Postprint: Response of Stoichiometric Characteristics of Desert Black Goji Berry (Lycium ruthenicum) to Nitrogen and Phosphorus Addition Ratios and Levels

Authors: Li Jinxia

Date: 2021-12-14T00:00:00+00:00

Abstract

Plant stoichiometric characteristics are crucial for elucidating the responses of biogeochemical and ecological processes to global change. Investigating the effects of different nitrogen and phosphorus (N, P) addition treatments on the ecological stoichiometric characteristics of desert plants can provide insights into plant responses to environmental changes from a stoichiometric perspective and offer ideas for predicting plant-nutrient interactions under global change scenarios. Using Lycium ruthenicum as the study material, three levels and ratios of N and P addition were established to examine the responses of L. ruthenicum C:N:P stoichiometric characteristics to N and P additions through a field experiment, with comparative analysis of stoichiometric traits among organs. The results showed that: (1) N and P additions had minor effects on carbon (C) content in different organs of L. ruthenicum; with increasing N and P addition amounts, fine root N content increased significantly; with increasing N:P addition ratios, non-root organ N content increased significantly while root system P content decreased significantly; the interactive effects of N:P addition ratio and amount significantly affected N and P contents in roots and fruits, as well as stem P content. (2) Low N:P addition ratio treatment decreased organ C/P ratio and increased C/N ratio, whereas high N:P addition ratio treatment showed the opposite pattern; N/P ratios in various organs remained relatively stable; L. ruthenicum offset changes in environmental elemental stoichiometry by adjusting nutrient conservation strategies through conservative nutrient utilization. (3) Stoichiometric characteristics of L. ruthenicum demonstrated functional differentiation among organs: leaf N content and N/P were significantly higher than other organs; stem C/N was the highest; coarse root C content and C/P were the highest; fine root N, P contents and N/P were relatively high; fruit P content was the highest. Relative to C, metabolically active organs (leaves, fine roots, fruits) required more N and P than metabolically inactive organs (stems, coarse roots). The findings contribute to a better understanding of desert plant stoichiometric responses to N and P additions from the perspective of element-plant functional relationships.

Full Text

Response of Stoichiometric Characteristics of Desert *Lycium ruthenicum* to Nitrogen and Phosphorus Addition Ratios and Levels

LI Jinxia, CHEN Nianlai, SUN Xiaomei, LI Fakui, YU Jieru
College of Resources and Environmental Sciences, Gansu Agricultural University, Lanzhou 730070, Gansu, China

Abstract

Plant stoichiometric characteristics are crucial for elucidating biogeochemical and ecological processes and their responses to global change. Investigating the effects of nitrogen (N) and phosphorus (P) addition treatments on the ecological stoichiometry of desert plants can help understand plant responses to environmental changes from a stoichiometric perspective and provide insights for predicting plant-nutrient interactions under global change scenarios. Using *Lycium ruthenicum* as the experimental material, we established three N:P supply ratios and three supply levels in a field experiment to examine how these factors affect the C:N:P stoichiometric features of different organs. The results indicated that: (1) N and P additions had minimal impact on carbon (C) content across organs, while nitrogen content in fine roots increased significantly with rising N,P supply levels. As the N:P supply ratio increased, nitrogen content in non-root organs rose substantially and phosphorus content in the root system declined. The interactive effects of N:P supply ratio and level significantly influenced the N and P contents in roots and fruits, as well as phosphorus content in stems. (2) Low N:P addition ratios decreased organ C:P ratios while increasing C:N ratios, whereas high N:P ratios produced the opposite pattern. Each organ maintained relatively stable N:P ratios, suggesting that *Lycium ruthenicum* offset environmental changes in elemental stoichiometry through conservative nutrient utilization strategies adjusted via nutrient retention mechanisms. (3) Stoichiometric characteristics exhibited clear organ-specific differences. Leaves showed significantly higher nitrogen content and N:P ratios than other organs, while stems had the highest C:N ratios, coarse roots had the highest carbon and phosphorus contents, fruits had the highest phosphorus content, and fine roots also exhibited elevated N:P ratios. Compared with carbon, metabolically active organs (leaves, fine roots, fruits) required substantially more nitrogen and phosphorus than structural organs (stems, coarse roots). These findings enhance our understanding of how desert plant stoichiometric properties respond to nitrogen and phosphorus additions from the perspective of elemental composition and plant functional ecology.

