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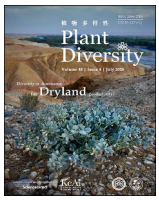

Research paper

Scaling and stoichiometry of seed nitrogen and phosphorus across Chinese grasslands

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ABSTRACT

Nitrogen (N) and phosphorus (P) play crucial roles in early seedling establishment, influencing germination, survival, and overall performance. However, large-scale multispecies seed element survey data are extremely scarce, and studies on the N, P concentrations and N:P ratios as well as scaling relationships of N and P in seeds remain limited. To examine the N versus P scaling relationship and N:P stoichiometry in seeds, we conducted a large-scale survey and collected 1652 seed samples from 446 species in 51 families spanning 236 sites across the Chinese grasslands, including typical steppe, desert steppe, and alpine meadow. We found that the arithmetic means of seed N and P concentrations and N:P ratios were 28.95 ± 0.32 mg/g, 4.26 ± 0.05 mg/g, and 7.24 ± 0.07, respectively. Seed N, P concentrations and N:P ratios varied across different plant groups and grassland types. For example, N-fixers had the highest N, P concentrations and N:P ratios across plant groups. Among the grassland types, alpine meadow displayed the highest N and P concentrations but the lowest N:P ratios. Using a recent bootstrapping approach to resolve data imbalance, the overall seed N vs. P scaling exponent was 0.75, supporting the growth rate hypothesis. We also detected strong phylogenetic signals in these traits. After accounting for phylogeny, the scaling exponent in independently evolving lineages was 0.66. These findings highlight how both environment and evolutionary history regulate seed nutrient allocation, advancing our understanding of plant reproductive strategies and providing key parameters for modelling early plant growth.

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1. Introduction

Nitrogen (N) and phosphorus (P) are critical components of proteins, nucleic acids, and energy-transfer molecules (e.g., ATP) and are fundamental elements for plant growth, reproduction, and ecosystem productivity (Elser et al., 2000; Sterner and Elser, 2002). Specifically, N is essential for amino acid synthesis and chlorophyll production (Peoples and Craswell, 1992; Marschner, 2012), whereas P is an important component of nucleic acids and energy-transfer molecules, and thus supports protein synthesis (Ågren, 2004; Ghimire et al., 2017). Consequently, the N:P ratio in plant tissues emerges from biochemical optimization processes, in which nitrogen allocation to proteins is coordinated with phosphorus demands for rRNA synthesis—the dominant cellular P sink supporting protein production (Sterner and Elser 2002; Ågren, 2004). The concentrations of N and P in plant organs do not vary independently but change in a coordinated manner, which reflects plant investment strategies to optimize growth and nutrient storage (Aerts and Chapin, 2000). Consequently, the relationship between N and P in plant organs is pivotal to understanding plant survival strategies and ecosystem dynamics.

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Several studies have examined N and P concentrations and N:P ratios in different plant organs. These traits link elemental composition and allocation within plants to organismal metabolism and energy flow at the ecosystem level (Elser et al., 2010). In particular, the coordinated variation of N and P concentrations in plant organs can be represented as a scaling relationship expressed as the power function $N = \beta P^{\alpha}$, where β is a normalization constant and α is a scaling exponent (Niklas et al., 2005; Kerkhoff et al., 2006; Reich et al., 2010). The α is a critical parameter used to predict plant and ecosystem functioning (Elser et al., 2010). Values of $\alpha < 1$ indicate that P accumulates faster than N. This is because fast-growing organisms prioritize P acquisition to build P-rich ribosomal RNA and meet the demands of rapid protein synthesis, as predicted by the growth rate hypothesis (Sterner and Elser, 2002). Conversely, $\alpha > 1$ indicates that N accumulates faster than P (Elser et al., 2003). This simple equation reflects the plants' physiologically coordinated investment in N and P, resulting from their evolutionary adaptation to environmental changes such as soil nutrient availability.

Most previous studies have focused on N and P concentrations, N:P ratios, and N–P scaling relationships at regional (Han et al., 2005; Sardans et al., 2015; Tang et al., 2018) and global scales (Reich and Oleksyn, 2004). Leaf N:P is well established as an indicator of vegetation composition and nutrient limitation across ecosystems (Koerselman and Meuleman, 1996). However, the patterns and drivers of N and P concentrations and N:P ratios in seeds are not well understood, despite their central role in reproduction, early seedling growth, and fitness. Most existing work has focused on vegetative organs, and it is unclear whether seeds follow similar scaling relationships, or if they reflect distinct ecological and evolutionary pressures.

Several studies have revealed divergent N vs. P scaling exponents in leaves (Niklas, 2006; Reich et al., 2010; Tian et al., 2018), stems (Wang et al., 2022a,b; Gong et al., 2024a), and roots (Yuan et al., 2011; Wang et al., 2019, 2021). For example, Niklas (2006) observed a leaf N vs. P scaling exponent of 0.73, whereas Reich et al. (2010) found a scaling exponent of approximately 2/3 across plant functional groups and biomes. These differences in scaling exponents may be explained by evolutionary history and biome variation (Reich et al., 2010). For fine roots, Wang et al. (2019) observed a scaling exponent of 0.82. However, statistical variation in scaling exponents occurs among functional groups and locations (Niklas and Cobb, 2005; Tian et al., 2018; Wang et al., 2021; Zhao et al., 2021), likely reflecting evolutionary and environmental influences. Scaling exponents for leaves and fine roots increase from boreal to tropical regions (Tian et al., 2018; Wang et al., 2019). Strong phylogenetic signals in N and P concentrations have also been observed in leaves (Stock and Verboom, 2012; Sardans et al., 2015), stems (Broadley et al., 2004; Gong et al., 2024b) and roots (Valverde-Barrantes et al., 2017; Wang et al., 2022a,b), potentially influencing the N vs. P scaling exponent (Kerkhoff et al., 2006). While extensive research has addressed vegetative organs, knowledge about N vs. P scaling in seeds is still very limited despite the importance of seeds for reproduction.

