

# Ecological Stoichiometry within Plant Organs of Four Forest Trees in Sygera National Forest

Jiaxiang Wang,<sup>a</sup> Luqi Wang,<sup>b</sup> and Yueyao Li<sup>c,\*</sup>

Four typical forest types in Sygera Mountain, namely, *Pinus armandii* (PA), *Picea likiangensis* var. *linzhiensis* (PLL), *Abies georgei* var. *smithii* (AGS), and *Juniperus saltuaria* (JS) were considered using methods such as analysis of variance and stoichiometry. Effects of changes of nutrient content and stoichiometric ratio of various organs of arbor plants were evaluated. Compared with global plant nutrients, this study area had lower N and P contents. The growth of the *Juniperus saltuaria* forest was jointly restricted by N and P, and as the environmental gradient decreased, the growth of the other three forest types changed from N and P joint restrictions to N restrictions. The distribution order of element content in various organs among different forest types was consistent as follows: leaf>branch>root>trunk. There was a strong domestication reaction between N and P contents. This led to a significantly higher C/N ratio of the square branch Berlin compared to the other three forest types, while the C/P and N/P ratios were opposite. This may be due to the "optimal allocation principle" of nutrients in various organs under different environmental conditions. The nutrient allocation patterns of plant organs in different forest types were not the same, which reflects the differences in life strategies and nutrient utilization among different forest species.

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Contact information: a: School of Chemical and Environmental Engineering, Wuhan Polytechnic University, Wuhan 430023, China; b: Anhui Agricultural University, Anhui 230036, China; c: Institute of Tibet Plateau Ecology, Tibet Agricultural & Animal Husbandry University, Nyingchi 860000, China; \* Corresponding author: liyueyao370@163.com

## INTRODUCTION

Ecological stoichiometry uses the correlation of multiple components of ecological processes to orderly regulate the proportion of nutrients in ecosystems (Zhou *et al.* 2018; Ba *et al.* 2023). The method elucidates the stoichiometric patterns of nutrients such as C, N, and P in ecosystems (Li *et al.* 2012). It is used to reveal the interactions and constraints between elements and to analyse the ecological chemical elemental mass balance and its impact on ecological interactions (Elser *et al.* 1996; Tian *et al.* 2021) and is an important method for exploring the transport and distribution relationships of nutrient elements in ecosystem processes (He and Han 2010; He *et al.* 2013; He and Wang 2018). Of these, C plays the role of a structural element, while N and P are important constituents of a wide range of proteins and genetic material. They are closely linked to plant growth, nutrient use efficiency, environmental adaptation mechanisms and the coupled nutrient cycling characteristics of ecosystem function (Agüero *et al.* 2014), and so are regarded as major limiting factors in ecosystems. As important physiological indicators, C/N and C/P ratios reflect plant growth rates and are related to the availability of N and P. N/P ratios are used

in the determination of limiting elements, and nutrient allocation of limiting element indicators is an important strategy for plants to cope with environmental changes, reflecting plant evolution, growth and development, and the balance of multiple functions (Sternier and Elser 2003; Bai *et al.* 2016). In order to maintain an optimal allocation of plant growth to sustain its own metabolic activity, plants must balance nutrient allocation between organs under different stresses (Wang and Yu 2008). Studying the nutrient allocation strategies of plants is therefore essential for understanding their own characteristics.

