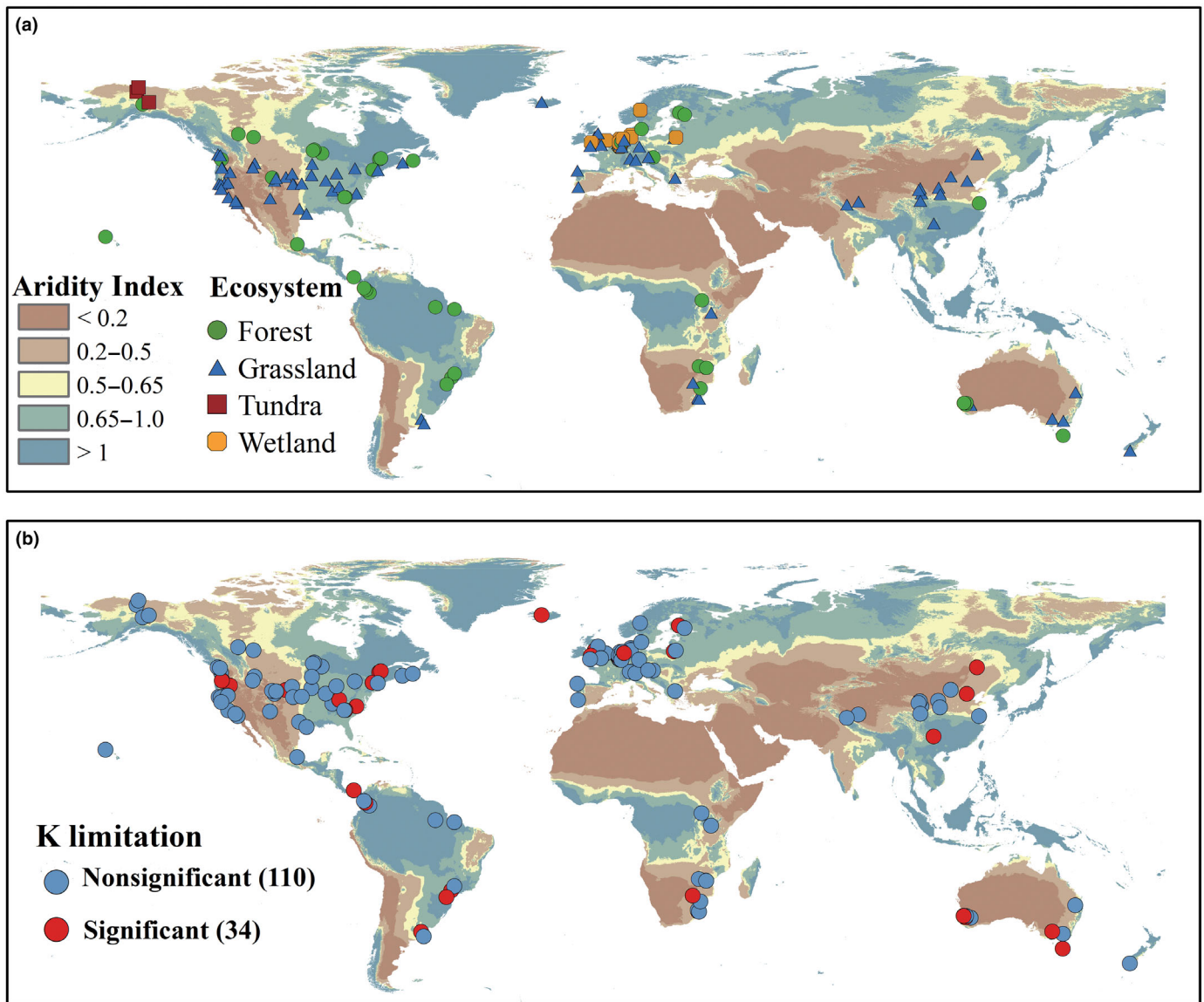
Fig. 1 Geographical distribution of 144 experimental sites used in the meta-analysis. (a) The terrestrial ecosystems were classified into four groups: forest, grassland, tundra, and wetland. (b) Assessment of effect of K addition: experiment with LNRR (log-transformed response ratio of aboveground production to K additions) > 0.22, K limitation is considered to be significant (for details see the Materials and Methods section). Aridity Index is calculated as the ratio of mean annual precipitation to potential evapotranspiration (Antonio & Robert, 2019), and data were acquired from: 10.6084/m9.figshare.7504448.v4.