The seed stage is crucial for plant establishment and population regeneration (De Frenne et al., 2011; Lambers and Poorter, 1992; Cochrane et al., 2015; Chen et al., 2020; Huang et al., 2020a, 2020b). During germination and early seedling growth, plants rely on internal N and P reserves in tissues such as the endosperm or cotyledons (Bewley et al., 2013). These reserves are mobilized to support rapid germination, seedling performance, and survival (Muthukumar and Udaiyan, 2000; Naegle et al., 2005; Bewley et al., 2013; Cheng et al., 2015; Jiménez-Alfaro et al., 2016). Seed N and P also affect interactions with nitrogen-limited seed predators and seed dispersal (Soltani et al., 2006; Delatte and Chabrerie, 2008; De Menezes et al., 2010). Notably, the N vs. P scaling exponents in leaves, stems, and roots are typically less than 1, indicating allometric growth. Unlike leaves and roots, which are associated with resource acquisition, seeds are primarily storage organs for nutrients and energy for the next generation, and may have distinct N and P patterns (Wang et al., 2020). It remains unclear whether seeds follow the same allometric scaling observed in other organs, or whether this varies among plant groups and grassland types. A more complete understanding of N and P concentrations and scaling relationship in seeds may improve predictions of plant life-history strategies and ecosystem functioning.

Grasslands are the dominant landscape in China, covering > 40% of the country's land area with abundant seed production (Te et al., 2025), and are important to biodiversity conservation, carbon sequestration and the maintenance of human livelihoods (Kang et al., 2007). Herbaceous species in Chinese grasslands have evolved uniquely rapid growth and fast life histories (Adler et al., 2014; Yao et al., 2025), small seed size (Turnbull et al., 2012) and high nutrient content (Körner, 1989), in response to environmental stresses in different grassland types. Chinese grasslands thus provide an ideal biome to investigate the scaling relationship of N and P in herbaceous plants.

Here, we conducted a large-scale field survey across grasslands in China, covering three major grassland types (typical steppe, desert steppe and alpine meadow) over a transect of more than 3000 km. We collected mature seeds of herbaceous species to explore the N vs. P scaling relationship. We address three questions: (1) Are there substantial variations in seed N and P concentrations and N:P ratios across different plant groups and grassland types?; (2) Do the seed N vs. P scaling exponents converge across different plant groups and among different grassland types, respectively?; (3) Is there a phylogenetic signal in seed N and P concentrations and N:P ratios, and if so, does phylogenetic history influence the N vs. P scaling exponent?

2. Materials and methods

2.1. Study area

We conducted a large-scale field survey of the Chinese grasslands from 2022 to 2024. The study area encompassed the alpine meadows on the Qinghai-Xizang Plateau and Xinjiang mountain areas, the desert steppes, and the typical steppes on the Inner Mongolia Plateau (Fig. 1a). The mean annual temperature (MAT) and mean annual precipitation (MAP) across the sampling sites ranged from −4.8 to 13.1 °C and from 158 to 888 mm, respectively (Fig. 1b). The grassland types reflect distinct environmental conditions. Alpine meadows are characterized by cold temperatures (MAT: −4.78 to 7.5 °C; MAP: 160–888 mm) and support vegetation dominated by *Kobresia* species. Desert steppes experience arid conditions (MAT: 2.2–13.1 °C; MAP: 160–306 mm) and are characterized by xeric shrubs. In contrast, typical steppes exist under semi-arid conditions (MAT: −2.8 to 7.9 °C; MAP: 222–440 mm) and are primarily dominated by *Stipa* species. To address potential confounding effects of interannual climate variability, we ensured sufficient spatial representation across diverse vegetation types and climate gradients, which minimized the impact of interannual fluctuations relative to spatial environmental heterogeneity.

2.2. Sample collection and N and P measurements

We selected sites that received no grazing or human disturbance. At each site, we first selected a large typical plot

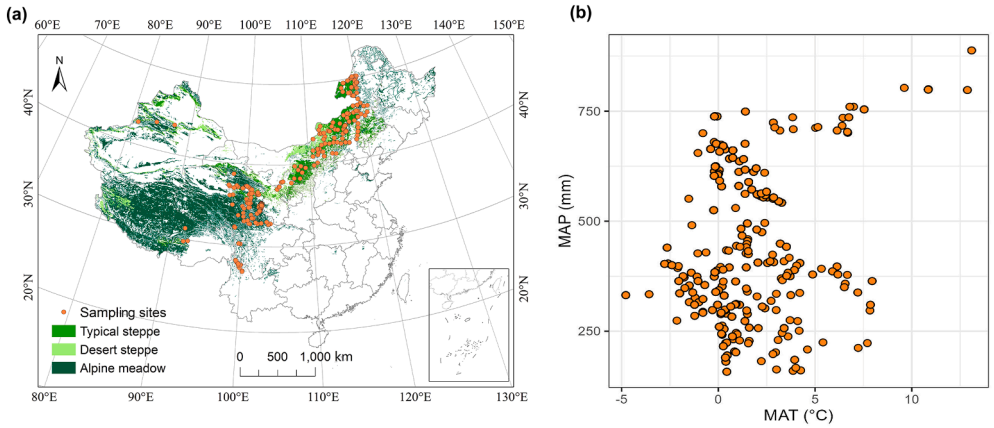

Fig. 1. The distribution of the 236 sampling sites used in this study (a). The spread of mean annual temperature (MAT) and mean annual precipitation (MAP) across these sites (b).