Keywords: stoichiometric characteristics; N,P supply level; N,P supply ratio; *Lycium ruthenicum*

1. Materials and Methods

Carbon, nitrogen, and phosphorus are the most important elements for plant construction and metabolic processes. As essential nutrients for plant growth, they determine key physiological processes such as photosynthetic carbon fixation and cellular biosynthesis, and typically become limiting elements for primary production. Changes in ecosystem nutrient cycles may alter the C:N:P stoichiometry in soil-plant systems. Conversely, the flexibility of plant organ stoichiometry can influence natural ecosystem material cycling, composition, structure, and function by altering plant physiological activity. Plant tissue nutrient content and concentration ratios reflect the balance between carbon fixation and nutrient uptake during growth, holding significant importance for fundamental ecological processes like primary production and material cycling. Plant responses to nitrogen addition and climate change are mediated through changes in C:N:P stoichiometry, which affects critical ecological processes including litter decomposition, species diversity, and environmental stress tolerance. However, the mechanisms by which nitrogen addition alters plant organ stoichiometry remain unclear, and understanding of plant growth processes and mechanisms is limited.

Plant metabolic demands for specific elements are influenced by environmental supply and biological stress factors. Numerous studies have linked plant and soil nutrient concentrations to infer soil nutrient limitations and plant responses to environmental changes based on C:N:P stoichiometric relationships. To date, most studies on plant stoichiometry have focused exclusively on leaves or entire plants. Kerkhoff et al. analyzed C:N:P stoichiometry across roots, stems, leaves, and reproductive organs in 1,280 seed plant species, finding that woody and herbaceous groups differed in nitrogen content and N:P ratios, with these differences being more pronounced in roots and stems than in leaves and reproductive structures. As plant tissues differentiate into roots, stems, leaves, and fruits, functional specialization occurs, leading to organ-specific C:N:P ratios based on function (photosynthesis, support, storage, reproduction). Leaves with high chloroplast proportions contain more nitrogen per unit dry weight than stems or roots and exhibit higher N:P ratios. Reproductive structures typically have higher nutrient concentrations than vegetative structures. Compared with leaves, stems and roots serve different nutrient functions and have longer lifespans, making them better indicators of long-term environmental changes. Plant size, biomass, and functional relationships depend on stoichiometric composition and its allocation between metabolically active and structural tissues. As support structures, stems require carbon-rich structural materials, while fastgrowing species invest in nitrogen-rich metabolically active tissues to rapidly convert photosynthates into growth. The extent to which stoichiometric patterns respond to environmental conditions, and which organs maintain relatively fixed elemental compositions to execute their functions, remains an unresolved question. Therefore, to better understand ecological stoichiometry from an element-function perspective, it is necessary to investigate different plant tissues rather than focusing solely on leaves.

The northwestern arid desert region represents a typical ecologically fragile and sensitive zone, where nitrogen and phosphorus are critical factors limiting plant growth. *Lycium ruthenicum* is an important species for desert control in this region, offering excellent ecological adaptability and comprehensive benefits that significantly impact species regeneration, community reconstruction, and ecosystem productivity. Nitrogen and phosphorus additions can improve plant growth and enhance community productivity, making studies on desert plant responses to nutrient additions crucial for vegetation restoration and maintenance of desert ecosystem productivity. Most research on plant organ stoichiometry has concentrated on nitrogen addition while neglecting phosphorus content and N:P ratios. Given the importance of roots and other organs, and the limited information on stoichiometric responses of desert plants to combined N and P additions, this study examined *L. ruthenicum* through field nutrient addition experiments to investigate how C:N:P stoichiometric characteristics respond to N:P supply ratios and levels, and to compare inter-organ stoichiometric differences. This research provides insights for interpreting organ functions and understanding survival adaptation strategies of desert plants in heterogeneous habitats, which is essential for ecosystem conservation, restoration, and sustainable management in northwestern arid desert regions.

The experiment was conducted in the Minqin Oasis at the lower reaches of the Shiyang River. Before fertilization, the basic physicochemical properties of the 0-20 cm sandy loam were determined: soil water content 12.79%, organic matter content 10.47 $g \cdot kg^{-1}$, total nitrogen 0.75 $g \cdot kg^{-1}$, total phosphorus 0.64 $g \cdot kg^{-1}$, available phosphorus 47.49 $mg \cdot kg^{-1}$, and alkali-hydrolyzable nitrogen 16.48 $mg \cdot kg^{-1}$.