Table 1 Effects of K addition on aboveground production (AP) and belowground production (BP) between inclusion and exclusion of published experiments that lacked variances.

Variable	Inclusion				Exclusion			
	n	Mean (%)	Lower CI (%)	Upper CI (%)	n	Mean (%)	Lower CI (%)	Upper CI (%)
AP	144	12.31	7.39	17.46	110	11.82	6.06	17.90
BP	42	9.63	−4.48	25.82	40	9.04	−5.82	26.26

CI, confidence interval; Mean, mean effect size of K addition; n, sample size.

points symmetrically distributed and $n > 5\ k + 10$ (where k is the number of experiments), the results could be considered reliable estimate of the real effect. In addition, we also explored the relationship between the LnRR of aboveground production to K addition and publication year, no significant correlation was found ($P = 0.8301$; Fig. S3). Between-group heterogeneity (Q_b) tests were conducted to assess whether different groups exhibited varied responses to K fertilization (Table S3).

Potassium limitation threshold

One objective of our meta-analysis was to determine the proportion of K-limited terrestrial ecosystems. Therefore, we defined a threshold value above which LNRR (log-transformed response ratio) was related to a real K limitation. To do this, we used a method described previously (Augusto *et al.*, 2017; Hou *et al.*, 2020) and collected the statistical response of aboveground production to K addition. We then investigated the distribution of LNRR values among significant and nonsignificant K addition groups. Finally, we identified the threshold value, which optimized the distinction between the two groups. In total, 68% of treatments that reported a significant K limitation had a LNRR value > 0.22. By contrast, 93% of treatments that reported a nonsignificant K effect had a LNRR value < 0.22. The maximum percentage of correct classification was obtained for an LNRR value of 0.22 in the two combined groups (86.5% correct classification; Fig. 2). Therefore, 0.22 was used to distinguish significant from nonsignificant K limitation in our database, which is close to thresholds used in previous study (LNRR of 0.23; Hou *et al.*, 2020).

MetaForest analysis

In this study, we used a MetaForest analysis to identify the relative importance of climate, soil properties, ecosystem types, and the fertilization regimes in influencing the response of aboveground biomass to K addition. MetaForest is a random forest-based algorithm. It considers unequal weights among different experiments, various predictors, and their interactions, as well as the nonlinear relationship between moderators and the predicted variables (Van Lissa *et al.*, 2020). We used 12 potential moderators (Table S4), which were AI, MAT, elevation, soil organic carbon (SOC), soil pH, soil exchangeable K, soil weathering stage, ecosystem type, the length of experimental duration, K application rate, and K fertilizer type, soil sand content. The proportion of predicted variables extracted from the original articles was listed in Table S4. The unreported soil exchangeable K values (0–15-cm layer) were obtained from Global Soil Dataset for use in Earth System (GSDE; Shangguan *et al.*, 2014). The experiments with missing data were excluded.

We conducted a preselection process of variables. All the predictors were included in MetaForest with 10 000 iterations and were replicated 100 times using a recursive algorithm from METAFOR (Viechtbauer, 2010). Only moderators that improved predictive performance during the preselection process were chosen to optimize the MetaForest model. Hereafter, the model parameters were optimized using the train function from the caret package (Kuhn, 2008). A tenfold cross-validated R^2 was calculated, the model with the smallest root mean square error (RMSE) was chosen.