(10 × 10 m), within which three 3 × 3 m subplots were randomly established. From each subplot, we collected mature and fresh seeds from multiple species, including both dominant and companion species, to obtain a representative community sample. The seeds collected were generally dark, brown, or yellow in color and had been dropped from the mother plant. For each species, more than 20 individuals were collected from each plot and pooled into a single sample, and we retrieved the seed maturity month for each collected species from the *Flora of China* (Appendix S1). In total, we collected 1652 samples from 446 species in 51 families spanning 236 sites across the Chinese grasslands (Fig. 1; Appendix S1). After collection, the seeds were stored in envelopes and oven-dried at 60 °C to constant weight and then ground to fine powder. The N and P contents were determined using an EcoChem Element Analysis system (Beijing Aozuo Ecological Instrument Co., Ltd).

2.3. Statistical analysis

The data were grouped into two life-form categories (annual and perennial), two functional groups (forb and graminoid), two N-fixing groups (N-fixing and non-N-fixing), and two phylogenetic groups (monocotyledon and dicotyledon). The data were also divided into three grassland types (typical steppes, desert steppes, and alpine meadows) based on the Chinese Grassland Vegetation Classification System (https://igsnrr.cas.cn/cbkx/kpyd/zybk/cdzy/) and dominant vegetation composition. Differences in N and P concentrations and N:P ratios between plant groups were evaluated using independent-samples t-tests, while comparisons among the three grassland types were performed using one-way ANOVA followed by LSD *post hoc* tests.

To address data imbalance and skew in frequency distributions (Fig. S1), we used the *balancR* package in R (michaletzlab.github.io/balancR/) to implement a bootstrapping method that generates balanced datasets. This approach leverages existing data to estimate the sampling distribution at each point across the abscissa, resolving data imbalance in biological scaling analyses and improving the accuracy of slope and confidence interval (CI) estimates (Simovic and Michaletz, 2025a, 2025b). First, we set a minimum threshold of $n = 5$ original observations per bin for parameter estimation. While Simovic and Michaletz (2025a) recommend at least 10 observations per bin for robust bootstrapped scaling analyses, sample size limitations required a lower threshold, potentially increasing uncertainty in estimates for bins with lower replication. We then divided seed P concentration into equally spaced logarithmic bins of size 0.44 (yielding 4 bins), then used bootstrapping within each bin (sampling with replacement) so that all bins contained the same number of observations as the most populated bin in the original data ($n = 1018$), yielding a balanced dataset ($n = 4072$).

Reduced major axis (RMA) regression in the lmodel2 function in '*lmodel2*' package was used to determine the numerical values of N vs. P scaling exponents for the plant groups and grassland types, using $\log_{10}$-transformed values of N and P concentrations (Warton et al., 2006; Legendre, 2018). The heterogeneity of the numerical values among the plant groups and grassland types was assessed using likelihood ratio tests.

To assess the effect of phylogenetic relatedness among species on the N vs. P scaling exponent in seeds, we first detected phylogenetic signals in seed N and P concentrations and N:P ratios using Blomberg's K and Pagel's λ indices, calculated with the "phylosignal" function in the R package "*picante*" (version 1.8.2). The statistical significance of Blomberg's K was assessed using a permutation test (with 1000 permutations), while the significance of Pagel's λ was evaluated using a likelihood ratio test. $K > 1$ or λ close to 1 indicates a strong phylogenetic signal, while $K < 1$ or λ close to zero indicates a weak signal (Pagel, 1999; Blomberg et al., 2003). A significant P value from the respective test indicates a significant phylogenetic signal. A significant P value indicates a significant phylogenetic signal. We then constructed a phylogenetic tree for the 446 species using *V.PHYLOMAKER* package in R (version 0.1.0; Jin and Qian, 2019). N and P concentration and N:P ratio were binned into 0.05, 0.25, 0.50, 0.75, and 0.95 quantile bins to aid visualization. We further calculated phylogenetically independent contrasts (PICs) using the *APE* package in R to disentangle N vs. P scaling relationships while accounting for shared evolutionary history (Felsenstein, 1985). For a tree with N species, N−1 contrast values were generated by weighting trait differences between sister groups at internal nodes by branch lengths, providing phylogenetically corrected residuals for subsequent RMA regression analysis. All statistical analyses were performed using the statistical software R 4.4.1 (R Core Team, 2024).

3. Results

3.1. Seed N and P concentrations and their ratios in different plant groups and grassland types

The overall arithmetic mean values of seed N and P concentrations and N:P ratios were 28.95 ± 0.32 and 4.36 ± 0.05 mg g^{-1}

and 7.24 ± 0.07, respectively. However, N and P concentrations and N:P ratios varied across different plant groups and grassland types (Table 1). For instance, N-fixing species exhibited significantly higher seed N (50.84 ± 1.34 mg g^{-1}) and P (5.36 ± 0.20 mg g^{-1}) concentrations than non-N-fixing species (27.12 ± 0.29 mg g^{-1} and 4.28 ± 0.06 mg g^{-1}, respectively). Similarly, forbs had higher N (34.45 ± 0.38 mg g^{-1}) and P (5.20 ± 0.07 mg g^{-1}) concentrations than graminoids (19.02 ± 0.28 mg g^{-1} and 2.86 ± 0.05 mg g^{-1}, respectively). In contrast, annual species showed a higher P concentration (4.75 ± 0.12 mg g^{-1}) than perennial species (4.27 ± 0.06 mg g^{-1}), whereas no significant difference was observed for N concentration. Dicotyledons also displayed markedly higher seed N and P concentrations (34.67 ± 0.40 mg g^{-1} and 5.27 ± 0.07 mg g^{-1}, respectively) than monocotyledons (20.14 ± 0.32 mg g^{-1} and 2.98 ± 0.05 mg g^{-1}, respectively). With the exception of the N-fixing groups, the N:P ratios did not differ significantly among these plant functional groups. N-fixers had higher N:P ratios (10.49 ± 0.36) than non-fixers (6.97 ± 0.07). Among the different grassland types, alpine meadow had the highest N (32.45 ± 0.41 mg g^{-1}) and P (5.05 ± 0.07 mg g^{-1}) concentrations, but the lowest N:P ratios (7.08 ± 0.09), whereas typical steppe had the lowest N (22.29 ± 0.45 mg g^{-1}) and P (3.14 ± 0.07 mg g^{-1}) concentrations. Desert steppe had the highest N:P ratios (8.11 ± 0.27).

