

Article

Divergent Nitrogen, Phosphorus, and Carbon Concentrations among Growth Forms, Plant Organs, and Soils across Three Different Desert Ecosystems

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Abstract: Quantifying the dryland patterns of plant carbon (C), nitrogen (N), and phosphorus (P) concentrations and their stoichiometric values along environmental gradients is crucial for understanding ecological strategies. To understand the plant adaptive strategies and ecosystem nutrient concentrations across three desert ecosystems (e.g., desert, steppe desert, and temperate desert), we compiled a dataset consisting of 1295 plant species across three desert ecosystems. We assessed the element concentrations and ratios across plant growth forms, plant organs, and soils and further analysed the leaf vs. root N, P, and N:P scaling relationships. We found that the leaf N, P, and C concentrations were significantly different only from those of certain other growth forms and in certain desert ecosystems, challenging the generality of such differences. In leaves, the C concentrations were always greater than the N and P concentrations and were greater than those in soils depending on the soil chemistry and plant physiology. Thus, the element concentrations and ratios were greater in the organs than in the soils. The values in the leaf versus the root N, P, and N:P scaling relationships differed across the three desert ecosystems; for example, α_N (1.16) was greater in the desert, α_P (1.10) was greater in the temperate desert ecosystem, and $\alpha_{N:P}$ (2.11) was greater in the desert ecosystem. The mean annual precipitation (MAP) and mean annual temperature (MAT) did not have significant effects on the leaf elemental concentrations or ratios across the desert ecosystems. This study advances our understanding of plant growth forms and organs, which support resource-related adaptive strategies that maintain the stability of desert ecosystems via divergent element concentrations and environmental conditions.

Keywords: desert ecosystems; plant organs; growth forms; elemental concentrations; climatic variables



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1. Introduction

Nitrogen (N), phosphorus (P), and carbon (C) are essential limiting elements in terrestrial ecosystems that often constrain plant growth and ecological functions [1–3]. They are important for the function and biogeochemical C cycles of terrestrial ecosystems [4,5] and help sustain the stability of ecosystems worldwide [2,6]. However, plant responses to increased carbon dioxide (CO₂) can be constrained and modulated by other growth conditions, including insufficient nutrient levels [7]. Additionally, plant leaf C:N and C:P ratios help to assimilate C in plants under N or P accumulation [8] and thereby help increase plant growth rates. Exploring the dynamics of N and P in plant life history strategies can advance our understanding of the requirements of plant growth, which represents an important nutrient-use adaptation strategy to help fulfil plant defence strategies [9], influencing soil–plant nutrient cycling and ecosystem processes [10,11]. Hence, the N:P ratio is considered to determine nutrient limitations in plant populations and communities [5]. Therefore, plant C:N:P stoichiometry is considered to play an important role in the study of

environmental changes, with an impact on ecosystem functions and nutrient limitations for biogeochemical cycling [10,12], which highlights the importance of environmental changes in plant tissue nutrients. It is important to understand how and why plant growth patterns and organs respond differently across three desert ecosystems, namely, deserts, steppe deserts, and temperate deserts, especially in terms of nutrient concentrations and climatic factors, at scales ranging from the regional scale to the global scale [13–15].

Previous studies have focused mainly on N and P absorption within a single organ type, including leaves [16,17], stems [16,18], and fine roots [19,20]. According to the leaf economics spectrum (LES), leaves are a basic part of plants that are sensitive to the external environment; therefore, plant functional traits have the potential to explain the adaptive strategies of species and their responses to environmental changes [21]. Leaves are sensitive to C fixation [22], while roots help water and nutrient transport [23] and soil C chemistry [24,25]. For example, plants allocate limited amounts of P and N to stabilize their metabolic rate by changing their allocations under water stress and soil nutrient limitations. Such coordination of different plant characteristics, also called the whole-plant economic spectrum (PES), occurs during slow and fast growth [26], suggesting that the fundamental constraints on fast and slow growth depend upon the coordination of different organs [26]. For example, if plant N and P allocation strategies also depend on the PES, it would be reasonable to assume that a scaling relationship between the N and P contents exists for all organs because nutrients and water are integrated across different organs to achieve an appropriate growth rate [27].

Thus, an increase in the distribution of N to leaves is an adaptive response to low photosynthetic rates and reduced stomatal conductance, which enhances water use efficiency in desert conditions [28,29]. Moreover, plants absorb atmospheric CO₂ through photosynthesis, by which CO₂ is converted into biomass; hence, C accumulates in plant leaves and roots [30]. Thus, plant root systems can easily increase water and nutrient uptake from the soil environment, which has a positive effect on stomatal conductance and photosynthesis [7]; therefore, an increase in CO₂ decreases stomatal conductance more in water-limited plants [7]. However, in the soil, more P is allocated to leaves with increasing soil P, and vice versa; when soil N increases, a larger proportion of N is allocated to roots [31]. The LES explains that plant species adopt ecological strategies, such as those used by conservative species (slow-growing, i.e., N-poor leaves) and acquisitive species (fast-growing, i.e., N-rich leaves), which could cause basic changes in ecosystem stability when resource availability is altered [13,32].

Studies have revealed clear geographical patterns in the compositions of leaf N and P contents in terrestrial plants at regional/global scales [13,33]. Therefore, biogeographic N and P gradients could occur because of the effect of temperature on plant physiology [13,34], while other climatic variables, such as precipitation, could also influence the changes in N and P [13] in plant organs. Dryland covers approximately 45% of the global terrestrial area and is expected to increase because of climate change [2]. Reports on drylands have shown that aridity has no negative or positive influence on the C, N, or P content in plant organs. Aridity does not affect foliar N or P concentrations in temperate desert plants [35]. In addition, it was reported that aridity does not affect the C and N concentrations in terrestrial ecosystems that are composed of grasses, N-fixing shrubs, or trees [36]. Based on the results from various reports, it remains controversial whether plant C contents decrease with increasing aridity in grasslands in China [37]; in contrast, several studies have reported that the C, N, and P concentrations in plants are positively correlated with aridity. This inconsistency in the positive and negative effects of aridity on C, N and P concentrations is possibly due to differences in geographic areas, plant types, soil types, and climatic conditions [2]. Therefore, herbaceous species require more nutrients for faster growth, and woody species need less nutrients for slow growth under dryland conditions [38]. There is a need for a better understanding of whether the shifts in these nutrient concentrations are because of the growth forms and their organs across desert ecosystems.