Assessment validity

To assess the reliability of N : K and K : P thresholds in detecting K limitation, we examined whether the type of K limitation
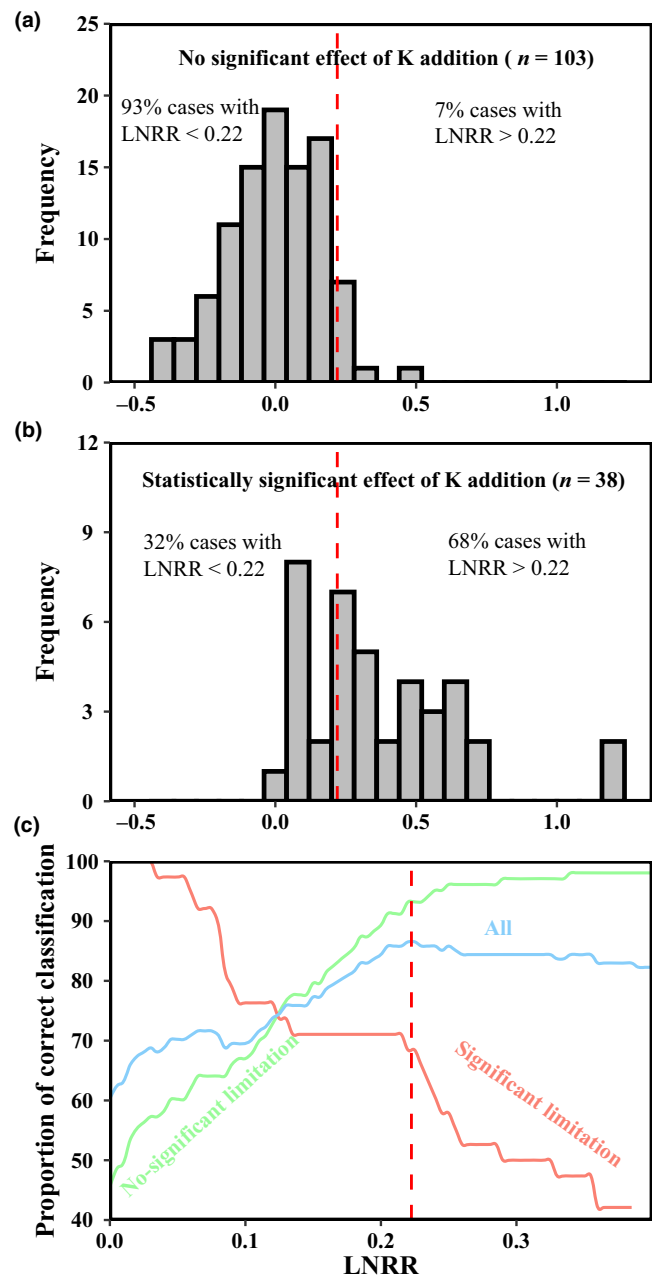

Fig. 2 Distribution of the log-transformed response ratio (LNRR) of aboveground production to K additions (a–c). Dashed line in all three subplots indicates the threshold value of LNRR (0.22).

predicted by stoichiometric threshold (N : K > 2.1 and K : P < 3.4) corresponded with that identified through the aboveground production response to K addition (Yan *et al.*, 2017). First, we selected 48 experiments, which simultaneously included aboveground production responses to K addition, and plant N : K and K : P ratios from unfertilized control plots. Subsequently, a ternary diagram was constructed in which the stoichiometric N : P : K ratios, and the type of K limitation determined by aboveground production response to K addition were plotted (Fig. S4).

Results and Discussion

Global distribution of K limitations

Our meta-analysis, using synthesized field K addition experiments, demonstrated that K limitation can occur in most terrestrial ecosystems and regions. K addition significantly increased aboveground production in all terrestrial ecosystems by 12.3% (95% CI: 7.4–17.5%) except in tundra, where only three experiments were available (Fig. 3; Tables 1, S5). The effects of K addition on aboveground production among ecosystem types did not differ significantly. These results emphasize the significance of K for terrestrial ecosystem production and are consistent with a previous study showing that single- or multiple-nutrient K limitation occurred at 21 of 42 grassland sites (Fay *et al.*, 2015). Furthermore, aboveground production increased with K addition in tropical, subtropical, and temperate regions, which cover a large part of the earth's land area (Fig. 3). Globally, 34 of 144 experiments (23.6% of the experiments) showed that K significantly limited aboveground production (Fig. 1b; Table S5). Taken together, these results suggest a global distributed K limitation in terrestrial ecosystems. As expected, fine root biomass decreased with K fertilization, likely due to alleviation of nutrient limitation and less plant investments to root for nutrient acquisition (Wright *et al.*, 2011; Yavitt *et al.*, 2011; Santiago *et al.*, 2012; Wurzburger & Wright, 2015). However, K addition did not significantly change belowground production in this meta-analysis (Table 1).