3.2. Seed N versus P scaling exponents across different plant groups and grassland types

Across all bootstrap-balanced data, seed N increased with increasing seed P, and the N vs. P scaling exponent was 0.75 (95% CIs = 0.74–0.76, $R^2 = 0.83$, $P < 0.001$) (Fig. 2a and Table 2). However, scaling exponents varied significantly among plant groups (Fig. 2b-f and Table 2). For example, the scaling exponent for annuals (0.66) was lower than for perennials (0.76). In contrast, the scaling exponent for graminoids (0.67) was greater than for forbs (0.60). Similarly, monocotyledon species (0.69) had a higher scaling exponent than dicotyledons (0.60). Likewise, compared to N-fixer species, non-N-fixer species showed numerically higher N vs. P scaling exponents (0.57 vs. 0.73). In addition, the N vs. P scaling exponents showed significant numerical differences among the grassland types (Fig. 2f and Table 2). The scaling exponents decreased from 0.77 in the typical steppes to 0.70 in the desert steppes and 0.67 in the alpine meadows.

Table 1
The arithmetic mean values of seed N and P concentrations and N:P ratios for different plant groups and grassland types. Data are presented as arithmetic mean ± standard error (SE). Different letters represent significant differences at 0.05 level.

Plant group	*n*	N (mg·g^{-1})	P (mg·g^{-1})	N:P ratios
All	1652	28.95 ± 0.32	4.36 ± 0.05	7.24 ± 0.07
Life form groups				
Annual	323	29.33 ± 0.55 a	4.75 ± 0.12 a	7.08 ± 0.20 a
Perennial	1329	28.86 ± 0.38 a	4.27 ± 0.06 b	7.28 ± 0.07 a
Functional groups				
Forb	1063	34.45 ± 0.38 a	5.20 ± 0.07 a	7.37 ± 0.10 a
Graminoid	589	19.02 ± 0.28 b	2.86 ± 0.05 b	7.00 ± 0.09 a
N-fixation groups				
N-fixing	127	50.84 ± 1.34 a	5.36 ± 0.20 a	10.49 ± 0.36 a
Non-N-fixing	1525	27.12 ± 0.29 b	4.28 ± 0.06 b	6.97 ± 0.07 b
Phylogeny groups				
Dicotyledon	1002	34.67 ± 0.40 a	5.27 ± 0.07 a	7.36 ± 0.10 a
Monocotyledon	650	20.14 ± 0.32 b	2.98 ± 0.05 b	7.05 ± 0.08 a
Grassland types				
Desert steppe	116	24.96 ± 1.04 b	3.28 ± 0.13 b	8.11 ± 0.27 a
Typical steppe	483	22.29 ± 0.45 c	3.14 ± 0.07 b	7.37 ± 0.10 b
Alpine meadow	1053	32.45 ± 0.41 a	5.05 ± 0.07 a	7.08 ± 0.09 b

3.3. Phylogenetic effects on the seed N versus P scaling exponent

There were strong phylogenetic signals in seed N and P concentrations and N:P ratios (Fig. 3). Based on PICs analysis, across all observations, the numerical value of N vs. P scaling exponent was 0.66 (95% CIs = 0.62–0.7, $R^2 = 0.57$, $P < 0.001$) (Fig. 4a and Table 3). In contrasting plant groups, the numerical values of N vs. P scaling exponents varied significantly. For example, the numerical values of N vs. P scaling exponents ranged from 0.51 in annuals to 0.81 in monocots (Fig. 4b, c, e and Table 3). The N vs. P scaling exponents in different plant groups for the PICs regressions were similar to those observed in the analyses of bootstrapping data. However, the N vs. P scaling exponents did not show significant numerical differences among different grassland types (Fig. 4f and Table 3).

4. Discussion

This study presents a comprehensive dataset of seed N and P stoichiometry in herbaceous species across Chinese grasslands to examine N vs. P scaling relationships and N:P ratios. Analyses of bootstrap-balanced data yielded a scaling exponent of 0.75 for the seed N vs. P relationship, as predicted by the growth rate hypothesis. Mean seed N and P concentrations and N:P ratios, as well as scaling exponents, varied among plant groups and grassland types. Strong phylogenetic signals were detected in seed N and P concentrations and N:P ratios, but accounting for phylogenetic relatedness did not substantially alter the scaling exponent as compared with the bootstrap-balanced data. Together, these results provide new insights into nutrient allocation strategies in seeds and advance our understanding of stoichiometry and nutrient cycling in plant reproductive organs.

4.1. Variation in seed N and P concentrations and N:P ratios across plant groups and grassland types

Our data showed that the arithmetic mean value of seed N concentration (28.95 mg g^{-1}) are nearly identical to leaves (29.07 mg g^{-1}; He et al., 2008), but markedly higher than fine roots (11.38 mg g^{-1}; Geng et al., 2014) for herbaceous species in Chinese grasslands. The arithmetic mean value of seed P concentration (4.36 mg g^{-1}) is higher than leaves (1.90 mg g^{-1}; He et al., 2008) and fine roots (0.83 mg g^{-1}; Geng et al., 2014). These results underscore the function of seeds as nutrient storage organs. Although seeds are dormant and exhibit low metabolic activity, they are provisioned with high concentrations of N and P compared to leaves or fine roots. This storage supports the high metabolic demands of rapid germination and ensures the robustness of early seedling establishment under diverse environmental conditions (Bu et al., 2008; Soriano et al., 2011; Bewley et al., 2013).