The log–log scaling relationships between N and P and the stoichiometric relationships between these elements in plant organs are important for understanding plant ecology

and desert ecosystem patterns at the local and global levels. Earlier studies have provided evidence that the foliar N versus P scaling relationships are similar at local, regional, and global scales, although changes occur because of environmental differences; that is, the scaling exponent for the N versus P relationship has been reported to range from 0.62 to 0.78 [39,40]. Based on a wide-ranging study (i.e., approximately 2500 species), a general $2/3$ scaling exponent was proposed [39] for the global foliar N versus P scaling relationship, with the relationships for plant functional types and vegetation biomes all having a similar scaling exponent. Additionally, based on 763 terrestrial plant species, a 0.82-power “law” was proposed for the global root N vs. P contents across different plant groups and ecosystems [19]. According to this sparse information, we hypothesized that the N vs. P and N:P ratio scaling relationships for roots and leaves will differ for the three different desert ecosystems, namely, desert, steppe desert, and temperate desert.

The leaf C, N, and P contents and their ratios in dryland plants have been extensively studied; however, the variations in C, N, and P across three desert ecosystems, namely, desert, steppe desert, and temperate desert ecosystems, especially among the growth forms and their organs, are unclear. Thus, we hypothesized that shifts in nutrient concentrations possibly cause plant growth forms and their organs to adapt, mediating a shift in plant adaptive strategies across the three desert ecosystems. Here, we compiled 1295 different plant growth forms (e.g., herbs, shrubs, trees, and grasses) along with soil and environmental conditions that were identified in previous studies across three desert ecosystems, namely, desert, steppe desert and temperate desert, focusing only on “drylands”. Our main objectives were (1) to quantify the changes in N, P, and C and their ratios in plant organs (leaves versus roots) and the soil and across the growth forms in three desert ecosystems; (2) to test whether differences in stoichiometric scaling exponents exist between root and leaf N, P, and N:P ratios across desert ecosystems; (3) to analyse the effects of temperature and precipitation on the leaf N, P, and C contents and their stoichiometry across desert ecosystems; and (4) to further quantify the element concentrations between deciduous and evergreen species and between N-fixing and non-N-fixing species from all the pooled data for the three different deserts.

2. Materials and Methods

2.1. Data Sources

Using the Web of Science (<http://apps.webofknowledge.com>, accessed on 10 February 2024) and Google Scholar (<http://scholar.google.com>, accessed on 10 February 2024), we surveyed studies that were published from 2005 to 2022, and additional references that were published between 1982 and 1991 were also checked for potential data (because some of the published literature used datasets covering 1982–1991). The following keywords were used: “nitrogen (N)”, “phosphorus (P)”, “carbon (C)”, “stoichiometry”, “N:P:C”, “leaves” and “roots”; and “soil”. We searched for these key terms using Google Scholar and the Web of Science, each in combination with the following terms: “deserts”, “mean annual temperature (MAT)” and “mean annual precipitation (MAP)”, which represented climatic variables. We compiled a dataset of a total of 1295 desert plant species (Supplementary Materials) from the literature (sources and literature information) can be found in the Supplementary Materials). After compiling the dataset, we divided the desert vegetation into (1) desert (D) (496 species), (2) steppe desert (SD) (363 species), and (3) temperate desert (TD) (436 species) based on the descriptions of the whole dataset that were provided in the original articles (Supplementary Table S1). The geographic locations, climatic variables, element concentrations and stoichiometric ratios, plant growth forms, and plant species collected from different desert ecosystems were compiled from the dataset. A complete list of information is provided in Supplementary Materials. The selected sites have different climatic conditions, with MAPs varying from 20 to 502 mm and MATs ranging from -2.17 to 13.9 °C; the geographical locations cover longitudes varying from 1.6° E to 129.18° E and latitudes varying from 11.18° N to 57.32° N in China. A complete description of the geographical locations and climatic variables for each desert vegetation type is provided in Supplementary Table S1 if this information was not specified

in the original research papers. Basic climatic parameter values (e.g., MAP and MAT) were obtained from the global biodiversity information facility (gbif.org, USA) based on the site locations if site climate information was not provided in the source papers.

The datasets were extracted from Supplementary Materials, and the data in the figures were extracted using GetData Graph Digitizer 2.26 (<http://getdata-graph-digitizer.com>, accessed on 10 February 2024) software. If the element contents (in milligrams per gram) were provided, rather than the element ratios, in table, text, or figure form, we then calculated the element ratios (i.e., N:P, C:N, and C:P) for the leaves, roots, and soil. As a result, the references in the literature were also checked for data (sources and the literature information in the Supplementary Materials [14,25,41–56]). Plant species were explored for N fixation (N-fixing and non-N-fixing) and growth (herbs, shrubs, trees, and grass), and plant species were further categorized according to their growth habit, i.e., deciduous or evergreen. The data pertain to desert vegetation and therefore cover an enormous range of environmental conditions and ecosystem types. Some publications did not provide root and soil data; in those cases, we simply used Student's *t*-tests (between two groups) and one-way ANOVA (more than two groups). Therefore, all the elemental concentrations and their stoichiometries are expressed as means $\pm$ standard errors (means $\pm$ SEs), with lowercase letters indicating significant differences (Supplementary Table S1). We also compared the N and P contents and their stoichiometric ratios in the leaves and roots between N-fixing and non-N-fixing plants and the leaf N, P, and C concentrations between deciduous and evergreen plants (Figures S1 and S2).

2.2. Statistical Analysis

We used SPSS version 19.0 (Armonk, NY, USA) for statistical analysis, and the figures were created with SigmaPlot 12.5. The differences in elemental concentrations and their ratios in plant organs and soils and among the growth forms across three different desert vegetation categories were tested using the least significant difference (LSD) test following one-way ANOVA (Figures 1 and 2). Furthermore, the data were log-transformed prior to analyses of the effects of climatic factors on element contents and their ratios among the different desert types. The correlations between the leaf element concentrations and environmental variables (MAP and MAT) were tested using simple linear regressions to adjust the r^2 and *p*-values. We also performed Student's *t*-tests (between two groups) to assess the differences between N-fixing and non-N-fixing plant organs and the element concentrations between deciduous and evergreen species.