Generally, terrestrial ecosystem productivity is thought to primarily be limited by N or P (Elser *et al.*, 2007; Vitousek *et al.*, 2010), and that K limitation might only emerge where N and P limitations are ameliorated. However, our findings showed that some degree of K limitation in aboveground production existed in most terrestrial ecosystems, despite the average K limitation strength (12.3%) was smaller than N (29%) and P limitation (34%; LeBauer & Treseder, 2008; Hou *et al.*, 2020). The global occurrence of terrestrial ecosystem K limitation may be explained by the K demands of core biochemical machinery (Elser *et al.*, 2007; Sardans & Peñuelas, 2015), large differences in soil properties, climate, and plant characteristics with regions, and several other mechanisms (Vitousek *et al.*, 2010), which can cause K deficiency (similar to other rock-derived nutrients, such as P) such as: K depletion, low-K parent materials, transactional limitation (slow release of K from mineral forms relative to supply of other resources), and anthropogenic changes (for example elevated atmospheric CO_2 and N deposition increased plant biomass production and subsequently increased plant K demand (Luo *et al.*, 2004)). Thousands of studies have emphasized the fundamental functional role of K, including xylem–phloem solute transport, cellular growth, wood formation, and stress responses, all of which may cause plant demand for K to outstrip supply (Sardans & Peñuelas, 2015). Whether K limits ecosystem productivity or not depends on K demand and soil K supply. Spatial climate heterogeneity, soil properties, and mineralogical composition have all resulted in high soil K variations in terrestrial ecosystems (T. Li *et al.*, 2021). Substantial variation in soil K concentrations and relatively similar proportion of plant K
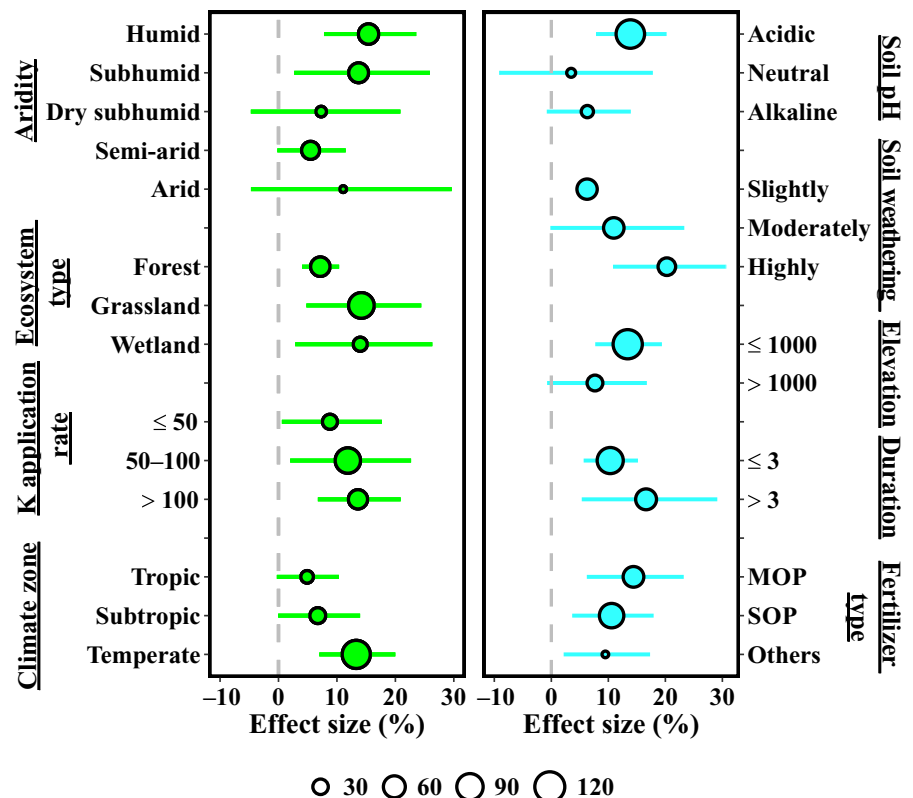
Fig. 3 Effects of K addition on aboveground production classified by the degrees of aridity, ecosystem type, K application rate (kg ha^{-1} yr^{-1}), climate zones, soil pH values, soil weathering stage, elevation (m), the length of experimental duration (year), and fertilizer type. Values represent effect sizes with 95% confidence intervals (CI). The circle size indicates the sample size (detailed information of experimental sites are shown in Supporting Information Table S5). The dashed lines indicate no-fertilization effect. SOP refers Sulfate of Potash (K_2SO_4) and MOP refers Muriate of Potash (KCl).