In contrast, the arithmetic mean N:P ratios in seeds (7.24) is considerably lower than leaves (15.3; He et al., 2008) and fine roots (13.04; Geng et al., 2014) of herbaceous plants in Chinese grasslands. A possible reason is that seedlings are adapted for rapid growth, functioning with lower N:P ratios compared to other plant organs, which have different functions less related to overall plant growth (Turnbull et al., 2012). Similarly, the significantly lower N:P ratio in seeds strongly aligns with the growth rate hypothesis, wherein rapid growth is sustained by high P investment in ribosomal RNA for protein synthesis, thereby lowering the N:P ratio (Sterner and Elser, 2002). This P reserve is pivotal for generating ATP, phospholipids for new membranes, and nucleic acids during germination, facilitating seedling establishment before photosynthetic independence (Bewley et al., 2013). Conversely, leaves invest heavily in N-rich photosynthetic proteins (e.g., Rubisco), and root stoichiometry is shaped by structural and foraging

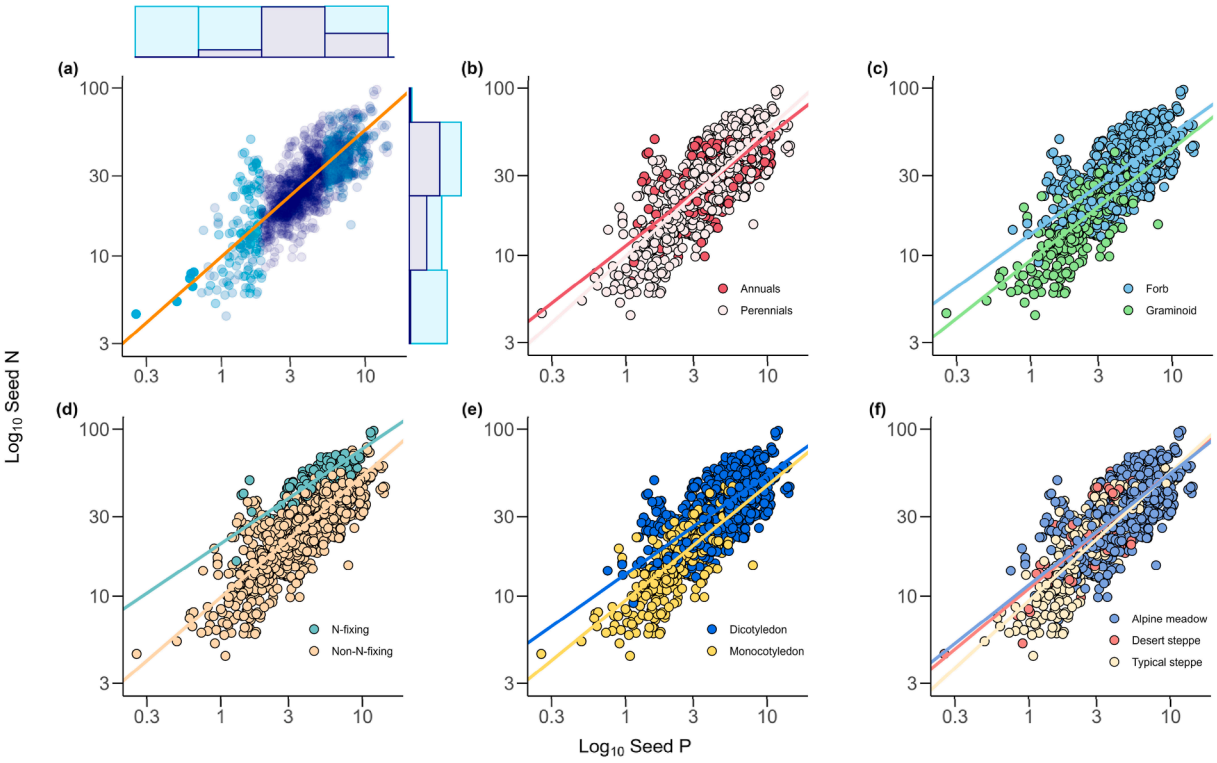

Fig. 2. Scaling relationships of seed nitrogen (N) and seed phosphorus (P) for all data pooled using the bootstrapping method implemented in balancR (a), and for plants in two life form groups (annual, perennial) (b), two functional groups (forb, graminoid) (c), two N-fixation groups (N-fixing, non-N-fixing) (d), two phylogeny groups (dicotyledon, monocotyledon) (e) and three grassland types (typical steppe, desert steppe, and alpine meadow) (f).

Table 2
Summary of reduced major axis (RMA) regression results of log-transformed seed N versus P for herbaceous species in Chinese grasslands across different plant groups and grassland types (all relations were statistically significant with $P < 0.001$). *n*, the number of observations after bootstrapping, and letters represent significant differences in exponents based on a likelihood ratio test.