1.1 Experimental Material and Design Using three-year-old *L. ruthenicum* as experimental material, plants were arranged in furrow-ridge planting with row spacing of 1.8 m and plant spacing of 0.7 m, achieving a planting density of 0.8 $plants \cdot m^{-2}$. Following Güsewell' s protocol, we established three N:P supply ratios (5:1, 15:1, and 45:1) and three N,P supply levels (low, medium, and high), creating nine treatment combinations. The supply levels were calculated based on pure N and P_2O_5 application rates of 148.35 $kg \cdot hm^{-2}$, 49.45 $kg \cdot hm^{-2}$, and 16.48 $kg \cdot hm^{-2}$, respectively. Urea (46% N) and superphosphate (18% P_2O_5) were applied as fertilizers in mid-June through single-plant hole application, followed by immediate irrigation. Each treatment was replicated three times.

1.2 Sample Collection and Measurement In early September, three plants with similar growth vigor were selected from each plot. From each plant, three branches of the same order were cut, and fully expanded leaves from the middle of branches without pest damage were collected. Mature fruits from the same branch order were harvested, and corresponding underground root systems were obtained using excavation methods. After washing, roots were separated into coarse roots (diameter $ 2*mm*)*andfineroots*(*diameter* < 2*mm*).*Allcollectedcoarseroots*, *fineroots*, *stems*, *leaves*, *andfruitswereoven* − *driedat*105°*Cfor*0.5*h*, *thenat*75°*Ctoconstantmass*, *andfinallygroundandpassedthrougha*0.15*mmsieveforC*, 1 *dried*, *andsievedthrougha*1*mmmesh*.*Plantandsoilorganiccarbon*, *totalnitrogen*, *andtotalphosphorusweremea* *heatingmethod*, *Kjeldahlnitrogendeterminationmethod*, *andmolybdenum* − *antimonycolorimetricmethod*, *respectively*, *withresultsexpressedasnutrientcontentperunitmass*(*mg*· *g*^{-1}$).

1.3 Data Analysis Two-way ANOVA was used to test the effects of N,P supply level, supply ratio, and their interactions on *L. ruthenicum* organ C:N:P stoichiometric characteristics. One-way ANOVA was employed to examine differences in C:N:P stoichiometric ratios among organs under the same supply level or ratio, with Duncan' s method for multiple comparisons. Statistical analysis was performed using SPSS 18.0, and graphs were created with GraphPad Prism 8.

2. Results

2.1.1 Root Stoichiometric Responses to N and P Addition Nitrogen-phosphorus supply ratio significantly or extremely significantly affected coarse root nitrogen content, C:P ratio, and N:P ratio; N,P supply level significantly or extremely significantly influenced coarse root phosphorus content and C:N ratio; and their interaction significantly or extremely significantly affected coarse root nitrogen content, phosphorus content, and C:N ratio (Table 1). Under the same N:P supply ratio or level, coarse root C, N, P contents and ratios did not show consistent patterns with changing supply levels or ratios (Fig. 1). At N:P ratio of 5:1, coarse root C:N ratio decreased with increasing supply level, while phosphorus content first increased then decreased. At N:P ratio of 15:1, coarse root C:N ratio first decreased then increased, with the medium supply level being significantly lower than high and low levels.

Nitrogen-phosphorus supply level significantly affected fine root nitrogen content, while supply ratio and its interaction with supply level significantly affected fine root nitrogen, phosphorus, and C:N ratio (Table 1). Under the same N:P ratio, fine root nitrogen content showed no significant change with supply level, while phosphorus content first increased then decreased. At N:P ratio of 5:1, fine root C:N ratio first decreased then increased, showing opposite trends at N:P ratios of 15:1 and 45:1. Under the same supply level, fine root nitrogen content significantly decreased with increasing N:P ratio, while C:N ratio significantly increased (Fig. 2). Mean coarse root and fine root C:N:P ratios were

367.5:15.8:1.8 and 367.5:20.2:1.9, respectively.

