frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 13 December 2022
DOI 10.3389/fevo.2022.1093474

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 09 November 2022
ACCEPTED 24 November 2022
PUBLISHED 13 December 2022

CITATION
Jia N, Niklas KJ, Yao B and Wang Z (2022) Altitude patterns of seed C, N, and P concentrations and their stoichiometry in an alpine meadow on the eastern Tibetan Plateau.
Front. Ecol. Evol. 10:1093474.
doi: 10.3389/fevo.2022.1093474

Altitude patterns of seed C, N, and P concentrations and their stoichiometry in an alpine meadow on the eastern Tibetan Plateau

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Understanding the altitudinal patterns of plant stoichiometry in seeds is critical for characterizing important germination and dormancy strategies, soil seed bank composition, seed predation probability, efficiency of seed dispersal and seedling performance, and to predict how biodiversity might be influenced by climate change. However, our understanding of the altitudinal patterns of seed stoichiometry is extremely limited. In this study, we measured the concentrations of carbon (C), nitrogen (N) and phosphorus (P) in the seeds of 253 herbaceous species along an altitudinal transect (2,000–4,200m) on the eastern Tibetan Plateau, China, and further to characterize seed C:N:P stoichiometry. The geometric means of C, N, and P concentrations were 569.75mg/g, 34.76mg/g, and 5.03mg/g, respectively. The C:N, C:P, and N:P ratios were 16.39, 113.31, and 6.91, respectively. The seed C, N, and P concentrations and C:N:P ratios varied widely among major plant groups and showed significant altitudinal trends. In general, C, N, and P concentrations increased, whereas seed C:N:P ratios decreased with elevation. These results inform our understanding of the altitudinal patterns of seed stoichiometry and how to model ecosystem nutrient cycling.

KEYWORDS

alpine meadow, carbon, nitrogen, phosphorus, seed, stoichiometry

Introduction

Ecological stoichiometry provides a framework for understanding plant strategies dependent on or influenced by the differential allotment of multiple chemicals in different organs. This framework is important because it sheds light on ecosystem functionalities and is a valuable method for indirectly assessing the biogeochemical cycling of terrestrial ecosystems (Elser et al., 2000; Sterner and Elser, 2002; Wang et al., 2022a). Carbon (C), nitrogen (N), and phosphorus (P) are the three essential elements and play important roles in regulating plant growth and development (Aerts and Chapin, 2000; Vitousek, 2004). For example, the C:N:P ratios of plant organs have been used to evaluate potential terrestrial nutrient limitations (Güsewell, 2004; Reich and Oleksyn, 2004) and to characterize biogeochemical cycling of ecosystems (Güsewell and Gessner, 2009; Wang et al., 2015). In addition, the C:N:P ratios of plant organs vary significantly among different environmental gradients (McGroddy et al., 2004; Reich and Oleksyn, 2004; Yuan et al., 2011; Wang et al., 2020a). Therefore, evaluating the patterns of C:N:P ratios of plant organs along environmental gradients can improve our understanding the effects of climate change on global C, N, and P coupling cycles.

Changes in elevation are correlated with changes in a number of environmental factors including temperature, CO_2 concentration, light, precipitation, and soil-type, which in turn can lead to differences in plant C, N, and P concentrations and their ratios (Sundqvist et al., 2011; Wang et al., 2020b). These environmental differences are also correlated with changes in the types of selection pressure on plant survival, growth and physiological function, thereby resulting in different adaptions (Lord, 1994). For example, leaf N and P concentrations decline and N:P ratios increase with increasing elevation as a result of low temperature suppression of soil nutrient mineralization and the decomposition of organic matter, both of which limit root nutrient uptake (Reich and Oleksyn, 2004). Moreover, increasing elevation is reported to affect the accumulation of inorganic P in leaves with an attending downward trend in N:P (Reich and Oleksyn, 2004). Similarly, fine root N and P concentrations decrease with increasing elevation, whereas fine root N:P ratio increasing (Zhao et al., 2016). Climate and soil variables jointly influence fine root C, N, and P concentrations and their ratios (Yuan et al., 2011; Wang et al., 2021a).