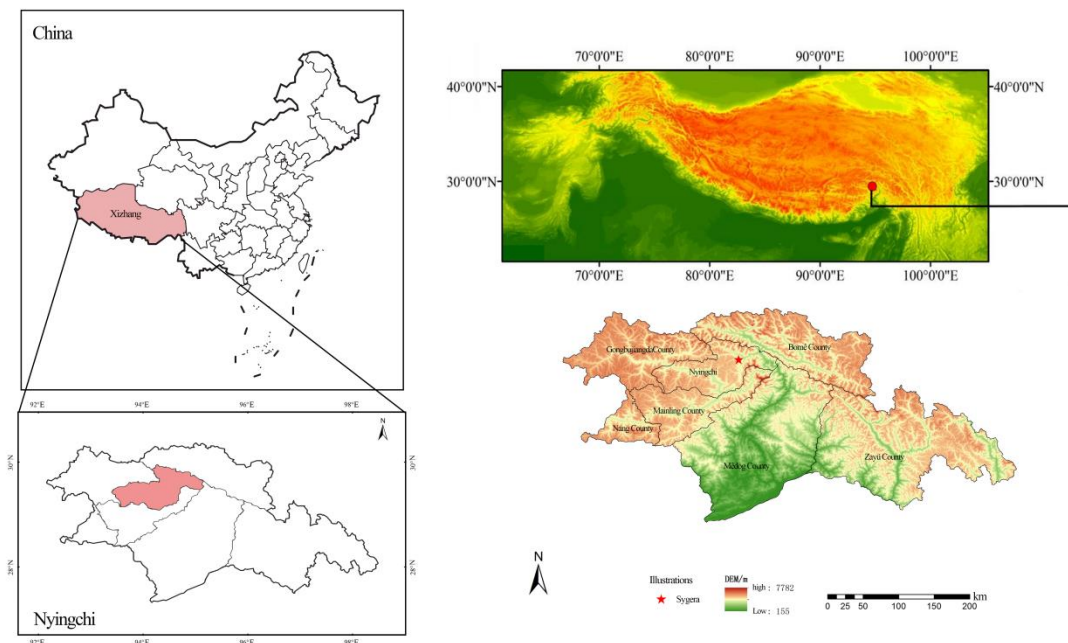
Located in the south-eastern region of Tibet, the Sygera Mountains can reach 26% forest cover and are an important part of the south-eastern Tibetan state forest region in China (Xin *et al.* 2004). The special geographical conditions make the forest ecosystem rich in climate change, unique tree species composition and a wide range of vegetation types. In recent years, studies on ecological chemometric characteristics have mostly focused on their different altitudes (Pan *et al.* 2022; Guo *et al.* 2023) and different stand ages (Liu *et al.* 2022; Jia *et al.* 2023), but most of these studies have mainly focused more on systematic analyses of plant leaf organs, litter fall matter, and soil nutrients, compared to relatively few studies on ecological chemometric characteristics of various organs of tree plants in forest communities in this study area. In fact, different plant organs play different roles in keeping plants alive. For example, the leaf organs are mainly responsible for photosynthesis and transpiration, the branch organs are mainly responsible for plant support and thinning, the root organs are mainly responsible for nutrient uptake and support, and the trunk organs are responsible for transport and accumulation. There are significant differences in stoichiometric characteristics among different species, which are the result of their own attribute characteristics and long-term adaptation to habitats. Usually, the more active organs have the highest demand for essential elements. Therefore, it is hypothesized here that more active organs will have higher nutrient content for optimal material and energy efficiency (Stable Hypothesis). At the same time, temperature is also an indispensable environmental factor for plant growth, especially in high latitude areas. The temperature difference caused by altitude changes the biochemical processes of plants and has a significant impact on the survival of alpine plants. For example, the carboxylation ability of low-temperature plants (Liu *et al.* 2022), the allocation of antifreeze nutrients (Zang *et al.* 2018), and cold tolerance (Takahashi *et al.* 2021) can potentially reflect the response of ecosystems to climate change. Therefore, studying the variation patterns of plant nutrient content and stoichiometry on different environmental stands is of great significance. In order to gain a deeper understanding of the distribution of nutrients among different forest types in the plant body of Sygera Mountain in southeastern Tibet, the plan was to answer the following two questions: What are the nutrient allocation trade-off strategies between plant tissues (leaves, branches, roots, trunks)? In addition, are nutrient limitations in the ecological stoichiometry of different forest types of trees? Thirdly, are the limiting indicators consistent across habitats?