2.1.2 Stem Stoichiometric Responses to N and P Addition Nitrogen-phosphorus supply ratio extremely significantly affected stem nitrogen content, C:P ratio, and N:P ratio; supply level significantly affected stem phosphorus content and C:N ratio; and their interaction significantly affected stem phosphorus content and C:N ratio (Table 1). Under the same N:P ratio, stem nitrogen content first increased then decreased with rising supply level, while phosphorus content showed no consistent pattern (Fig. 3). At N:P ratio of 5:1, stem C:N ratio decreased with increasing supply level, while C:P ratio increased. Under the same supply level, stem nitrogen content generally decreased with increasing N:P ratio, while C:N ratio first decreased then increased, with medium and high supply levels significantly higher than low level. At high supply level, stem nitrogen content significantly decreased with increasing N:P ratio, while C:P ratio increased. Mean stem C:N:P ratio was 367.5:15.8:1.8, with ranges of 32.3-38.0 mg · g^{-1} for carbon, 1.6-2.1 mg · g^{-1} for nitrogen, and 15.2-22.6 mg · g^{-1} for phosphorus.

2.1.3 Leaf Stoichiometric Responses to N and P Addition Nitrogen-phosphorus supply ratio significantly or extremely significantly affected leaf nitrogen content, phosphorus content, C:N ratio, C:P ratio, and N:P ratio; supply level significantly affected leaf C:N ratio and C:P ratio; and their interaction significantly affected leaf C:N ratio (Table 1). Under the same N:P ratio, leaf nitrogen content showed an initial increase followed by a decrease with rising supply level, while phosphorus content remained essentially unchanged (Fig. 4). At N:P ratio of 5:1, leaf C:N and C:P ratios decreased with increasing supply level. Under the same supply level, leaf nitrogen content decreased with increasing N:P ratio, while C:N ratio first decreased then increased. At low and medium supply levels, leaf C:P ratio significantly decreased with increasing N:P ratio. Mean leaf C:N:P ratio was 367.5:36.2:1.8, with ranges of 11.3–39.0% for carbon, 19.1-24.7 mg · g^{-1} for nitrogen, and 1.2-2.5 mg · g^{-1} for phosphorus.

2.1.4 Fruit Stoichiometric Responses to N and P Addition Nitrogen-phosphorus supply ratio extremely significantly affected fruit nitrogen content, phosphorus content, C:N ratio, C:P ratio, and N:P ratio; supply level significantly affected fruit C:N ratio and C:P ratio; and the interaction between ratio and level significantly affected fruit C:N ratio (Table 1). Fruit nitrogen and phosphorus contents did not change significantly with N:P ratio or supply level. Fruit C:N and C:P ratios generally decreased with increasing supply level (Fig. 5). Under the same supply level, fruit C:N and C:P ratios increased with increasing N:P ratio. At low N,P supply level, N:P ratios of 15:1 and 45:1 increased C:N ratio by 39.0% and 81.5%, and C:P ratio by 18.4% and 31.9%, respectively, compared with N:P ratio of 5:1. Mean fruit C:N:P ratio was 367.5:20.2:1.9.

2.2 Soil Stoichiometric Responses to N and P Addition Nitrogen-phosphorus supply level significantly affected soil total phosphorus; supply ratio significantly or extremely significantly affected soil total nitrogen and soil N:P ratio; and their interaction significantly affected soil N:P ratio (Table 2). Soil organic carbon, total nitrogen, and total phosphorus contents showed no consistent patterns with N:P ratio or supply level (Fig. 6). Organic carbon content first increased then decreased with increasing N:P ratio at low and medium supply levels. Total nitrogen content increased with both supply level and N:P ratio, while total phosphorus content decreased with increasing N:P ratio and supply level. Mean soil organic carbon, total nitrogen, and total phosphorus contents were 5.94 $g \cdot kg^{-1}$, 0.64 $g \cdot kg^{-1}$, and 0.63 $g \cdot kg^{-1}$, respectively, with C:N:P ratios ranging from 4.93–7.03 $g \cdot kg^{-1}$, 0.53–0.81 $g \cdot kg^{-1}$, and 0.52–0.76 $g \cdot kg^{-1}$. Soil N:P ratio varied considerably across treatments, reaching maximum values (12.62) at medium supply level with N:P ratio of 45:1, and minimum values (6.54) at medium supply level with N:P ratio of 5:1.

2.3 Inter-Organ Differences in Stoichiometric Characteristics The C:N:P stoichiometry of *L. ruthenicum* differed significantly among organs (Fig. 7). For nitrogen content, coarse roots, fine roots, stems, and fruits were 124.6%, 75.8%, 58.9%, and 30.3% higher than leaves, respectively. For phosphorus content, fruits were significantly higher than other organs. For carbon content, coarse roots were highest, followed by stems and fine roots, with leaves being lowest. For C:N ratio, stems were highest, followed by coarse roots, fine roots, and fruits, with leaves being lowest. For C:P ratio, coarse roots were highest, followed by stems and fine roots, with leaves being lowest. For N:P ratio, leaves were significantly higher than other organs, while fine roots were also relatively high. These differences reflect that metabolically active organs require more nitrogen and phosphorus than non-metabolically active structural organs.