To compare the numerical values of the scaling exponents (α) for the leaf and root element contents and their ratios among the three desert vegetation categories, we performed reduced major axis (RMA) regressions using the lmodel2 function of the R package LMODEL2 (Figure 3, Table 1) [1,57]. The data were log-transformed prior to performing the RMA regressions (Figure 3 and Table 1) to determine the scaling relationships of leaf vs. root N, P, and N:P for the three different desert ecosystems. The allocation of N and P concentrations among plant organs was assessed using a scaling relationship that may be described as a log–log scaling relationship, taking the form:

$$Y = \beta X^\alpha \quad (1)$$

Taking the log on both sides results in the following:

$$\log Y = \log \beta + \alpha \log X \quad (2)$$

where α and β represent the slopes of the *Y* versus *X* regression curves (the scaling exponent), respectively [18,29]. The scaling exponent α explains the allocation of N with respect to the allocation of P in plant organs. This simple equation provides a useful empirical model in which α can be used to predict plant and ecosystem functioning [10]. Therefore, the numerical values of the scaling exponents for the plant growth forms and ecosystems were determined using RMA regressions as explained above.

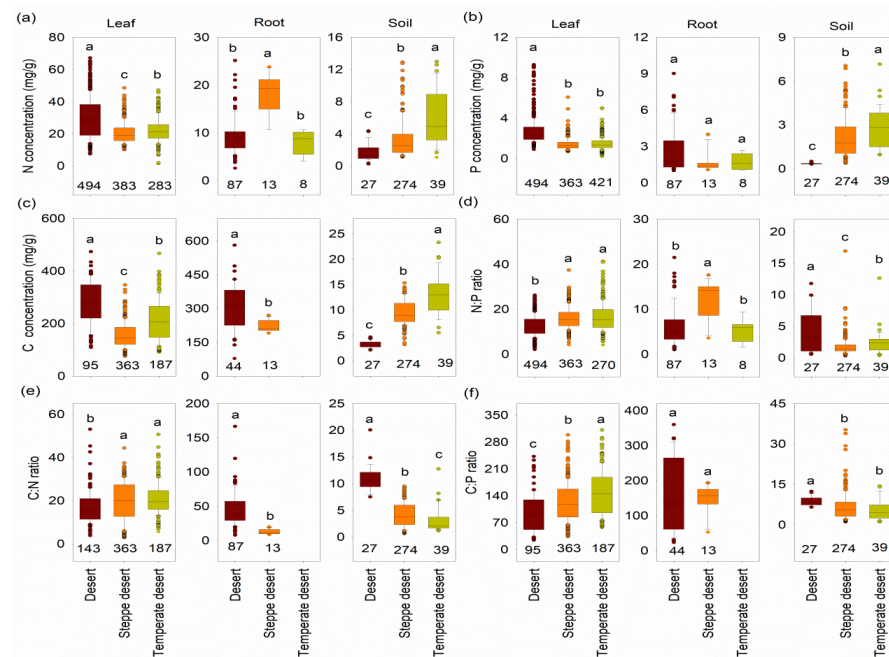


Figure 1. Comparisons of the nitrogen (N), phosphorus (P), and carbon (C) concentrations and their stoichiometric ratios in the leaves, roots, and soil of three ecosystem types (e.g., desert, steppe desert, and temperate desert). Here, (a–c) show the N concentrations, P concentrations, and C concentrations and (d–f) show the N:P, C:N, and C:P ratios, respectively, in two organs (e.g., leaves and roots) and in soil when all growth forms (e.g., herbs, shrubs, trees, and grasses) were pooled together. The different letters in each graph indicate significant differences among the three ecosystem types and differences in elements among leaves, roots, and soil (one-way ANOVA, $p < 0.05$). The numbers (n) under the box plot represent the number of species in each group.

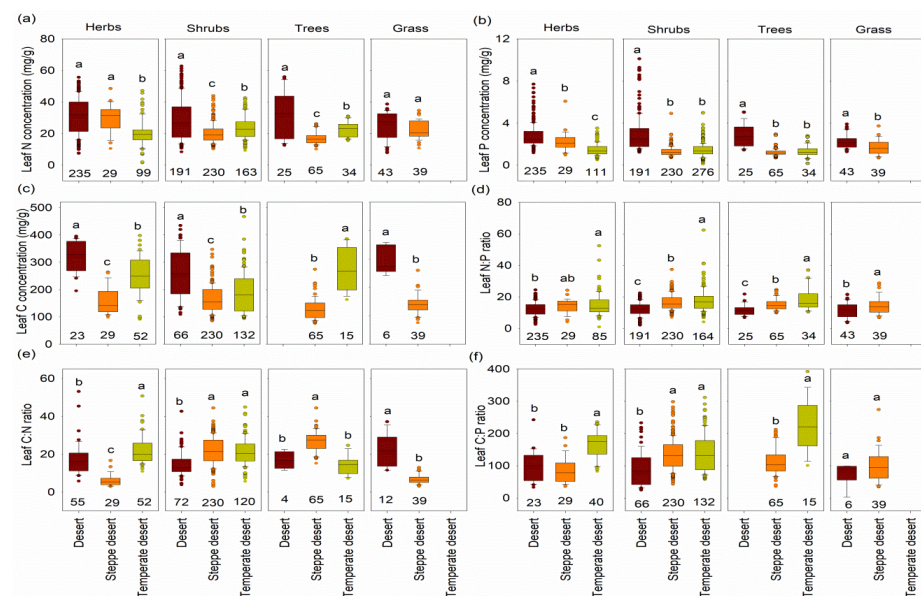


Figure 2. Comparisons of the nitrogen (N), phosphorus (P), and carbon (C) concentrations and their stoichiometric ratios in the leaves of plants with different growth forms (e.g., herbs, shrubs, trees, and grasses) among the three ecosystem types (e.g., desert, steppe desert, and temperate desert). Here, (a–c) show the N concentrations, P concentrations, and C concentrations and (d–f) show the N:P, C:N, and C:P ratios, respectively, in leaves. The different letters in each graph indicate significant differences in the elements across the three ecosystem types and among growth forms (one-way ANOVA, $p < 0.05$). The numbers (n) under the box plot indicate the number of species in each group.