requirements (Knecht & Göransson, 2004) can lead to imbalanced supply and demand, thus resulting in K limitation at many sites. K limitation in humid tropic regions may be attributed to K depletion, which is caused by the high leaching and prolonged weathering of this cation from soil. Furthermore, other anthropogenic activity, such as deforestation, remove considerable amounts of K stored in biomass, possibly resulting in K limitation in forest systems (Tripler *et al.*, 2006).

We also discovered that previous N : K and K : P thresholds potentially introduce a large uncertainty when applied to detect K limitation in other ecosystems, based on the following two findings. First, among the 48 K addition experiments, only 14.5% of sites exhibited a N : K ratio > 2.1 and K : P ratio < 3.4, which was much less than the percentage of K limitation inferred from aboveground vegetation production (*c.* 25.0%; Fig. S4). Second, plants with a N : K ratio > 2.1 and K : P ratio < 3.4 could be significantly K limited ($n = 3$) or not significantly K limited ($n = 4$). Similarily, plants with an N : K ratio < 2.1 or K : P ratio > 3.4 also showed a significant K limitation ($n = 9$) or no K limitation ($n = 32$; Fig. S4). Consequently, K limitation types determined by the previous N : K and K : P threshold are inconsistent with those determined by aboveground production response to K addition. Thus, the N : K and K : P ratio thresholds cannot accurately detect K limitation, and the use of this threshold may cause large errors and is not advisable. This inconsistency could be attributed to different biological mechanisms, such as luxury consumption of soil nutrients (Chapin *et al.*, 1990; Van Wijk *et al.*, 2003), species-specific N : K and K : P thresholds, and plant adaption to soil nutrient (Coley *et al.*, 1985).

Factors regulating the response of aboveground production to K addition

The Metaforest analysis showed Aridity Index (AI) to be the most important factor influencing the effect of K addition on aboveground production, and LNRR (natural log-transformed response ratio) was significantly and positively correlated with AI ($P = 0.025$; Figs 4a,b, S5). Aboveground production increased significantly with K addition in humid and subhumid regions by 15.4% (95% CI: 7.8–23.6%), and 13.7% (95% CI: 2.7–25.9%), respectively, but was not significant in dry humid, semiarid, and arid regions (Fig. 3). Moreover, LNRR exhibited a positive correlation with MAP, although this correlation was not statistically significant (Fig. S6a). These findings may imply that wetter regions were more likely to be K limited, which was consistent with previous work showing foliar K concentrations to be negatively correlated with MAP (Han *et al.*, 2011). This phenomenon can be elucidated through considerations of plant K demand, soil K supply, and water use efficiency (WUE). In humid regions, substantial soil K leaching and high vegetation productivity contributed to lower soil K supply and greater plant K demand. Meanwhile, K-induced increases in plant WUE were larger in humid regions than in arid regions (Yang *et al.*, 2023). Consequently, K fertilization would have a more pronounced stimulatory effect on plant growth in humid areas. Soil organic

carbon was the second most important factor influencing K addition effect on aboveground production, and LNRR was positively correlated with SOC ($P = 0.064$; Figs 4a,c, S5). This finding aligns with the literature reporting a linear positive correlation between the effect size of K fertilization on crop WUE and SOC at field-population and whole-plant scales (Yang *et al.*, 2023). Soil organic carbon could help stabilize soil structure and increase soil cation exchange capacity (CEC), both of which are crucial for nutrient retention. Under identical K fertilization conditions, soils with higher SOC could store a larger amount of plant-available K (Kai-lou *et al.*, 2022). Consequently, sites rich in SOC exhibit a greater magnitude of aboveground production response to K fertilization (Johnston *et al.*, 2009; Bai *et al.*, 2015).