3. Discussion

3.1 Effects of N and P Supply Conditions on Ecological Stoichiometry Stoichiometric characteristics reflect plant nutrient utilization strategies and are susceptible to environmental changes. Nitrogen and phosphorus additions significantly increased nitrogen content in *L. ruthenicum* organs while decreasing leaf phosphorus content. The carbon content in roots, stems, and leaves decreased with increasing N:P supply ratio, yet nitrogen and phosphorus additions did not significantly alter carbon content across organs, leading to changes in organ C:N:P stoichiometry. These patterns align with previous studies. Carbon, as a structural element, plays a skeletal role in plants and is less affected by environmental changes. When N:P supply ratio was 5:1, organ nitrogen content increased with supply level, while leaf nitrogen content decreased with increasing N:P ratio. At high N:P ratios, soil phosphorus limitation and increased plant biomass after fertilization may have caused nutrient dilution effects. Nitrogen addition significantly increased nitrogen content in stems and leaves of woody and herbaceous plants but did not significantly affect root nitrogen content. In this study, increasing N,P supply level significantly enhanced nitrogen content in all organs. When N:P ratio was 5:1, organs maintained relatively high nitrogen content, indicating strong nitrogen retention capacity in nitrogen-rich environments. At N:P ratio of 45:1, organ nitrogen content decreased, suggesting that phosphorus limitation under high nitrogen addition affected nitrogen retention capacity. Due to long-term adaptation to specific abiotic and biotic environments, elemental stoichiometry undergoes evolutionary trade-offs under particular strategies. Homeostatic regulation is the biological mechanism controlling internal elemental composition. The effects of N,P addition on plant stoichiometry may be influenced by soil nutrient content, climate, vegetation type, and other factors. *Lycium ruthenicum* adjusted its nutrient retention strategy to offset changes in elemental stoichiometry, minimizing dependence on soil nutrients.

3.2 Relationship Between Stoichiometric Characteristics and Organ Function Plant organs perform multiple biological functions ensuring normal growth and successful reproduction. Resource absorption by roots, support and hydraulic processes by stems, photosynthetic carbon fixation by leaves, sexual reproduction by seeds, and vegetative regeneration and resource storage by clonal organs all depend on organ form, quantity, and elemental composition. Nutrient allocation includes strategic utilization of different nutrients within specific organs and allocation of the same nutrient among organs, reflecting relative investment in different organs. The allocation of limiting resources like nitrogen and phosphorus represents an important plant adaptation strategy to environmental change. Many studies have found stoichiometric differences among organs. This study revealed that N,P addition significantly altered C:N:P stoichiometry in roots, stems, leaves, and fruits of *L. ruthenicum*, demonstrating clear organ-specific differences. Nutrients can limit plant growth and play important roles in plant function, with different organs having varying nutrient requirements based on their functions.

The N:P ratio is recognized as an effective indicator of plant responses to environmental nutrient status and homeostatic regulation of nutrient assimilation. Leaf function depends on nutrients absorbed by fine roots. Studies show leaf nitrogen and phosphorus concentrations are higher than in other organs, consistent with our results. This primarily reflects high metabolic and photosynthetic activity in leaves containing abundant nitrogen-rich Rubisco, while plants in arid environments tend to have higher nutrient concentrations in leaves. The leaf nitrogen content of *L. ruthenicum* ($35.43\ \mathrm{mg \cdot g^{-1}}$) was significantly higher than global, national, and northern desert region averages (20.1, 20.2, and $24.45\ \mathrm{mg \cdot g^{-1}}$, respectively), while leaf phosphorus content ($1.84\ \mathrm{mg \cdot g^{-1}}$) approximated these scales (1.77, 1.46, and $1.74\ \mathrm{mg \cdot g^{-1}}$), indicating certain conservatism in leaf phosphorus content. Stems serve as important intermediates connecting leaves and roots, facilitating nutrient and water transport to support root and leaf functions. The certain nitrogen content in stems supports high rates of photosynthate transport and photosynthetic activity, though stems contain fewer nutrients than leaves and fine roots at the individual level. Studies have shown higher C:N ratios in stems compared with other organs, consistent with our findings on *L. ruthenicum*, indicating that lignin-rich structural organs require more carbon-rich structural materials, reflecting high carbon investment in support structures.