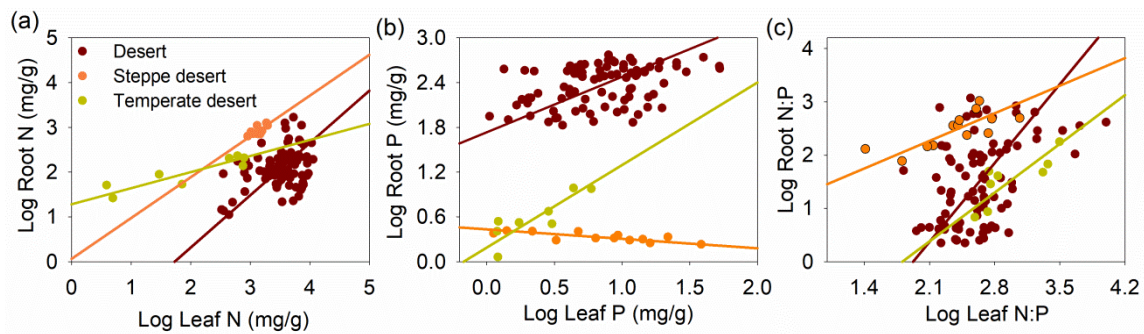


Figure 3. Scaling relationships of the nitrogen (N) and phosphorus (P) concentrations and N:P ratios between roots and leaves among the three vegetative types (e.g., desert, steppe desert, and temperate desert). The results of the reduced major axis (RMA) regressions are shown as comparisons between root and leaf N (a), between root and leaf P (b), and between root and leaf N:P ratios (c) across desert, steppe desert, and temperate desert ecosystems. All the results are described in Table 1.

Table 1. Summary of the reduced major axis (RMA) regressions of the log-transformed leaf nitrogen (N), phosphorus (P), and N:P ratios pooled across all species. α_{RMA} and β_{RMA} represent the scaling exponent and intercept, respectively. n represents the number of individuals. Lowercase letters indicate the differences among the three ecosystem types (shown by the exponents) based on likelihood-ratio tests at $p < 0.05$.

Ecosystem Type	n	α_{RMA} (95% CLs)	β_{RMA} (95% CLs)	r^2	p
N					
All	108	0.817 (0.677; 0.985)	−0.559 (−1.090; −0.029)	0.039	=0.041
Desert	87	1.169 (0.956; 1.424) ^a	−2.022 (−2.847; −1.197)	0.147	<0.01
Steppe desert	13	0.912 (0.572; 1.455) ^a	0.061 (−1.319; 1.441)	0.469	<0.01
Temperate desert	8	0.360 (0.237; 0.548) ^b	1.279 (0.943; 1.615)	0.812	<0.01
P					
All	108	2.102 (1.749; 2.528)	0.290 (−0.076; 0.655)	0.074	<0.01
Desert	87	0.742 (0.609; 0.905) ^a	1.735 (1.595; 1.875)	0.145	<0.01
Steppe desert	13	−0.128 (−0.195; −0.084) ^b	0.434 (0.381; 0.486)	0.578	<0.01
Temperate desert	8	1.106 (0.665; 1.838) ^a	0.190 (−0.064; 0.443)	0.718	<0.01
N:P					
All	108	1.987 (1.653; 2.389)	−3.606 (−4.589; −2.622)	0.077	<0.01
Desert	87	2.111 (1.734; 2.568) ^a	−4.060 (−5.174; −2.946)	0.161	<0.01
Steppe desert	13	0.740 (0.484; 1.130) ^b	0.713 (−0.067; 1.493)	0.568	<0.01
Temperate desert	8	1.307 (0.747; 2.289) ^{ab}	−2.362 (−4.674; −0.050)	0.651	=0.016

3. Results

3.1. Patterns of Element Concentrations and Stoichiometry among Plant Organs across Growth Forms and in the Soil across Three Desert Ecosystems

3.1.1. Changes in Concentrations and Ratios among Leaves, Roots, and Soils

According to our results, leaves had higher N and P concentrations and N:P ratios than roots and soils. Across the three desert ecosystems, plants in desert ecosystems had higher N, P, and C contents than those in the steppe and temperate desert ecosystems. Surprisingly, the lowest N, P, and C contents were found in the soils of the desert ecosystem, while the desert ecosystem had higher leaf and root C contents than did the other two desert ecosystems. However, the steppe and temperate desert ecosystems had higher P and C contents in their soils than did the plant organs. Among all the element contents and their ratios, the highest C storage was found in organs and soils. Furthermore, the N:P, C:N, and C:P ratios in the leaves, roots, and soils varied significantly across the three different desert ecosystems (Figure 1d). The soil N:P ratios were significantly greater in the desert ecosystem than in the other ecosystems. The soils had considerably greater

C:N ratios than the leaves and roots in the desert ecosystem. In the desert ecosystem, compared with those in the soils and roots, the C:P ratios in the leaves were significantly lower, but the differences were not significant. Finally, substantial variations were found in the ratios across organs and roots and across the desert ecosystems. However, within the plant organs and soils, almost all the leaf and root element contents and ratios significantly differed between the plant species that were associated with the three desert ecosystems (Figure 1), indicating that plant traits are also dependent on soil status and maintain different ecosystem stabilities under such conditions.