Plant group	*n*	Intercept	Exponent	95%CI	R^2	*P*
All	4072	1.00	0.75	(0.74–0.76)	0.83	< 0.001
Life form groups						
Annuals	605	1.06	0.66 b	(0.62–0.70)	0.38	< 0.001
Perennials	3467	1.00	0.76 a	(0.75–0.77)	0.85	< 0.001
Functional groups						
Forb	1899	1.12	0.60 b	(0.58–0.62)	0.42	< 0.001
Graminoid	2173	0.97	0.67 a	(0.65–0.68)	0.80	< 0.001
N-fixation groups						
N-fixing	255	1.31	0.57 b	(0.52–0.63)	0.47	< 0.001
Non-N-fixing	3847	1.00	0.73 a	(0.72–0.74)	0.84	< 0.001
Phylogeny groups						
Dicotyledon	1814	1.13	0.60 b	(0.58–0.62)	0.41	< 0.001
Monocotyledon	2258	0.97	0.69 a	(0.68–0.70)	0.82	< 0.001
Grassland types						
Desert steppe	399	1.04	0.70 b	(0.68–0.72)	0.92	< 0.001
Typical steppe	1834	0.97	0.77 a	(0.76–0.79)	0.80	< 0.001
Alpine meadow	1839	1.06	0.67 b	(0.65–0.69)	0.41	< 0.001

functions, explaining their higher N:P ratios (Güsewell, 2004; Liang et al., 2026).

Seed N and P concentrations differed significantly across plant groups and grassland types (Table 1), reflecting differences in morphology, nutrient availability and adaptive strategy. For example, annual species exhibited higher seed N and P concentrations than perennial species, supporting the notion that short-lived, fast-growing species tend to have higher N and P concentrations than those of long-lived, slow-growing species (Aerts, 1996; Güsewell, 2004). Similarly, forb species have higher seed N and P concentrations than graminoid species, possibly because they have relatively larger seeds with high nutrient reserves than the smaller seeds in graminoid species. Larger seeds possess more endosperm or cotyledon storage space to accumulate nitrogen-rich (e.g., proteins) and phosphorus-rich (e.g., nucleic acids, phytic acid) compounds, and forbs also adopt a nutrient-intensive germination strategy that requires more N and P reserves to support early seedling establishment, whereas graminoids with smaller seeds rely more on post-germination soil nutrient uptake (Bonfil, 1998; Soriano et al., 2011). This “quality over quantity” strategy supports seedling vigor in competitive or variable environments.

High seed N and P concentrations were also observed for N-fixing species compared with non-N-fixing species, aligned with their ability to absorb N in root nodules (Peoples and Craswell, 1992) and relatively high phytate in legumes species, comprising 60–90% of total seed P (Lott et al., 2000). Dicotyledons also tended to have markedly higher seed N and P concentrations than monocotyledons, providing evidence that cotyledons accumulate protein reserves (N-rich) and phytate (P-rich) (Lambers and Poorter, 1992).

Among grassland types, alpine meadows had higher seed N and P concentrations than typical and desert steppes. This phenomenon supports the idea that plants growing under low temperatures and short growing seasons may contain higher N and P concentrations to compensate for reduced metabolic rates (Reich and Oleksyn, 2004; Wang et al., 2015, 2023). Notably, seed N:P ratios were not observed to vary across plant groups, with the exception of N-fixation groups and grassland types (Table 1). This observation may reflect a fundamental constraint on seed N:P ratios, despite wider variation in their concentrations.

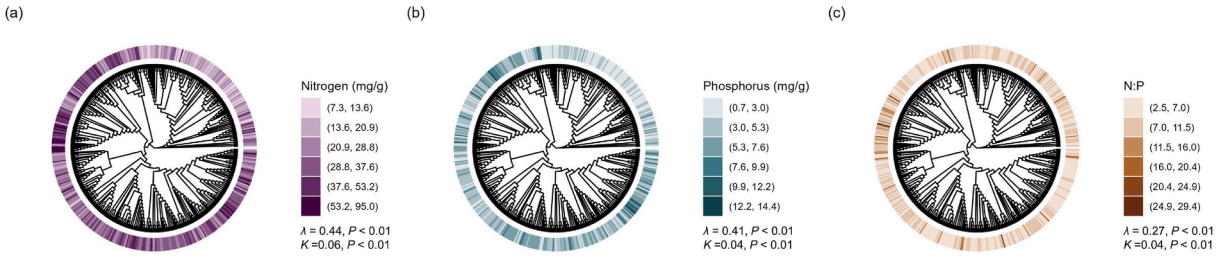

Fig. 3. Phylogenetic distribution of seeds N (a), P (b) and N:P ratios (c) across phylogenetic tree of 446 herbaceous species representing 51 families. Purple represents the N concentration, blue represents the P concentration, and orange represents the N:P ratio. Color brightness represents 0.05, 0.25, 0.5,0.75, and 0.95 quantile bins.