The effect size of K addition on aboveground production varied with the soil weathering stage. Highly weathered soils (20.3%, 95% CI: 10.8–30.5%) responded more strongly to K addition than moderately (10.7%, 95% CI: −0.1 to 22.8%) and slightly weathered soils (6.3%, 95% CI: 4.6–8.0%; Figs 3, 4a, S5). This finding may be the result of K^+ depletion after long-term primary mineral weathering (Aerts & Chapin, 1999). It is not surprising that soil exchangeable K was a major driver of K addition responses, and LNRR was negatively correlated with soil exchangeable K ($P = 0.024$; Figs 4a,e, S5), because it determines soil K supply. The effect of K addition on aboveground production was larger at application rates of > 50 kg ha^{-1} yr^{-1} compared with ≤ 5 kg ha^{-1} yr^{-1} (Fig. 3). More K input increased soil K availability and relieved K deficiency. Initial soil pH values also significantly impacted the response of aboveground production to K enrichment, and LNRR was negatively correlated with soil pH ($P = 0.044$; Figs 4a,d, S5). Acidic soils had a larger effect with K addition on aboveground production (13.8%, 95% CI: 7.8–20.1%) compared with neutral (3.5%, 95% CI: −9.1 to 17.8%) and alkaline soils (6.3%, 95% CI: −0.8 to 13.9%; Fig. 3). The negative soil pH relationship and the strong acidic soil response may be ascribed to reduced soil K availability (Bowman *et al.*, 2008). During acidification, the soil is buffered by a multitude of soil chemical reactions, thus leading to the replacement of exchangeable base cations (Ca^{2+}, Mg^{2+}, K^+, and Na^+) by H^+ and Al^{3+} at the cation exchange sites, which limits soil cation adsorption capacity (Rahman *et al.*, 2018). Therefore, essential nutrient cations for plants (such as Ca^{2+}, Mg^{2+}, and K^+) easily leach out from soils. Atmospheric N deposition has reportedly caused a significant decrease in global soil pH by 0.26 (Tian & Niu, 2015) and has promoted top soil K loss (Lucas *et al.*, 2011). Furthermore, N deposition increased aboveground production, thus increasing K demand. We therefore expect that the occurrence of K limitation will likely increase in regions where N deposition is high (Li *et al.*, 2016; Wassen *et al.*, 2021).