The shrubs in the different desert ecosystems had varying element concentrations and ratios as follows: desert ecosystem (means $\pm$ SEs) N (5.75 ± 0.71), P (3.20 ± 0.31), and C (13.93 ± 0.95) contents; steppe desert ecosystem N (3.31 ± 0.16), P (2.18 ± 0.09), and C (9.20 ± 0.16); and desert ecosystem N (1.21 ± 0.3), P (0.34 ± 0.01), and C (3.04 ± 0.19). Regarding the ratios, shrubs in the desert ecosystem had means $\pm$ SEs of N:P (3.49 ± 0.87), C:N (10.65 ± 0.3), and C:P (8.51 ± 0.39); those in the steppe desert had means of N:P (1.86 ± 0.1), C:N (3.99 ± 0.15), and C:P (6.37 ± 0.34); and those in the temperate desert had means of N:P (2.22 ± 0.28), C:N (3.30 ± 0.5), and C:P (4.73 ± 0.67) (Supplementary Table S2). The results also demonstrated that the means $\pm$ SEs of the element concentrations and their ratios were greater in the roots of different growth forms than in the soils associated with the growth forms across the different ecosystems.

3.1.2. Changes in Leaf Concentrations and Ratios among Growth Forms

We found that trees (woody), herbs, shrubs (woody), and grasses had higher N contents, while woody species had higher P contents than herbs and grasses in the desert ecosystem. Higher leaf N and P contents were observed in the herbaceous species than in the grasses and woody species (shrubs and trees) of the steppe desert. Additionally, lower leaf N and P contents were found in grass species than in herbaceous and woody species in the desert ecosystem. We observed that woody species exhibited higher N:P ratios than herbaceous species and grasses. We determined that the plants in the desert ecosystem had the lowest P concentrations and highest C concentrations, which demonstrates the importance of different growth forms and their organs in desert ecosystems for nutrient storage and photosynthetic activity under harsh conditions.

We found significant relationships between N-fixing and non-N-fixing plants in terms of the leaf and root N and P concentrations, except for the root and leaf N:P ratios, which were not significant (Supplementary Figure S1). For example, the leaf N and P concentrations were significantly greater for N-fixing species than for non-N-fixing species, while the leaf N:P ratios were not significantly greater for N-fixing species than for non-N-fixing species across the three desert ecosystems. The root N and P concentrations were significantly greater for N-fixing species than for non-N-fixing species, and the root N:P ratios were not significantly greater for non-N-fixing species than for N-fixing species (Supplementary Figure S1). Across all the pooled data for the three desert ecosystems, the leaf N contents were greater for deciduous species than for evergreen species, and the leaf P contents were greater for evergreen species than for deciduous species, although the difference was not significant; however, the leaf C contents were significantly greater for evergreen species than for deciduous species (Supplementary Figure S2).

3.2. *N* vs. *P* Scaling Exponents across Desert Ecosystems

According to the reduced major regression (RMA) analysis of log-transformed Equation (1) (Figure 3 and Table 1), we pooled all the data for the three desert ecosystems, where the leaf N vs. root N and leaf P vs. root P scaling exponents (α_N and α_P , respectively) were 0.81 (95% CIs = 0.677–0.985; Table 1) and 2.10 (95% CIs = 1.749–2.528; Table 1), respectively, and the leaf N:P versus root N:P scaling exponents ($\alpha_{N:P}$) were 1.98 (95% CIs = 1.653–2.389; Table 1).

We also observed that the α_N , α_P , and $\alpha_{N:P}$ values varied across the three different desert ecosystems; for example, α_N was greater (1.16) in the desert ecosystem than in the steppe desert (0.91) and temperate desert (0.36), whereas α_P was greater (1.10) in the

temperate desert than in the desert (0.74) and steppe desert (0.12), and $\alpha\text{N:P}$ was greater (2.11) in the desert than in the temperate desert (1.30) and steppe desert (0.74). There were significant differences among the three desert ecosystems in terms of the scaling exponents (αN , αP , and $\alpha\text{N:P}$) based on the RMA regressions ($p < 0.05$). Furthermore, we observed that αN , αP , and $\alpha\text{N:P}$ were weakly correlated across all the pooled data; no correlations were found in the desert ecosystem ($r^2 = 0.039$ to $r^2 = 0.0747$), but a weak positive correlation was found among the three desert ecosystems ($r^2 = 0.14$ to $r^2 = 0.81$). The ratio of N to P among the three desert ecosystems was generally statistically greater than 2/3 (or 0.66), which is close to/greater than 1, whereas α was statistically less than 2/3 for temperate desert ($\alpha\text{N} = 0.36$) and steppe desert ($\alpha\text{P} = 0.12$) ecosystems.

3.3. Effects of Climate on Leaf Elements and Stoichiometry

The overall effects of climatic factors (mean annual precipitation (MAP) and mean annual temperature (MAT)) explained the significant variations in leaf N, P, and C contents and their ratios (Figure 4) that were found by using data for all species and plant types across the three desert ecosystems. Overall, the leaf N concentrations increased with increasing MAP from high to low in the following order: desert > steppe desert > temperate desert; leaf N concentrations decreased with increasing MAT from high to low as follows: desert > steppe desert $\approx$ / or > temperate desert; leaf P concentrations increased with increasing MAP from high to low as follows: desert $\approx$ steppe desert > temperate desert; and leaf P concentrations decreased with decreasing MAT from high to low as follows: desert > steppe desert > temperate desert. The ranking of leaf C contents showed negative relationships with increased MAP in the desert, and the order in which leaf C contents increased with increasing MAP was similar to the relationship of steppe desert $\approx$ temperate desert. While the leaf C contents increased with increasing MAT in the desert, the ranking of leaf C content decreased with increasing MAT from high to low in the following order: temperate desert > steppe desert. Leaf N, leaf P, and temperate desert had lower slope relationships ($r^2 = 0.11$, $p < 0.43$ and $r^2 = 0.002$, $p < 0.32$) with MAT than did the other two desert ecosystems. The steppe desert leaf C content had the lowest values, with no significant difference in the relationship with MAT ($r^2 = 0.004$, $p < 0.21$) when compared to the other two ecosystems.