When characterizing plant ecological strategies, nutrient allocation to reproductive tissue plays a central role. *Lycium ruthenicum* fruits had relatively high nitrogen and phosphorus contents, reflecting the nutrient demands and metabolic activity of reproductive organs. This study also found that root C:N ratio increased with root diameter, while root N:P ratio decreased with increasing diameter, consistent with Ma et al. Different diameter roots differ in morphological, anatomical, and physiological characteristics. Fine root growth depends on carbohydrates fixed by leaves and is metabolically most active, participating in water and nutrient capture. Fine roots serve as key elements for carbon sequestration and play important roles in nutrient cycling in terrestrial ecosystems. Root stoichiometry aligns with the physiological functions of corresponding root diameters, with many studies demonstrating high nitrogen content in fine roots, exhibiting higher respiration rates, turnover rates, and active nutrient absorption. In contrast, coarse roots with low nitrogen content perform water transport and nutrient storage functions, having lower respiration rates. Fine root nitrogen content in *L. ruthenicum* was 22.0% higher than in coarse roots, representing relatively high nutrient returns, while coarse roots showed the highest C:N ratio. Nitrogen addition changes belowground carbon allocation and nutrient distribution in ecosystems, altering plant growth strategies. Fine root nitrogen and phosphorus contents were 11.4% and 72.4% higher than in stems, respectively, indicating high metabolic activity in fine roots and greater nitrogen demand for synthesizing carrier enzymes that actively absorb soil nutrients. Additionally, desert plants adapted to arid habitats tend to invest more nitrogen in fine roots to improve water and nutrient use efficiency.

4. Conclusions

1) Nitrogen and phosphorus additions primarily affected *L. ruthenicum* growth by altering organ nitrogen and phosphorus contents, yet each organ maintained relatively stable C:N:P stoichiometry. *Lycium ruthenicum* offset changes in elemental stoichiometry through adjusted nutrient retention strategies and conservative nutrient utilization.

2) Organ stoichiometric characteristics in *L. ruthenicum* reflected functional differences, demonstrating higher nutrient returns in metabolically active tissues and high carbon investment in storage and support structures. Metabolically active organs (leaves, fine roots, fruits) required more nitrogen and phosphorus than structural organs (stems, coarse roots).

References

[1] Zhou Xin, Zuo Xiao' an, Zhao Xueyong, et al. Ecological stoichiometry of plant and leaf carbon and nitrogen in different habitats of Horqin Sandy Land[J]. Arid Land Geography, 2015, 38(3): 565-575.

[2] Sterner R W, Elser J J. Ecological stoichiometry: The biology of elements from molecules to the biosphere[M]. Princeton: Princeton University Press, 2002.

[3] Li Congjuan, Xu Xinwen, Sun Yongqiang, et al. Stoichiometric characteristics of C, N, P for three desert plants leaf and soil at different habitats[J]. Arid Land Geography, 2014, 37(5): 996-1004.

[4] Peñuelas J, Poulter B, Sardans J, et al. Human induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe[J]. Nature Communications, 2013, 4(1): 2934, doi: 10.1038/ncomms2934.

[5] Imran M, Gurmani Z A. Role of macro and micro nutrients in the plant growth and development[J]. Science, Technology and Development, 2011, 30(3): 36-40.

[6] Marklein A R, Houlton B Z. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems[J]. New Phytologist, 2012, 193(3): 696-704.

[7] Huang W J, Houlton B Z, Marklein A R, et al. Plant stoichiometric responses to elevated CO_2 vary with nitrogen and phosphorus inputs: Evidence from a global-scale meta-analysis[J]. Scientific Reports, 2015, 5(1): 1-8.

[8] Mo Q F, Zou B, Li Y W, et al. Response of plant nutrient stoichiometry to fertilization varied with plant tissues in a tropical forest[J]. Scientific Reports, 2015, 5: 14605, doi: 10.1038/srep14605.

[9] Sardans J, Rivas-Ubach A, Peñuelas J. The C:N:P stoichiometry of organisms and ecosystems in a changing world: A review and perspectives[J]. Perspectives in Plant Ecology, Evolution & Systematics, 2012, 14(1): 33-47.

[10] Sardans J, Peñuelas J. Climate and taxonomy underlie different elemental concentrations and stoichiometries of forest species: The biogeochemical niche[J]. Plant Ecology, 2014, 215(4): 441-455.