## EXPERIMENTAL

### Study Areas

The Sygera (94°12' to 35'E, 29°15' to 50'N) is located in Nyingchi County, southeastern Tibet. The area belongs to the intersection of the eastern section of the Nyingchi Tanggula and Himalayan Mountain systems, with very rich climatic zones and vegetation types, and a high altitude, with the main peak around 5300 m above sea level

and a vertical height difference of nearly 3000 m (Luo *et al.* 2021). They are in the central transition zone of the wet and semi-humid mountains of southeastern Tibet and are in the watershed between the Niyang River basin and the Parlung Zangbo. The region is a subalpine cold temperate humid climate zone, with the characteristics of warm winters and cool summers, and obvious changes in the dry and wet seasons. The average annual temperature is around  $-0.73\text{ }^{\circ}\text{C}$ , with the highest monthly average temperature of  $9.23\text{ }^{\circ}\text{C}$  in July and the lowest monthly average temperature of  $-13.98\text{ }^{\circ}\text{C}$  in January. The rainy season is from June to September with abundant rainfall, accounting for 82 % of the annual precipitation, which can reach an average annual precipitation of around 1134 mm. There is a frost-free period of 178 d, an annual average relative humidity of 79.1 %, and an annual sunshine hour of 1150 h. The soils are mainly mountain brown loam. The mountains are relatively rich in biological resources and biodiversity and are the core area of the eastern section of the priority biodiversity conservation area in the southeastern Himalaya. The area is one of the components of the northern route of the Yarlung Tsangpo River Grand Canyon National Nature Reserve, and an important natural barrier to ecological security in China. The four main forest vegetation types studied in this paper are evergreen coniferous forests (see Fig. 1).



**Fig. 1.** Location map of the research site in Sygera Forest Park

### Sampling Method

The forest communities in southeastern Tibet are all montane forests with large altitude differences and spatial heterogeneity. Accordingly, in order to minimize the influence of site conditions, the sample plots were selected from a comprehensive and most representative range of *Pinus armandii* forest (PA), *Picea likiangensis* var. *linzhiensis* forest (PLL), *Abies georgei* var. *smithii* forest (AGS), and *Juniperus saltuaria* forest (JS) as the subjects of the study. One  $30\text{ m} \times 30\text{ m}$  sample square was set up in each typical forest ecosystem type, and the height, diameter at breast height and related information of all representative tree species in the sample square were measured and recorded (Table 1).

**Table 1.** Basic Characteristics of the Main Stand Plants in Sygera Mountain

Elevation (m)	Forest type	Slope (°)	CD (%)	TH (m)	DBH (cm)	MAT (°C)	Lifestyle	Major understory vegetation
2560	PA	33	50	26.0±0.8	128.4±4.3	7.10 to 11.20	E-N-A	<i>Cupressus gigantea</i> , <i>Pinus densata</i> , <i>Rosa sericea</i> Lindl., <i>Cotoneaster microphyllus</i> Wall.ex Lindl
3308	PLL	7	40	20.8±0.7	156.2±6.8	3.70 to 7.10	E-N-A	<i>Betula utilis</i> , <i>Quercus aquifolioides</i> , <i>Larix gmelinii</i> , <i>Abies georgei</i> var. <i>smithii</i> , <i>Sinarundinaria setosa</i> Yi
3900	AGS	32	80	21.4±1.4	177.4±7.2	0.41 to 3.70	E-N-A	<i>Spiraea schneideriana</i> , <i>Sorbus rehderiana</i>
4420	JS	25	50	10.2±0.7	90.8±4.5		E-N-A	<i>Rhododendron pingianum</i> , <i>Salix lindleyana</i> , <i>Rhodiola fastigiata</i> Rh. <i>aganniphum</i> Balf.f.et Ward

Note: CD: canopy density; TH: tree height; DBH, diameter at breast height; PA: *Pinus armandii*; PLL: *Picea likiangensis* var. *linzhiensis*; AGS: *Abies georgei* var. *smithii*; JS: *Juniperus saltuaria*; E-N-A: Evergreen-needleleaf-arbor.