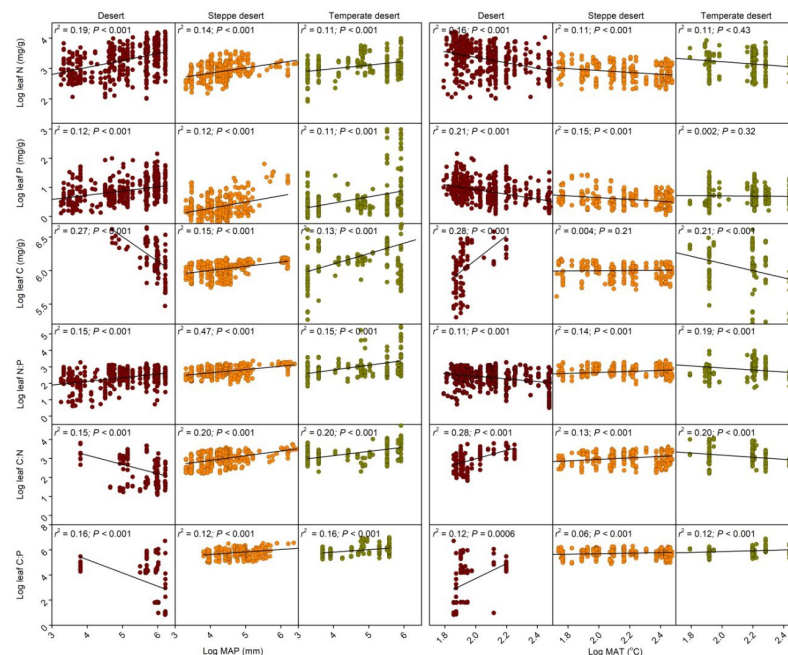


Figure 4. Comparison of the leaf nitrogen (N), phosphorus (P), and carbon (C) concentrations and stoichiometric ratios (C:N and C:P) in relation to the mean annual precipitation (mm) (MAP) and mean annual temperature (°C) (MAT) among desert, steppe desert, and temperate desert ecosystems. The fitting results (r^2 and p -values) are shown in Figure 4.

Furthermore, compared with those of MAP, the leaf N:P ratios were weakly related to MAT across the three desert ecosystems. The leaf C:N and C:P ratios showed negative relationships with MAP and positive relationships with MAT in the desert, while positive relationships of leaf C:N and C:P ratios with MAP and the leaf C:N and C:P ratios remained constant with increasing temperature in the steppe desert and temperate desert. The steppe desert showed weak relationships ($r^2 = 0.06$, $p < 0.001$) compared with the other desert ecosystems.

4. Discussion

By using a dataset of species from three desert ecosystems and a scaling approach, we found variations in stoichiometric scaling exponents across desert ecosystems for the leaf N, root N, and root P contents, reflecting the influences of plant traits and the stability strategies of species found in various geographic locations on nutrient allocation. From an ecological and evolutionary perspective, the nutrient distribution patterns across growth forms and desert ecosystems improve the understanding of species adaptation and ecosystem functioning to overcome climatic challenges. Therefore, we divided the typical desert into three different desert ecosystems, despite earlier studies having focused only on typical deserts.

4.1. Variations in Elements and Stoichiometry among Growth Forms of Organs According to Soil Factors across Three Desert Ecosystems

Our results support previous studies [27,58] showing that leaves display greater N and P concentrations and N:P ratios than roots and soils, possibly due to the metabolic requirements for photosynthetic activities under limited water and nutrient concentrations. These results support previous studies of the steppe region in Xinjiang, China [59], including Northwest China [2,11]. The results from this study showed that leaf traits and N and P patterns possibly cause basic changes across the three desert ecosystems when resource availability and climate conditions are altered, which follow the predictions of the LES. These results also support those of previous studies [29,60]. Furthermore, these results support the hypothesis that desert plants allocate more N and P to leaves than roots, supporting previous findings [59], probably because plants specifically allocate more N for photosynthetic activity [27,58]. Our results showed that the N:P ratios in leaves and roots were affected more by the N content than by the P content, so a total decrease in P in soils was found across terrestrial ecosystems in China [11,43]; this is why N:P ratios are considered good indicators of soil N and P. Furthermore, in desert ecosystems, the C contents were greater in leaves than in roots, consistent with the findings of a previous study showing that high proportions of protein and other C-rich compounds were enriched in leaves [61]. These results are inconsistent with a previous report on a steppe desert [61] in which a lower C content was observed in the leaves than in the roots. This suggested that temperate ecosystems follow a conservative strategy with investment in structure and defence [12,62]. Our analyses revealed that roots, soils, and both growth forms (Figures 1b and 2b) had the lowest P concentrations in the steppe and temperate desert ecosystems of Northeast China, which is consistent with the findings of low leaf P concentrations in previous reports, possibly reflecting low soil P concentrations in Chinese desert ecosystems [2,43]. Overall, studies have shown that the concentrations of N and especially P are lower in Chinese dryland regions. However, these harsh conditions increase the stability of certain general plant organ growth characteristics that could be applied to a wide range of habitats of various species in different desert ecosystems.

Higher N concentrations were detected in the leaves of trees (woody), herbs, shrubs, (woody) and grasses, while higher P concentrations were detected in woody species than in herbs and grasses in the desert ecosystem. The results for the N concentrations are inconsistent with the findings for trees, consistent with the findings for woody shrubs [58], and inconsistent with the findings for P concentrations, which were greater in woody species than in herbaceous plants [2,58] and grass species in desert ecosystems. Compared with herbaceous species, a positive relationship was reported between the soil and organ N

contents for woody species; indeed, woody species use deep roots to acquire soil N, which is why organ N levels may reflect soil N contents [19]. Higher N and P concentrations were detected in the leaves of herbaceous species than in those of grasses or woody species in the steppe desert ecosystem, which is consistent with previous reports [2]. The N:P ratios in the leaves of woody species were greater than those in the leaves of herbaceous plants and grasses, which indicates that different species are variably susceptible to N and P limitations. Compared with those of herbaceous and woody species, lower N and P concentrations were observed for grass species in desert ecosystems, which supports the findings of a previous report [19,62] suggesting that the roots of grasses exhibit somewhat low metabolic activity and slow absorption rates [63,64]. This finding demonstrates the importance of trade-offs in determining the P and C patterns in plants in global desert ecosystems (drylands). Across the different desert ecosystems, lower P concentrations were observed with higher C concentrations; such plants showed conservative nutrient strategies and displayed lower P contents but higher C contents [62,63].