The effects of elevation on specific plant organs, such as leaves (Soethe et al., 2008; Hoch and Körner, 2012; Zhao et al., 2014), stems (Yao et al., 2015; Wang et al., 2018, 2022b) and roots (Yuan et al., 2011; Wang et al., 2022c) as well as soil microbes (He et al., 2019; Wang et al., 2021b) have been widely investigated and have significantly improved our understanding of plant responses to differences in elevation. However, our understanding of the effects (if any) on seed C:N:P stoichiometry is poor. Yet, during the earlier stages of plant ontogeny, many developmental and physiological processes depend on seed reserves (Bewley et al., 2013). For example, the C, N and P reserves in seeds are critical components affecting growth (Bu et al., 2018) because C is the most abundant component of dry matter, whereas N affects protein synthesis and P is essential for the synthesis of nucleobases (Elser et al., 2000; Sterner and Elser, 2002). Therefore, seed reserves might influence seed dormancy, germination, and survival with different nutrient elements having different effects on each stage. Given the importance of C, N and P to seedling growth and survival, it is important to evaluate see C:N:P stoichiometry, particularly along elevational gradients.

The goal of this paper was to evaluate the effects of elevation on seed stoichiometry in the eastern Tibetan Plateau, which represents one of the largest alpine meadows in the world, covering more than 60% of the area of the alpine steppe and alpine meadow (Yang et al., 2015). In this study, we compiled a dataset on C, N and P seed concentrations for 253 herbaceous species along an altitudinal gradient to determine the seed C, N, and P concentrations and C:N:P ratios across different plant groups, and examine the elevational patterns of the seed C, N, and P concentrations and C:N:P ratios.

Materials and methods

Study area description

This study area is located on the eastern edge of the Tibetan Plateau in China (100°44′-104°45′E, 33°06′-35°34′N; Figure 1). The climate is cold and humid, and the elevation rises from 2000 to 4,200 m. The mean annual temperature ranges from 1.2°C-4.6°C and the mean annual precipitation increased from 450 to 780 mm and growing season is short (from late May to late September; Bu et al., 2016, 2018). The main vegetation types in typical alpine meadow dominated by various graminoids (e.g., Cyperaceae and Poaceae) and herbs (e.g., Asteraceae, Fabaceae, Gentianaceae, Polygonaceae, Ranunculaceae, and Scrophulariaceae). All these factors make it an optimal site to explore the altitudinal patterns of seed C:N:P stoichiometry.

Seed collection and measurements

The mature seeds of 253 species from 37 families were examined along an altitudinal gradient from late August to September in 2015. The time of collection was based on prior extensive field observations on seed development and dispersal time. See maturity was determined using a number of physical cues including see color, pericarp consistency, and the ease of detaching them. Mature seeds were sampled randomly from over 30 individual of each species from sites differing in 50 m across the elevational gradient. Intact seeds were stored in envelopes and oven-dried at 50°C to constant weight after which seeds were ground into a fine powder and C, N, and P concentrations were measured. Dry combustion in an elemental analyzer (Elementar TOC Vario, Germany) was used to measure C and N concentrations. The parts of fine powder were digested using microwave heating, and volumes of 5 ml of HNO_3 65% and 1 ml of H_2O_2 30% were added for the digestion. The molybdenum blue method on an automatic flow injection analyzer (Lachat Quickchem 8500, United States) was used to measure P concentrations as described by Wang et al. (2020b). The stoichiometric ratios of C:N, C:P and N:P ratios were calculated on a mass basis.