### Sample Collection and Processing

When selecting trees in advance, in order to ensure the uniformity of plant phenological stages under different forest stands, four forest types of sample plots were collected in August of the same year (growth period). Within each sample plot, 5 trees were selected as the standard for different forest types of tree species, and standard trees of the same size, relatively complete, and highly similar were selected as the sampling plants.

For leaf and branch organ sampling, high pruning shears were used to collect branches (1- to 2-year-old new branches) and leaves (1- to 3-year-old) of the sample plant to represent the whole plant. Branches and leaves were collected from the middle of the plant in four different orientations: east, west, south, and north. For trunk organ sampling, 5 cores were drilled to the pith of the tree at 1.3 m from the ground at breast height using a 5 mm inner diameter growth cone. Finally, butter grease was used to fill the holes left in the sampling area to prevent pathogens from attacking the sample plants. For root sampling, root samples were obtained by digging at a depth of 0 to 30 cm, washing and screening fine roots less than 2 mm as root samples.

In order to make their samples more representative, the above were mixed in proportion as single plants and sealed and refrigerated after being well labelled. After the samples were returned to the laboratory on the same day for pre-treatment such as splitting and washing, the samples were placed in an oven at 105 °C for deactivation of enzymes (15 min), then dried at 80°C to a constant weight, crushed and sieved (1 mm), placed in self-sealing bags and stored in a box with desiccant for backup.

### Determination of Plant Nutrient Elements

The samples were mainly analysed for the determination of the elemental content of C, N, and P between different organs of plants. In particular, the elemental analyser method (vario EL cube CHNOS Elemental Analyzer, Elementar Analysensysteme GmbH,

Germany) was used to determine the C and N contents of different organs of plants. The P content of different plant organs was determined by the HNO<sub>3</sub>-H<sub>2</sub>O<sub>2</sub> ablation-ICP-OES method (iCAP 6300 ICP-OES Spectrometer, Thermo Fisher, USA).

### Data Processing

Microsoft Excel 2021 was used to collate the initial data on the plants in the four typical forest ecosystem types of the Sygera obtained, and the statistical analysis of the data was done in SPSS 25.0 software, all passing the homogeneity of variance test and the normal distribution test with a significance level of  $\alpha = 0.05$ . Multi-factor ANOVA and Duncan's test were used for multiple comparisons to analyse the variability in nutrient content between organs of different stand types. Correlations between C, N and P ecological stoichiometric ratios were tested using Pearson correlation analysis and plotted in Origin 2021. The variation in the C, N and P content of the different organs of the plant body (roots, stem, branches and leaves) is expressed as the coefficient of variation CV (%) and is calculated as shown below.

### Equations

$$CV = (SD/M) \times 100 \%, \quad (1)$$

where CV denotes coefficient of variation, SD denotes standard deviation, and M denotes mean.  $CV \leq 10 \%$  is weak variation,  $10 \% < CV \leq 100 \%$  is moderate variation, and  $CV \geq 100 \%$  is strong variation (Lu *et al.* 2021).

## RESULTS AND DISCUSSION

### Effects of Forest Types and Organs on Plant Element Content and Stoichiometric Ratio

Through the analysis source of variation, it can be seen that the influence of element content and stoichiometric ratio on each component varied (Table 2). The interaction between organs and forest types had the greatest impact on C content, with Type IIISS reaching 13 572.73, but the impact of forest types on C content was insignificant ( $p > 0.05$ ). The N and P contents of different forest types were mainly influenced by organs (Type IIISS=1 384.22, 15.90). The difference was that the interaction between organs and forest types had the least impact on N content, while the forest type had the least impact on P content, reaching a significant level ( $p < 0.05$ ).