We found variations in the leaf and root N and P concentrations, which were greater in N-fixing species than in non-N-fixing species (Supplementary Materials, Figure S1). These results support the finding [65,66] that the maximum metabolic cost of N fixation is correlated with higher N concentrations [67] and, indirectly, that N-rich cellulose phosphatase leads to increased P concentrations [68]. However, the N:P ratios in leaves and roots were not significantly greater in N-fixing species than in non-N-fixing species (Supplementary Materials, Figure S1), possibly due to the close correlation of N with P contents. These results are in accordance with previous findings in terrestrial ecosystems [69] because N and P are required for plant metabolic activities [13,17]. Additionally, higher N and lower P and C contents were observed in deciduous species than in evergreen species (Supplementary Materials, Figure S2), which supports the findings of previous studies showing higher N contents but inconsistent P contents [1,5]; these results also depend on the lifespans and growth rates of species. It is suggested that the P contents were limited across the different desert ecosystems, which is consistent with previous reports in arid regions [37,70], following the “plant physiology hypothesis” [13,71]. In contrast to the findings of previous studies, especially in desert conditions, evergreen plants employ expensive strategies with high P and C gains [29], and deciduous species may follow conservative strategies and invest more in leaf formation [38]. Thus, this study expands our understanding of the effects of the dynamics of three different desert ecosystems (drylands) with limited element concentrations and ratios on nutrient allocation patterns, and the results are helpful for determining future nutrient limitations and climatic trajectories.

4.2. Variations in Leaf vs. Root N, P, and N:P Scaling Exponents in Different Desert Ecosystems

Our results revealed divergent root and leaf N and P concentrations and N:P ratio allocation strategies across three different desert ecosystems and overall, based on RMA, where α_N is >1 (i.e., more N is allocated to roots than to leaves). Our compiled data also revealed that α_P is <1 (i.e., less P is allocated to roots than to leaves). The changes in the numerical values of the scaling exponent that were reported among studies are expected given the differences in sample sizes [39]. The higher α_N (1.16) and lower α_P (0.74) in the desert ecosystem indicate that more N is allocated to roots than to leaves, while less P is allocated to roots than to leaves. Our results showed a greater metabolic rate in leaves than in roots because of the greater requirement of P for photosynthesis and C partitioning in light–dark cycling [72]; therefore, the leaf and root differences in α_N and α_P likely explain their divergent requirements for N and P in functional and physiological processes [73,74]. Our observations that $\alpha_P < 1$ in the desert ecosystem agree with the findings of [75], who demonstrated a disproportionate increase in leaf P content in relation to the increases in root P content. These results agreed with the “growth rate hypothesis”, which states that plants with greater growth rates need disproportionately more P than N to support rapid protein synthesis [15], thus leading to an N versus P scaling exponent that is less than 1.0 ($\alpha < 1$) [76]. Overall, the values for the three desert ecosystems ($\alpha_N = 0.81$, $\alpha_P = 2.10$,

and $\alpha\text{N:P} = 1.98$) differed from those reported previously, with slightly higher values than those reported at the global scale (0.76) [74] and the regional scale (0.79) [77] but lower values than those reported at the local scale (0.87) [40]. Furthermore, the higher leaf and root N:P ratios in desert (2.11) and temperate desert (1.30) ecosystems may support the soil substrate-age hypothesis, where greater precipitation in areas that are geologically older leads to lower fertility rates and areas that are more highly depleted of P than other areas [34,78]. The influence of soil substrate age on soil P and N availability depends on soil fertility in young and old soils [79], thereby enhancing N:P ratios in the leaves and roots of desert and temperate desert ecosystems.

The αN , αP , and $\alpha\text{N:P}$ ratios differed among the three desert ecosystems. For example, we found different values for αN (>1), αP (<1), and the $\alpha\text{N:P}$ ratio (>1) in desert ecosystems, indicating changes in the allocations of N and P to leaves and roots because of different combinations of stressors, e.g., high temperature and low-P soils [13]; as a result, physiological stressors became the cause of the N and P investments in leaves and roots, respectively. Therefore, N:P ratios are considered indicators of nutrient availability and limited N and P in terrestrial ecosystems [5] and are often considered to be positively correlated with stress tolerance. The relatively high N:P and C:P ratios among plants under dryland conditions reflect slow growth rates and high stress tolerance, possibly because these plants are limited by P compared with other nutrients and drought conditions. In agreement with our results, plants under desert conditions are possibly more limited by P than by C and N with greater aridity [2,19]. Although the N and P concentrations are low in plant metabolic organs (e.g., leaves and roots) in desert ecosystems, they are greater than those in steppe desert ecosystems, which is consistent and inconsistent, respectively, with the finding that both plant N and P contents are low in temperate deserts [35].

In some cases, the N and P concentrations and N:P ratios differed among plant organs, and the metabolic organs (e.g., leaves and roots) had increased nutrient concentrations and N:P ratios compared with structural organs (e.g., stems and coarse roots), which has been reported by previous researchers [27,80]. However, the possible reason that the leaves and roots are involved in the plant photosynthesis, respiration, and nutrient uptake processes is the need for greater nutrient concentrations to sustain plant physiological activity [70]. Consistent with the prediction of PES theory, our results revealed a scaling relationship between N and P in plant organs (e.g., leaves, stems, and roots). This suggested that the nutrient-use strategies of all the organs (surprisingly) varied across the growth forms in the three different desert ecosystems. Therefore, the results of both the present study and of previous studies demonstrate that the PES is applicable for water-related as well as C- and nutrient (i.e., N and P)-related traits across scales [26,27]. Our results indicate that similar and dissimilar isometric relationships between N and P occur among plant leaves and root organs, although previously reported observations showed that N increases rapidly with P in particular organs [29,39]. Thus, heterogeneous environmental conditions and various trade-off strategies caused different leaf and root N and P contents and different leaf and root N:P ratios across the three desert ecosystems.