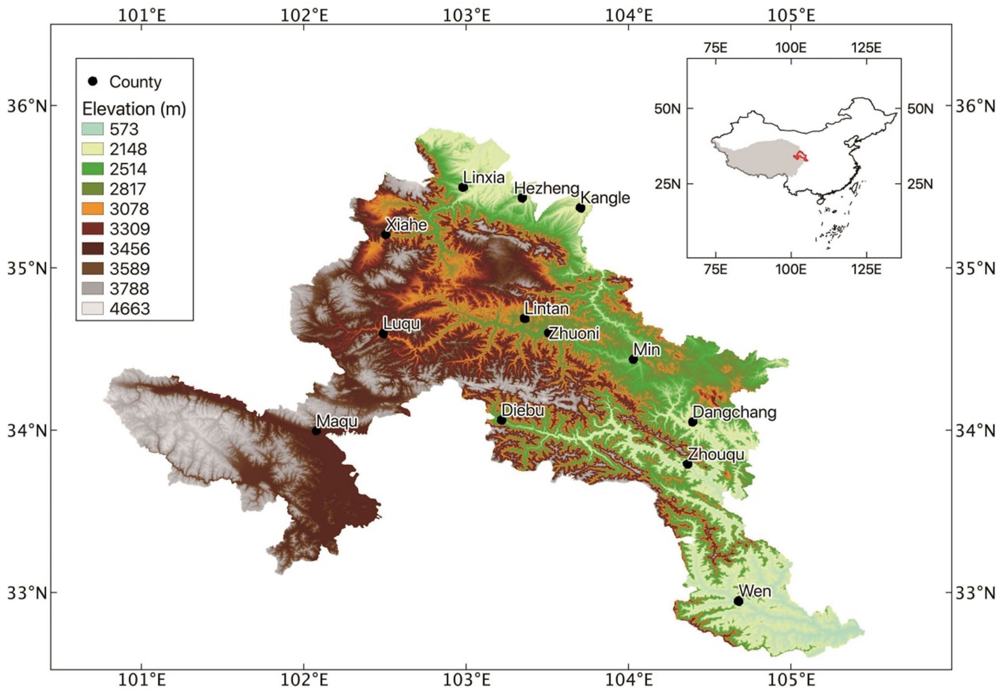

FIGURE 1
The study area and sampling sites along the elevation gradients.

Data analysis

The plant species were divided into two life-form groups (i.e., annual and perennial), two functional groups (i.e., forb and graminoid), two N-fixing groups (i.e., N-fixing and non-N-fixing), and two phylogenetic groups (i.e., monocotyledons and eudicots). We compared the differences in C, N, and P concentrations and C:N:P ratios of seeds across major functional groups using one-way analysis of variance (ANOVA) least-significant difference with (LSD) *post hoc* tests. The relationships between seed C, N, and P concentrations and C:N:P ratios and elevation were explored by ordinary least squares (OLS) regressions analysis after the seed C, N, and P, concentrations and C:N:P ratios were log-transformed to normalize frequency distributions. All statistical analyses were performed using R 2.15.2 (R Development Core Team, 2015).

Results

The geometric mean values of seed C, N, and P concentrations were 569.75 mg/g, 34.76 mg/g, and 5.03 mg/g, respectively (Table 1 and Figure 2). The C concentration ranged from 501.23 to 575.9 mg/g, N concentration ranged from 21.54–57.17 mg/g, whereas P concentration ranged from 2.87–5.18 mg/g (Table 1). The C:N:P ratios ranged from 8.77 to 24.65 for C:N, 99.11 to 185.27 for C:P, and 6.36 to 11.3 for N:P (Table 1). Seed C:N:P ratios differed significantly across different major plant groups. Seed C:N and C:P ratios were the highest in graminoids, whereas N-fixing species had the highest N:P ratios. In contrast, seed C:N and C:P ratios were the lowest in N-fixing species, whereas annual species had the lowest N:P ratios (Table 1).