[11] Wang Chuncheng, Ma Songmei, Zhang Dan, et al. Spatial genetic structure of *Lycium ruthenicum* in the Qaidam Basin[J]. Chinese Journal of Plant Ecology, 2020, 44(6): 661-668.

[12] Güsewell S. High nitrogen:phosphorus ratios reduce nutrient retention and second year growth of wetland sedges[J]. New Phytologist, 2005, 166(2): 537-550.

[13] Persson J, Fink P, Goto A, et al. To be or not to be what you eat: Regulation of stoichiometric homeostasis among autotrophs and heterotrophs[J]. Oikos,

2010, 119(5): 741-751.

[14] Huang J Y, Wang P, Niu Y B, et al. Changes in C:N:P stoichiometry modify N and P conservation strategies of a desert steppe species *Glycyrrhiza uralensis*[J]. Scientific Reports, 2018, 8(1): 1-9.

[15] Bao Shidan. Soil agro-chemistrical analysis[M]. 3rd ed. Beijing: China Agriculture Press, 2007: 268-270, 389-391.

[16] Wang Z N, Lu J Y, Yang M, et al. Stoichiometric characteristics of carbon, nitrogen, and phosphorus in leaves of differently aged *Medicago sativa* (lucerne) stands[J]. Frontiers in Plant Science, 2015, 6: 1062, doi: 10.3389/fpls.2015.01062.

[17] Tian H, Chen G, Zhang C, et al. Pattern and variation of C:N:P ratios in China' s soils: A synthesis of observational data[J]. Biogeochemistry, 2010, 98(1/3): 139-151.

[18] Liang Xingyun. Leaf functional traits and ecological stoichiometry of the dominant tree species along forest succession of Korean pine broad-leaved mixed forest in Changbai Mountain, northeastern China[D]. Beijing: Chinese Academy of Forestry, 2017.

[19] Li Yulin, Mao Wei, Zhao Xueyong, et al. Leaf nitrogen and phosphorus stoichiometry in typical desert and desertified regions, north China[J]. Environmental Science, 2010, 31(8): 1716-1725.

[20] Li W B, Jin C J, Guan D X, et al. The effects of simulated nitrogen deposition on plant root traits: A meta-analysis[J]. Soil Biology & Biochemistry, 2015, 82: 112-118.

[21] Li L, Liu B, Gao X P, et al. Nitrogen and phosphorus addition differentially affect plant ecological stoichiometry in desert grassland[J]. Scientific Reports, 2019, 9: 18673, doi: 10.1038/s41598-019-55110-0.

[22] Zhan S X, Wang Y, Zhu Z C, et al. Nitrogen enrichment alters plant N:P stoichiometry and intensifies phosphorus limitation in a steppe ecosystem[J]. Environmental and Experimental Botany, 2017, 134: 21-32.

[23] Chen G T, Tu L H, Peng Y, et al. Effect of nitrogen additions on root morphology and chemistry in a subtropical bamboo forest[J]. Plant and Soil, 2017, 412: 441-451.

[24] Mayor J R, Wright S J, Turner B L. Species-specific responses of foliar nutrients to long-term nitrogen and phosphorus additions in a lowland tropical forest[J]. Journal of Ecology, 2014, 102(1): 36-44.

[25] Kleyer M, Minden V. Why functional ecology should consider all plant organs: An allocation-based perspective[J]. Basic and Applied Ecology, 2014, 16(1): 1-9.

[26] Reich P B, Oleksyn J. Global patterns of plant leaf N and P in relation to temperature and latitude[J]. Proceedings of the National Academy of Sciences of the United States of America, 2004, 101(30): 11001-11006.

[27] Han W X, Fang J Y, Guo D L, et al. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China[J]. New Phytologist, 2005, 168(2): 377-385.

[28] Li H, Li J, He Y L, et al. Changes in carbon, nutrients and stoichiometric relations under different soil depths, plant tissues and ages in black locust plantations[J]. Acta Physiologiae Plantarum, 2013, 35(10): 2951-2964.

[29] Ma Yuzhu, Zhong Quanlin, Jin Bingjie, et al. Spatial changes and influencing factors of fine root carbon, nitrogen and phosphorus stoichiometry of plants in China[J]. Chinese Journal of Plant Ecology, 2015, 39(2): 159-166.

[30] Freschet G T, Cornwell W K, Wardle D, et al. Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide[J]. Journal of Ecology, 2013, 101(4): 943-952.