The K fertilizer formulation, experimental duration, soil sand content, and elevation also regulated K effects, although the variable importance is relatively low. For example, larger effects were found when experimental duration was longer than 3 yr relative to shorter than 3 yr (Fig. 3), which is in line with the findings that the effects of nutrients on living biomass increase over time (Seabloom *et al.*, 2021). Combined, these findings indicate that
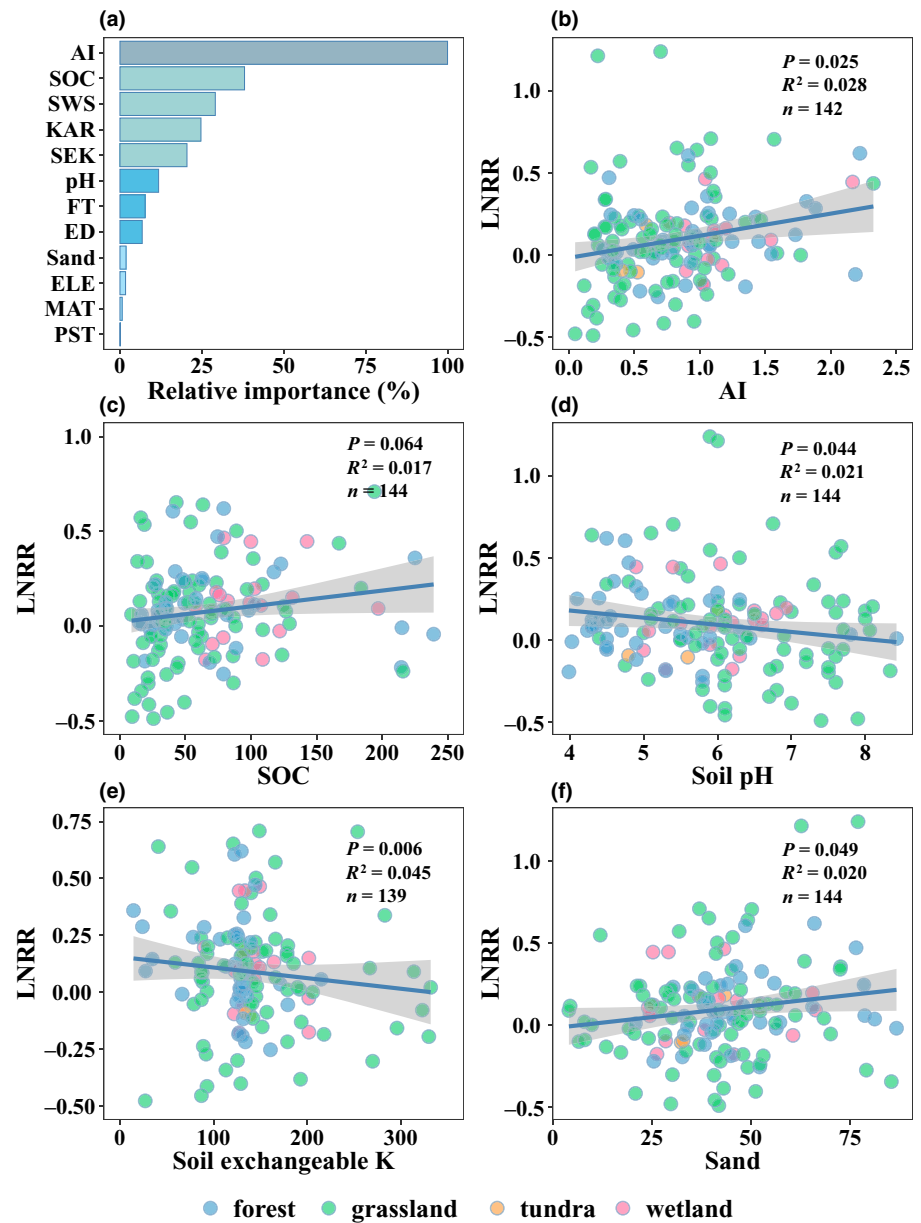
Fig. 4 Factors influencing the response of aboveground production to K addition. (a), Variable importance of predictors of the effects of K addition on aboveground production (AI, aridity index; ED, experimental duration; ELE, elevation; FT, fertilizer type; KAR, K application rate; MAT, mean annual temperature; pH, soil pH value; PST, ecosystem type; Sand, soil sand content; SEK, soil exchangeable K; SOC, soil organic carbon; SWS, soil weathering stage). Relationships of LNRR with aridity index (b), with soil organic carbon (g kg^{-1}) (c), with soil pH values (d), with soil exchangeable K (mg kg^{-1}) (e), with soil sand content (%) (f). The axes scale sometimes was reshaped to make graphs readable, which would make a few outliers invisible, but they were still considered for the statistics. LNRR, natural log-transformed response ratio of aboveground production to K additions.

climate, soil properties, fertilizer regimes, and ecosystem types simultaneously determine the effects of K addition. Complex interconnections and interactions among these factors result in great variation in K effects.