Seed C, N, and P concentrations and C:N:P ratios were significantly correlated with altitude ($p < 0.05$; Figure 3). C, N, and P concentrations increased significantly with elevation ($p < 0.05$; Figures 3A–C), whereas seed C:N:P ratios decreased with increased elevation ($p < 0.01$; Figures 3D–F).

Discussion

Variations of seed C, N, and P and C:N:P ratios

Our results indicate that seed C, N and P concentrations on the eastern Tibetan Plateau have geometric means that are 569.75 mg/g, 34.76 mg/g, and 5.03 mg/g, respectively, and thus higher than that of leaves (435 mg/g, 29.2 mg/g, and 2 mg/g, respectively) reported by He et al. (2006) and fine roots (447.6 mg/g, 11.09 mg/g, and 0.91 mg/g, respectively) reported by Geng et al. (2014) for herbaceous species in an alpine meadow. These findings support the fact that compared to leaves or fine roots, germinating seeds manifest higher metabolic activity and thus require higher amounts of nutrients for germination and primary growth (Bu et al., 2008) until seedlings become established and autotrophic (Soriano et al., 2011; Bewley et al.,

TABLE 1 Geometric means and standard deviations of seed C, N, and P concentrations and their ratios for major plant groups.

Taxonomic group	*n*	C (mg/g)	N (mg/g)	*p* (mg/g)	C:N	C:P	N:P
All	711	569.75 ± 71.14	34.76 ± 13.02	5.03 ± 2.36	16.39 ± 6.16	113.31 ± 75.07	6.91 ± 3.50
Life from groups							
Annual	175	570.24 ± 84.03a	31.22 ± 8.31b	4.91 ± 2.22a	18.26 ± 5.58a	116.13 ± 65.65a	6.36 ± 4.34a
Perennial	536	569.58 ± 66.47a	36.01 ± 13.91a	5.08 ± 2.42a	15.82 ± 6.26b	112.41 ± 77.95a	7.11 ± 3.17a
Functional groups							
Forb	681	571.52 ± 71.77a	35.51 ± 12.83a	5.15 ± 2.34a	16.10 ± 5.75b	110.88 ± 70.43b	6.89 ± 3.64a
Graminoid	30	530.98 ± 35.04b	21.54 ± 9.39b	2.87 ± 1.76b	24.65 ± 8.62a	185.27 ± 118.66a	7.52 ± 4.13a
N-fixation groups							
N-fixing	55	501.23 ± 47.14b	57.17 ± 13.28a	5.06 ± 2.14a	8.77 ± 2.08b	99.11 ± 47.91b	11.30 ± 4.63a
Non-N-fixing	656	575.90 ± 69.63a	33.34 ± 11.24b	5.03 ± 2.39a	17.27 ± 5.86a	114.59 ± 76.70a	6.63 ± 3.12b
Phylogeny groups							
Monocotyledon	54	533.02 ± 48.95b	25.86 ± 11.67b	3.50 ± 1.65b	20.61 ± 8.75a	152.29 ± 101.24a	7.39 ± 3.32a
Dicotyledon	657	572.88 ± 71.76a	35.62 ± 12.88a	5.18 ± 2.37a	16.08 ± 5.73b	110.59 ± 71.35b	6.88 ± 3.51a

n represents the number of samples. Different letters denote significant differences at the 0.05 level.