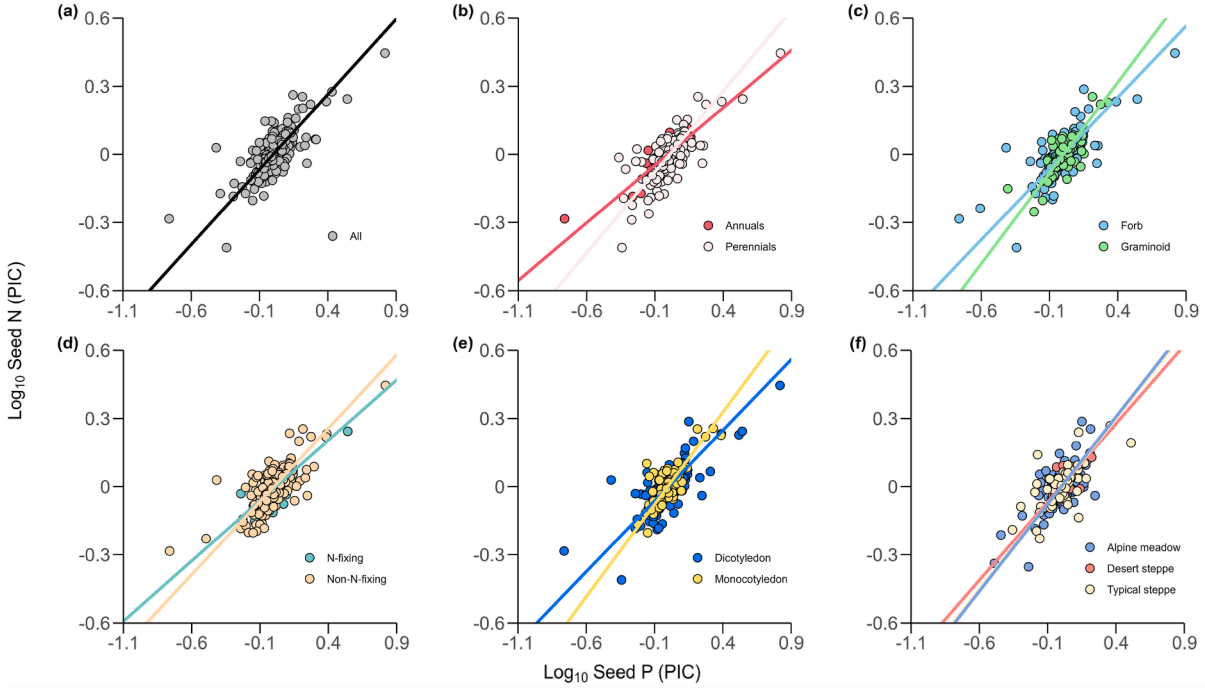

Fig. 4. Phylogenetically independent contrasts of scaling relationships of seed nitrogen (N) and seed phosphorus (P) for all species (a), and for plants in two life form groups (annual, perennial) (b), two functional groups (forb, graminoid) (c), two N-fixation groups (N-fixing, non-N-fixing) (d), two phylogeny groups (dicotyledon, monocotyledon) (e) and grassland types (typical steppe, desert steppe, and alpine meadow) (f).

Table 3
Summary of reduced major axis (RMA) regression results of log-transformed phylogenetic independent contrasts of seed N versus P for herbaceous species across different plant groups and grassland types (all relationships were statistically significant with $P < 0.001$). *n*, the number of observations, and letters represent significant differences in exponents based on a likelihood ratio test.

Plant group	*n*	Intercept	Exponent	95%CI	R^2	*P*
All	445	0.00	0.66	(0.62–0.70)	0.57	< 0.001
Life form groups						
Annual	95	0.00	0.51 b	(0.45–0.57)	0.71	< 0.001
Perennial	350	0.00	0.71 a	(0.67–0.76)	0.57	< 0.001
Functional groups						
Forb	340	0.00	0.63 b	(0.59–0.67)	0.58	< 0.001
Graminoid	104	0.00	0.80 a	(0.70–0.91)	0.56	< 0.001
N-fixation groups						
N-fixing	41	0.01	0.53 b	(0.43–0.65)	0.61	< 0.001
Non-N-fixing	404	0.00	0.64 a	(0.60–0.69)	0.55	< 0.001
Phylogeny groups						
Dicotyledon	325	0.00	0.62 b	(0.58–0.67)	0.58	< 0.001
Monocotyledon	119	0.00	0.81 a	(0.72–0.92)	0.57	< 0.001
Grassland types						
Desert steppe	44	0.00	0.69 a	(0.61–0.92)	0.56	< 0.001
Typical steppe	142	0.00	0.75 a	(0.61–0.78)	0.43	< 0.001
Alpine meadow	329	0.00	0.77 a	(0.71–0.83)	0.46	< 0.001

4.2. Variation in the scaling exponent across plant groups and grassland types

Using bootstrap-balanced data (Simovic and Michaletz, 2025a, 2025b), our results show that the N vs. P scaling exponent is 0.75 for Chinese grassland herbaceous species, which reveals a clear allometric pattern in support of the growth rate hypothesis (Sterner and Elser, 2002). This value is consistent with the value of 0.73 previously reported for alpine meadows seeds (Wang et al., 2020). However, this value is slightly less than the 0.82 reported for herbaceous fine roots (Wang et al., 2019), but higher than the 0.66 reported for herbaceous leaves (Reich et al., 2010; Tian et al., 2018) (Fig. S2).

Clearly, there are many morphological, anatomical and physiological differences among seeds, fine roots, and leaves (Xiong et al., 2025). These differences could result in variations in their N and P concentrations (Yuan et al., 2011). As nutrient reserves, seeds may exhibit a tighter coupling between N and P for seedling establishment, where N is largely in proteins and P in phytate (Muthukumar and Udaiyan, 2000). This results in a steeper N vs. P scaling slope compared to leaves, where N and P are allocated to

more flexible photosynthetic and metabolic pools (Güsewell, 2004). The even higher scaling exponent in fine roots may indicate a preferential investment of P in energy metabolism (e.g., ATP) and membrane synthesis within these resource-acquiring tissues. Meanwhile, the N vs. P scaling exponents across plant organs were significantly less than 1. This pattern may represent a manifestation of evolutionary adaptations in internal resource coordination. It constitutes a fitness-optimizing strategy wherein plants differentially allocate N and P to organs based on functional priorities (e.g., immediate acquisition in leaves and roots vs. future establishment in seeds), while maintaining organism-level stoichiometric regulation.

The observed scaling exponent of 0.75 for seeds shows that P accumulates faster than N in Chinese grasslands, primarily reflecting reliance on P-rich mRNA reserves for protein synthesis during early germination (Slot et al., 2013). Beyond the universal allometric pattern, the numerical values of the scaling exponent varied significantly among contrasting plant groups and grassland types in China (Table 2 and Fig. 2). Compared to perennial species, annual species displayed lower N vs. P scaling exponents (0.76 vs. 0.66), supporting the growth rate hypothesis that annual plants demand more P to sustain higher growth rate (Sterner and Elser, 2002). Graminoid species showed significantly greater N vs. P scaling exponents (0.67) than forb species (0.60), potentially reflecting graminoids enhanced N uptake capacity to increase foliar biomass and productivity, and associated competitive advantages (Wright et al., 2004; Aerts and Berendse, 1989; Aerts, 1996). The N vs. P scaling exponent for non-N-fixing species (0.73) is higher than N-fixing species (0.57), indicating that N-fixing species with higher N:P ratios may have a competitive advantage for P absorption over non-N-fixing species. The lower scaling exponent observed in dicotyledon (0.60) compared to monocotyledons (0.69) may indicate divergent nutrient storage strategies (cotyledonary vs. endospermic reserves), perhaps reflecting selective pressure on plant physiology (He et al., 2006).