[31] Wang G, Fahey T J, Xue S, et al. Root morphology and architecture respond to N addition in *Pinus tabuliformis*, west China[J]. Oecologia, 2012, 171(2): 583-590.

[32] Treseder K K, Vitousek P M. Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests[J]. Ecology, 2001, 82(4): 946-954.

[33] Jing H, Zhou H X, Wang G L, et al. Nitrogen addition changes the stoichiometry and growth rate of different organs in *Pinus tabuliformis* seedlings[J]. Frontiers in Plant Science, 2017, 8: 1922, doi: 10.3389/fpls.2017.01922.

[34] Cui Q, Xiao T L, Wang Q B, et al. Nitrogen fertilization and fire act independently on foliar stoichiometry in a temperate steppe[J]. Plant and Soil, 2010, 334(1): 209-219.

[35] Sun Xiaomei, He Mingzhu, Zhou Bin, et al. Non-structural carbohydrates and C:N:P stoichiometry of roots, stems, and leaves of *Zygophyllum xanthoxylon* in responses to xeric condition[J]. Arid Land Geography, 2021, 44(1): 240-249.

[36] Shi Xianmeng, Qi Jinhua, Song Liang, et al. C, N and P stoichiometry of two dominant seedlings and their responses to nitrogen additions in the montane moist evergreen broad-leaved forest in Ailao Mountains, Yunnan[J]. Chinese Journal of Plant Ecology, 2015, 39(10): 962-970.

[37] Yu Hua, Pan Zongtao, Chen Zhiqiang, et al. Effects of nitrogen addition on soil chemical properties and leaf functional traits of *Dicranopteris dichotoma* in the red soil erosion area of southern China[J]. Chinese Journal of Applied and Environmental Biology, 2020, 26(4): 1-11.

[38] Elser J J, Fagan W F, Denno R F, et al. Nutritional constraints in terrestrial and freshwater food webs[J]. Nature, 2000, 408(6812): 578-580.

[39] Sistla S A, Schimel J P. Stoichiometric flexibility as a regulator of carbon and nutrient cycling in terrestrial ecosystems under change[J]. New Phytologist, 2012, 196(1): 68-78.

[40] Zhang S B, Zhang J L, Slik J W F, et al. Leaf element concentrations of terrestrial plants across China are influenced by taxonomy and the environment[J]. Global Ecology & Biogeography, 2012, 21(8): 809-818.

[41] Aerts R, Chapin F. The mineral nutrition of wild plants revisited: evaluation of processes and patterns[J]. Advances in Ecological Research, 1999, 30: 1-67.

[42] Agren G. Stoichiometry and nutrition of plant growth in natural communities[J]. Annual Review of Ecology, Evolution & Systematics, 2008, 39(1): 153-170.

[43] Minden V, Kleyer M. Internal and external regulation of plant organ stoichiometry[J]. Plant Biology, 2014, 16(5): 897-907.

[44] Güsewell S. N:P ratios in terrestrial plants: Variation and functional significance[J]. New Phytologist, 2010, 164(2): 243-266.

[45] Xu Z H, Chen C R, He J Z, et al. Trends and challenges in soil research 2009: Linking global climate change to local long-term forest productivity[J]. Journal of Soils and Sediments, 2009, 9(2): 83-91.

[46] Elser J J, Fagan W F, Kerkhoff A J, et al. Biological stoichiometry of plant production: Metabolism, scaling and ecological response to global change[J]. New Phytologist, 2010, 186(3): 593-608.

[47] Peñuelas J, Sardans J. The C:N:P stoichiometry of organisms and ecosystems in a changing world: A review and perspectives[J]. Perspectives in Plant Ecology, Evolution & Systematics, 2012, 14(1): 33-47.

[48] Wright S J, Turner B L. Species-specific responses of foliar nutrients to long-term nitrogen and phosphorus additions in a lowland tropical forest[J]. Journal of Ecology, 2014, 102(1): 36-44.

[49] Kerkhoff A J, Fagan W F, Elser J J, et al. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants[J]. The American Naturalist, 2006, 168(4): E103-E122.

[50] He J S, Wang L, Flynn D F B, et al. Leaf nitrogen:phosphorus stoichiometry across Chinese grassland biomes[J]. Oecologia, 2008, 155(2): 301-310.

Note: Figure translations are in progress. See original paper for figures.

Source: ChinaXiv —Machine translation. Verify with original.