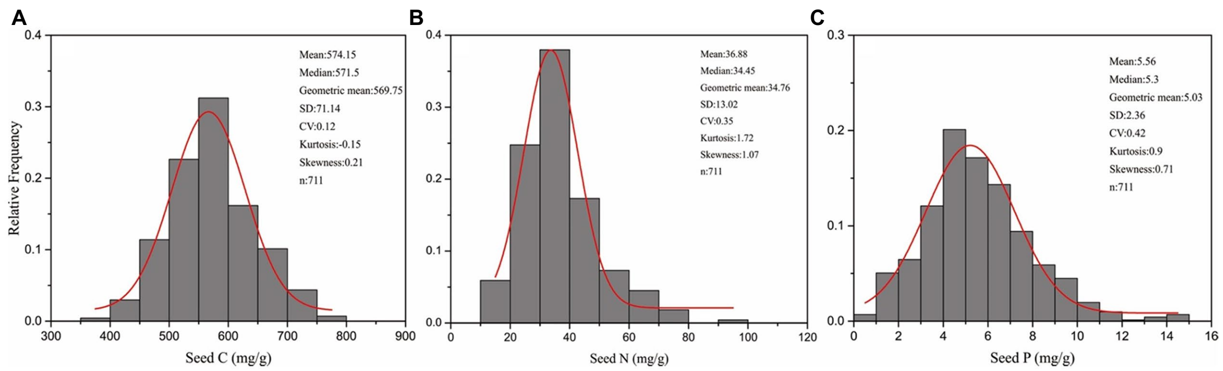

FIGURE 2
Frequency distribution of seed carbon (C) **(A)**, nitrogen (N) **(B)** and phosphorus (P) concentrations **(C)** for all 253 herbaceous species on the eastern Tibetan Plateau.

2013; Cheng et al., 2015). For example, P reflects nucleic acid content, which is required for the synthesis of the sugar-phosphate intermediates of photosynthesis and respiration (Sterner and Elser, 2002). P content can provide sufficient ribosomes for seed germination and rapid initial growth (Elser et al., 2003). Higher C, N, and P content in seeds may also reflect an adaptive strategy for survival and preservation. In contrast, the seed C:N, C:P, and N:P ratios on the eastern Tibetan Plateau have a geometric mean of 16.39, 113.31, and 6.91, respectively, which are lower than that fine roots (40.36, 491.87, and 6.91, respectively) reported by Geng et al. (2014) for herbaceous species in an alpine meadow. The lower C:N:P ratios of seeds supports the growth rate hypothesis, which postulates that fast-growing species have higher P content and lower C:P and N:P ratios because higher growth rates requires more P supported by P-rich rRNA than N to ensure rapid protein synthesis (Elser et al., 2000; Sterner and Elser, 2002).

Seed C, N, and P concentrations and C:N:P ratios differ across major plant groups (Table 1). These differences may reflect different nutrient availability strategies among different plant groups. We found significantly higher N concentrations for perennial species compared with annual species. This result is consistent with a previous study (Bu et al., 2008), suggesting that higher seed N content is positively correlated with germination success (de Frenne et al., 2011). The lower C:N ratios in perennial species than annual species is likely mainly due to larger N concentrations in perennial species. Forb species have markedly higher C, N, and P concentrations than graminoid species. These results might be attributed to forbs generally having more rapid germination rates and more vigorous seedlings compared to the seeds of grasses (Ching and Rynd, 1978). Similarly, eudicots generally have higher seed C, N, and P concentrations than monocotyledon, perhaps as a consequence of differences in their ability to store nutrients (Bonfil, 1998). The N concentrations of seeds was significantly higher in N-fixing species than non-N-fixing species owing to the ability to absorb N in fine roots (McCormack et al., 2015) and also perhaps because of the high