4.3. Effects of Environmental Conditions on Element Concentrations and Stoichiometry

Shifts in species ranges and abundances are expected to occur with climate change. We hypothesized that along with nutrient concentrations, MAP and MAT are also key drivers of the shifts in and stabilization of elemental concentrations and their ratios in desert ecosystems; for example, climate variables and nutrient limitations in soils influence the biogeographic patterns of root and leaf N and P allocations [13,74]. However, due to the lack of data on the C, N, and P concentrations and their ratios in the roots and soils in our dataset, our understanding of the N and P relationships in the roots and soils with climatic factors is still severely limited. We found that the leaf N and P contents increased with MAP and that the leaf N and P contents decreased with increasing MAT (except in the temperate desert ecosystem, Figure 4, $r^2 = 0.002$, $p = 0.32$). However, because the temperatures in temperate desert ecosystems (40–265 °C) are lower than those in the other

two desert ecosystems, there is no support for the hypothesis that N and P contents increase with MAT; for example, low temperatures suppress biogeochemical processes [13], and interactions with many other processes may limit the degree to which this increase occurs, especially at all but the lowest temperatures [81]. This result showed that biogeographic variations, along with climate variables, had different effects on the total nutrient contents across the desert ecosystems.

According to our results, the three desert ecosystems were limited by P, and these findings were consistent with the low precipitation and high evaporation present in the studied areas [82]. This suggested that these desert plants, through morphological and physiological adjustments, decreased their metabolism rates and resource demands [59] to cope with harsh desert conditions. This result is consistent with the hypothesis that leaf N contents decrease/increase with decreasing/increasing MAP [71] because of the higher leaf N contents of plants in desert ecosystems. These results are widely reported to indicate that plants increase their leaf N contents to increase light availability while decreasing stomatal conductance and transpiration rates [29,59]. Similarly, roots play a key role in nutrient cycling in desert habitats, but leaves are considered to be more important than roots and stems for supporting higher nutrient levels [35,60]. Our analyses showed that in all the studied desert plants, the leaves maintained greater N and P concentrations than did the roots and soil.

With increasing MAP in desert species, the leaf C contents decreased with increasing C:N and C:P ratios, which indicates that the plant leaf C contents in desert ecosystems are highly correlated with MAP in steppe desert and temperate desert ecosystems. At the leaf level, species displayed different responses to climatic variables in the different desert ecosystems. The finding that the C:N and C:P ratios increased (and the N and P contents decreased) with increasing MAT is consistent with previous plant physiology hypotheses that C:N and C:P ratios increase with increasing temperature (T) [13,83]. Surprisingly, the lowest P concentration was detected in roots, followed by leaves, but the P concentration was greater in the soils of the temperate desert ecosystem (Figure 1). Our results are consistent with those of previous studies [13,43]; that is, we did not observe a decrease in leaf N concentrations with decreasing MAT (Figure 4). However, MAT has a significant effect on leaf P concentrations in desert ecosystems, and the leaf P patterns are sensitive to temperature changes [13]; thus, temperature causes a shift in decreasing leaf P contents [27]. Our analyses showed that the leaf N:P ratios increased with MAP across the three desert ecosystems and that this increase was driven by leaf P concentrations, consistent with previous results [84].

The desert species had relatively high leaf N contents, which is explained by the adaptation of these plants to desert conditions and the accumulation of N compounds in their leaves to maintain the water balance [71]. The results demonstrated that roots are responsible for nutrient absorption and transport to leaves, resulting in the maintenance of metabolic activity, which is limited among desert plants by the nutrient contents [59]. This finding agrees with the hypothesis that N limits photosynthesis more than P [85]. Geographic cycles, climatic variables, and divergent N, P, and C contents and their ratios in plant organs and soil maintain plant distributions and ecosystem stability across different desert ecosystems. These results suggest that MAT and MAP play key roles in allocation strategies in leaves across desert ecosystems. Furthermore, the results indicate that leaf and root N, P, and N:P ratios play key roles in explaining variations in the numerical values of scaling exponents, which explains the shift in nutrients in organs of plant growth forms across the three deserts. The three desert ecosystems investigated in this study result from the collective influence of several drivers that led to a shift in nutrient allocation strategies across space. Through different adaptations to limited nutrients in the soil and environmental conditions, different desert plants have developed special survival strategies that help to determine species distributions and desert ecosystem stability. These results have important implications for understanding how plant species and their organs maintain nutrient allocation strategies across different geographic scales in deserts and

highlight the resource and photosynthetic capacities of plant roots and leaves in response to environmental variables.

5. Conclusions

To our knowledge, this is the first study to address the nutrient allocation strategies in plant organs and soil across three different desert ecosystems rather than focusing only on “drylands”. For instance, the plant species extracted from previous studies showed that even by using only three elements, namely, the N, P, and C concentrations in plants and soil, deserts can be differentiated from steppe desert and temperate desert ecosystems and characterized by the dependency of these elements on the organs, the soil, and the MAP and MAT. This study further revealed that the values of root and leaf N vs. P and N:P ratio scaling relationships vary for species growing across three desert ecosystems, which helps us to understand plant growth and ecosystem dynamics. This phenomenon needs to be tested in more diverse desert ecosystems where plant nutrient cycling is sensitive to limited soil nutrients, increased CO₂ concentrations, and climatic factors.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f15040607/s1>, Figure S1: Changes in nitrogen (N), phosphorus (P) concentrations and their stoichiometric ratios in the leaves and roots between N-fixing and Non-N-fixing. Here, (a)–(c) show the N concentrations, P concentrations and N:P ratios in leaves between N-fixing and non-N-fixing, and (d)–(f) show the N and P concentrations and N:P ratios in roots between N-fixing and non-N-fixing. The different letters in each graph indicates significant differences between N-fixing and Non-N-fixing in leaves and roots. Significant difference ($p < 0.05$) was calculated by Student’s *t*-test. The numbers (n) under the box-plot are the number of species for each group; Figure S2: Changes in nitrogen (N), phosphorus (P) and carbon (C) concentrations in the leaves between deciduous and evergreen species when all pooled data were together. Here, (a) show the comparison of N concentrations, (b) P concentrations, and (c) the C concentrations. Different letters in each graph indicates the significant differences between deciduous and evergreen species (Student’s *t*-test, $p < 0.05$). The numbers (n) under the box-plot are the number of species for each group; Table S1: Complete the basic information for the three different desert ecosystem and related climatic variables; Table S2: Comparison of the three different ecosystem types for different elements in root and soil for growth forms. References [14,25,41–56] are cited in the Supplementary Materials.

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