Significant variations in scaling exponents were also observed among different grassland types, decreasing from typical steppes (0.77) to alpine meadows (0.67) (Table 2 and Fig. 2). This phenomenon likely reflects differences in plant adaptive strategies in response to environmental conditions, particularly temperatures and soil nutrient availability (He et al., 2008). Chinese steppes are generally considered to be N and P co-limited (He et al., 2008; Bai et al., 2010). Thus, seeds need to maintain relatively balanced N and P investment to respond to resource limitation during the early germination stage. For example, compared with typical steppes, alpine meadows with low temperatures suppress microbial activity and slow N mineralization rates, leading to reduced N availability during germination (Aerts and Chapin, 2000). Moreover, plants growing in alpine meadows with relatively short growing seasons require seeds that maintain higher P content to support fast initial growth and individual survival (Bu et al., 2019; Xiong et al., 2022).

Meanwhile, the variation in intercepts across plant groups and among different grassland types suggests divergent strategies for nutrient allocation, particularly phosphorus. For instance, the intercept was higher in N-fixing species (1.31) and dicotyledons (1.13) than in non-N-fixing species (1.00) and monocotyledons (0.97). A higher intercept may indicate a greater proportional investment of P into reproductive structures like seeds, where it is primarily stored as phytate to support early seedling growth (Kerkhoff et al., 2006). This pattern underscores the substantial phosphorus investment required for seed development.

4.3. Phylogenetic signals in the N versus P scaling exponent

There were strong phylogenetic signals in seed N and P concentrations and N:P ratios (Fig. 3), confirming that seed nutrient relationships are constrained by phylogeny. The observed phylogenetic conservatism shows that closely related species tended to retain similar nutrient profiles due to shared ancestry, rather than converging independently under similar ecological conditions (Lord et al., 1995; Stock and Verboom, 2012). Using PICs analyses, the seed N vs. P scaling exponent for the PICs regression was found to be 0.66, similar to that observed from the bootstrapped data. When the effect of phylogeny was removed, N vs. P scaling exponents still differed significantly in contrasting plant groups (Table 3). This indicates that, despite strong phylogenetic constraints preserving legacy traits in seed N and P concentrations, both adaptive selection and character coevolution exerted measurable influences on N vs. P scaling exponent (Kerkhoff et al., 2006; Bu et al., 2019).

Interestingly, the absence of significant differences in N vs. P scaling exponents among grassland types suggests that broad-scale environmental gradients (e.g., temperature and soil fertility) may exert weaker selective pressures on seed N vs. P scaling exponent than intrinsic phylogenetic or functional group constraints. This aligns with the observation that PICs and bootstrapping data regressions yielded similar N vs. P scaling exponents, reinforcing the primacy of evolutionary history over local adaptation in shaping these allometric patterns. Such agreement is consistent with recent studies showing that bootstrap-balanced analyses yield reliable estimates of scaling exponents even when sampling distributions are highly uneven (Simovic and Michaletz, 2025a, 2025b).

5. Conclusion

This study is the first large-scale field survey of seed N and P concentrations, N vs. P scaling relationships, and N:P ratios in herbaceous species across Chinese grasslands. We document substantial variation in seed N and P concentrations and N:P ratios among plant groups and grassland types. For example, N-fixers species had the highest N and P concentrations and N:P ratios across plant groups. Among the grassland types, alpine meadow displayed the highest N and P concentrations but the lowest N:P ratios.

Although the pooled data followed a 3/4-power scaling relationship observed in leaves, seed N vs. P scaling exponents varied among contrasting plant groups and grassland types. For instance, seed N vs. P scaling exponents were higher in perennials, graminoids, non-N-fixers, and monocotyledons than in their counterparts (annuals, forbs, N-fixers, and dicotyledon, respectively). Furthermore, the scaling exponent decreased along the grassland types, from 0.77 in the typical steppes to 0.67 in the alpine meadows. Phylogeny had a significant effect on seed N and P concentrations and N:P ratios, and the scaling exponent in independently evolving plant lineages was 0.66. These findings emphasize that both environmental factors and evolutionary history together regulate N vs. P scaling relationships in seed. Overall, our results advance understanding of plant reproductive strategies and resource allocation in seeds and have important implications for refining early plant growth models.

CRediT authorship contribution statement

Nan Hu: Writing – original draft, Writing – review & editing, Conceptualization, Data curation, Formal analysis, Investigation,

Methodology, Visualization. **Li Zhang:** Writing – original draft, Writing – review & editing, Conceptualization, Data curation, Investigation. **Sean T. Michaletz:** Writing – review & editing, Methodology. **Milos Simovic:** Writing – review & editing, Methodology. **Josep Peñuelas:** Writing – review & editing. **Jordi Sardans:** Writing – review & editing. **Haiyang Gong:** Writing – review & editing, Visualization. **Haiyan Bu:** Writing – review & editing, Conceptualization, Supervision. **Zhiqiang Wang:** Writing – review & editing, Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision.

Data availability statement

All data are available in a permanent Zenodo archive of a GitHub repository: https://doi.org/10.5281/zenodo.16633323.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2026.03.006.

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