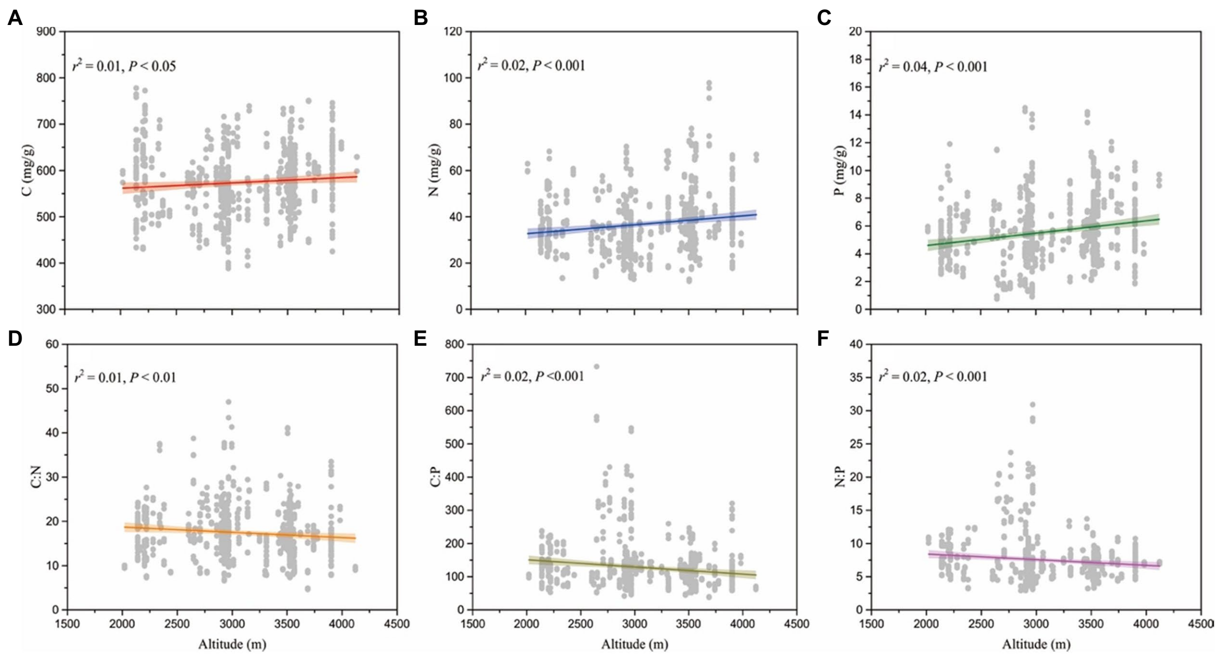

FIGURE 3
Changes in seed C, N, P **(A-C)** and C:N:P **(D-F)** ratios with the elevational gradients.

metabolic cost of N-fixation (Wardle and Greenfield, 1991). Interestingly, the seed N:P ratios in our study do not vary across the major plant groups, with the exception of N-fixers. This phenomenon may reflect a fundamental constraint on seed N and P concentrations and N:P ratios.

Altitudinal patterns of seed C, N, and P concentrations and C:N:P ratios

Seed C, N, and P concentrations and C:N:P ratios are closely correlated with the elevational patterns on the eastern Tibetan Plateau ($p < 0.05$). The variations of climate and the limitation of nutrient availability along an elevational gradient may interact to shape the elevational patterns of seed C, N, and P concentrations and C:N:P ratios. Seed C concentration increases significantly with altitude, supporting the notion that plant growth in higher elevations experiencing more stressed conditions require more non-structural C, including starch, low molecular weight sugars, and storage lipids to maintain cellular osmotic pressure and to resist freezing (Hoch et al., 2002; Millard et al., 2007; Hoch and Körner, 2012). Likewise, seed N and P concentrations increase with elevation, suggesting that for rapid initial growth, species from high elevation areas would take the opportunity to recruit seedlings. Thus, the high content of N and P in seeds of these species might be the result of natural selection for rapid initial growth. These patterns also support the Temperature-Plant Physiology and the Soil Substrate Age hypotheses (Reich and Oleksyn, 2004). Plants growing in high elevations tend to have greater N and P concentrations purportedly as a defense against the effects of low temperatures. This speculation is consistent with mechanisms that reduce N-rich enzymatic efficiency at low temperatures and P-rich RNA that can compensate for decreased rates of metabolic reactions (Weih and Karlsson, 2001; Reich and Oleksyn, 2004). In addition, our data indicate that seed C, N, and P concentrations are highly associated with one another ($p < 0.01$; Figure 4). This result indirectly supports the observation that seed C, N, and P concentrations follow the same trends along an elevational gradient.