Limitations and implications

Although we used a meta-analysis to quantitatively estimate the effects of K addition on aboveground production, our study still had limitations. First, the experimental site distribution in our analysis did not occur evenly over all the continents (48 sites were in Europe and 60 sites in North America, while there were only 14 sites in Asia, 11 sites in South America, and 10 sites in Africa) and ecosystems (49 sites were in forests, 19 sites in wetland, 87 sites in grassland, and only three sites in tundra; Fig. 1a, Tables S1, S5). Second, analysis uncertainty may also stem from

the paucity of available data and may likewise result from errors in soil pH and SOC values from SOILGRIDS2.0 (Batjes *et al.*, 2020; Poggio *et al.*, 2021), and soil exchangeable K values from GSDE (Shangguan *et al.*, 2014). This likely introduced bias into relative importance estimate in the Metaforest analysis. Additionally, our analysis did not account for the impact of plant adaptation to soil nutrient levels. Previous studies have pointed out that species adapted to low nutrient conditions typically exhibit a limited growth response to nutrient fertilization (Coley *et al.*, 1985; Wright *et al.*, 2018). This could contribute to high variation of K fertilization effect in Fig. 3.

An analysis using the 134 fertilization experiments revealed that N addition significantly reduced foliar K concentration (Mao *et al.*, 2020), suggesting that N deposition may cause plant K deficiency. However, other researchers (Lucas *et al.*, 2011) reported that foliar K concentration in boreal and temperate

forests did not change significantly with N addition for a long period of time (exceeding 5 yr). Furthermore, N deposition increases K uptake through increased enzyme production and mycorrhizal activity in heathland ecosystems (Rowe *et al.*, 2008). Hence, it remains unclear whether continuing N deposition would lead to lower tissue K concentrations and subsequently cause K become limiting to plant growth. Studies on atmospheric K deposition are highly lacking compared with atmospheric N and P deposition (Van Langenhove *et al.*, 2020), which may limit our understanding of the potential effects of atmospheric K deposition in terrestrial ecosystems.

To our knowledge, this is the first global meta-analysis study to evaluate the responses of ecosystem production to K addition in nonagricultural ecosystems, although agriculture has already recognized the central importance of K (Zörb *et al.*, 2014). Our meta-analysis showed that K limitation exists in most terrestrial ecosystems, and K can become a more prominent limiting nutrient. We also found the previous N : K and K : P thresholds to be poor indicators of K limitation, suggesting that these thresholds in detecting K limitation should be used with caution in future studies. Finally, this research emphasizes the importance of K in terrestrial ecosystems, and help to change the current belief that net primary productivity of natural ecosystems is primarily limited by N or P by showing that there is a common K limitation. It is imperative to incorporate K cycle into ecosystem process models.

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Competing interests

None declared.

Author contributions

BC, PC and SP designed the research. JF performed the analysis. BC and JF led the writing and editing of the manuscript. TAB, FW, SN, ZZ and YL contributed to the interpretation of the results, and all authors contributed to data and to the text.

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Data availability

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.23959320.v3.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 PRISMA flow diagram showing the procedure used for the selection of studies for this synthesis.

Fig. S2 Funnel plots for the effect of K addition on aboveground production.

Fig. S3 Relationship of the effect of K addition on aboveground production with publication years.

Fig. S4 Ternary diagrams showing N, P, and K stoichiometric relationships in red (significant K limitation sites based on aboveground production analysis) and gray (nonsignificant K limitation sites based on aboveground production analysis).

Fig. S5 Partial dependence graphs of K addition effect on aboveground production from the global 130 experiments.

Fig. S6 Relationships of K addition effects on aboveground production with different factors.

Note S1 List of 89 published papers from which response of aboveground production to K fertilization were extracted for this meta-analysis.

Note S2 List of 15 published papers from which response of belowground production to K fertilization were extracted for this meta-analysis.

Table S1 Summary of site characteristics and fertilization regimes in this study.

Table S2 K effect size grouped by the measure of aboveground production (CI indicates confidence interval).

Table S3 Effects of K fertilization between-group heterogeneity (Q_b) in relation to the response ratios of aboveground production.

Table S4 Predictors used in Metaforest analysis for examining the effects of K fertilization on aboveground production.

Table S5 Significant K limitation (LNRR > 0.22, LNRR: log-transformed response ratio of aboveground production to K fertilization) in all groups of experiments.

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