The data presented here indicate that seed C:N:P ratios decrease along an elevational gradient. Previous studies have shown that low temperatures can depress soil microbe activity, resulting in the slow decomposition of organic matter, thereby reducing the availability of N and P in soils and thus limiting N and P uptake by roots (Körner, 1989; Wang et al., 2019; Long et al., 2020, 2022). Moreover, aggravated P leaching in soils caused by the increased precipitation at higher elevations can reduce P availability (Hedin et al., 2003). The decreasing seed N:P ratio along an elevational gradient indirectly supports the Temperature-Physiological hypotheses, which states that leaf N:P ratios decrease with mean annual temperature (MAT) at a global scale as a result of both physiological acclimation and adaptation to temperature (Reich and Oleksyn, 2004; Lin et al., 2021; Wang et al., 2022d). Collectively, these elevational patterns probably are the result of the collective influences of climate and soil drivers that lead to a gradual shift in seed C:N:P stoichiometry from low to high elevations. However, due to the lack of data of soil nutrients (e.g., soil total C, N, and P) in our

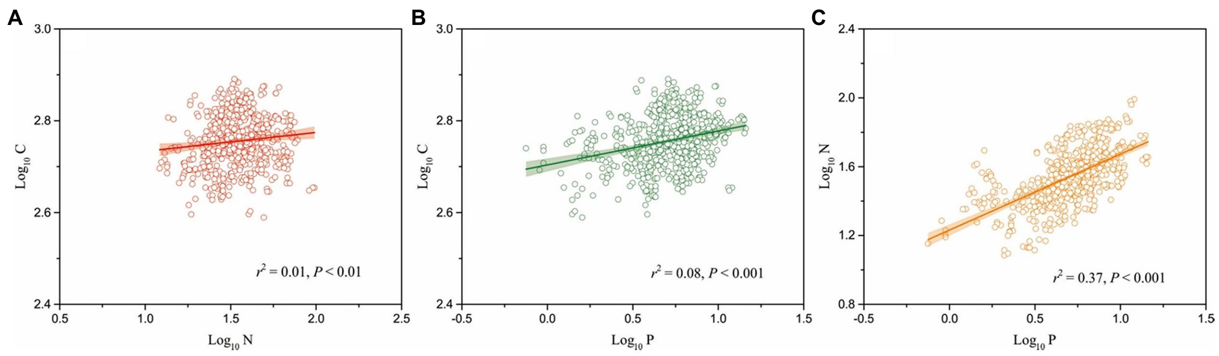

FIGURE 4
Relationships of seed carbon and nitrogen **(A)**, carbon and phosphorus **(B)**, nitrogen and phosphorus **(C)** concentrations for all 253 herbaceous species on the eastern Tibetan Plateau.

dataset, our understanding of the mechanisms driving the elevational patterns of seed C:N:P stoichiometry on the eastern Tibetan Plateau is still severely limited and warrants further investigation.

Conclusion

In summary, this study provides a comprehensive documentation of the seed C:N:P stoichiometry across different plant groups in an alpine meadow on the eastern Tibetan Plateau. The results presented indicate that the seed C, N, and P concentrations and C:N:P ratios differ across major plant groups. Seed C, N, and P concentrations and C:N:P ratios also exhibited a statistically robust elevational pattern on the eastern Tibetan Plateau. These results advance our understanding of plant stoichiometry and have important implications for ecosystem functioning across large environmental gradients.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

ZW conceived the idea and designed the research. NJ, KN, BY, and ZW performed the data analysis and wrote the paper. All authors contributed to the article and approved the submitted version.

Funding

This study was financially supported by the International Science and Technology Cooperation Project of Qinghai province of China (2022-HZ-817).

Acknowledgments

We are grateful to Jordi López-Pujol for the help with species identification.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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