The C/N and C/P ratios were mainly influenced by organs, with Type IIISS being 1,650,000 and 181,000,000, respectively. The second was the interaction between organs and forest types (Type IIISS = 225,0000 and 80,000,000), and the least affected was forest types. Except for the C/P ratio, which did not reach a significant level, all other differences reached significant levels ( $p < 0.05$ ). The degree of influence of the N/P ratio varied, mainly influenced by the interaction between organs and forest types (Type IIISS=205.76), followed by forest types, where organs were the least affected. The differences in the influence of the three factors on the N/P ratio were all significant ( $p < 0.05$ ).



**Table 2.** Analysis of Sources of Variation in C, N and P Contents and Stoichiometric Ratios in Different Forest Types

Parameters	Projects	Source of Variation				
		Type IIISS	DF	MS	F	P
C	Organ (O)	5182.03	3.00	1727.34	5.77	0.00
	Forest type (F)	729.90	3.00	243.30	0.81	0.49
	O*F	13572.73	9.00	1508.08	5.04	0.00
	Error	19157.66	64.00	299.34		
N	Organ (O)	1384.22	3.00	461.41	699.03	0.00
	Forest type (F)	40.33	3.00	13.44	20.37	0.00
	O*F	19.57	9.00	2.18	3.30	0.00
	Error	42.24	64.00	0.66		
P	Organ (O)	15.90	3.00	5.30	149.74	0.00
	Forest type (F)	0.55	3.00	0.18	5.19	0.00
	O*F	2.67	9.00	0.30	8.37	0.00
	Error	2.26	64.00	0.04		
C/N	Organ (O)	1646202.45	3.00	548734.15	103.99	0.00
	Forest type (F)	120366.71	3.00	40122.24	7.60	0.00
	O*F	224523.50	9.00	24947.06	4.73	0.00
	Error	337702.31	64.00	5276.60		
C/P	Organ (O)	180953956.37	3.00	60317985.46	14.27	0.00
	Forest type (F)	26217853.02	3.00	8739284.34	2.07	0.11
	O*F	80023073.91	9.00	8891452.66	2.10	0.04
	Error	270545591.24	64.00	4227274.86		
N/P	Organ (O)	77.92	3.00	25.97	6.77	0.00
	Forest type (F)	144.69	3.00	48.23	12.58	0.00
	O*F	205.76	9.00	22.86	5.96	0.00
	Error	245.38	64.00	3.83		

Note: Type IIISS is the sum of squares of deviations, and the greater the value, the stronger the factor's influence is.

The variation characteristics of C, N, P content and stoichiometric ratio in various organs of tree plants in this study area varied among different forest types. The variability of C content in various organs among different forest types was the smallest, belonging to weak variation (Table 3). The maximum coefficient of variation (26.53%, 25.56%) of N content in the trunk organs of *Pinus armandii* forest and the root organs of *Picea likiangensis* var. *linzhiensis* forest showed moderate variation. The coefficient of variation of P content in all organs of *Pinus armandii* forest had moderate variation, and the coefficient of variation of P content in the trunk organs of *Juniperus saltuaria* forest was relatively high (48.45 %). Among the four forest types, the C/N ratio had the smallest coefficient of variation of leaf organs, which exhibited weak variation. In the C/P ratio, except for the leaf organs of *Abies georgei* var. *smithii* forest and the leaf and branch organs of *Juniperus saltuaria* forest, which showed weak variation, the rest had moderate variation, and the coefficient of variation of trunk organs of *Pinus armandii* forest was the largest (92.12%), which was similar to high variation, In *Pinus armandii* forest, the maximum coefficient of variation (43.53%) of N/P ratio of trunk organs showed moderate variation, while the root organs were relatively stable in different forest types, and their coefficient of variation was low.

**Table 3.** Coefficient of Variation Between Different Forest Types and Organs (%)

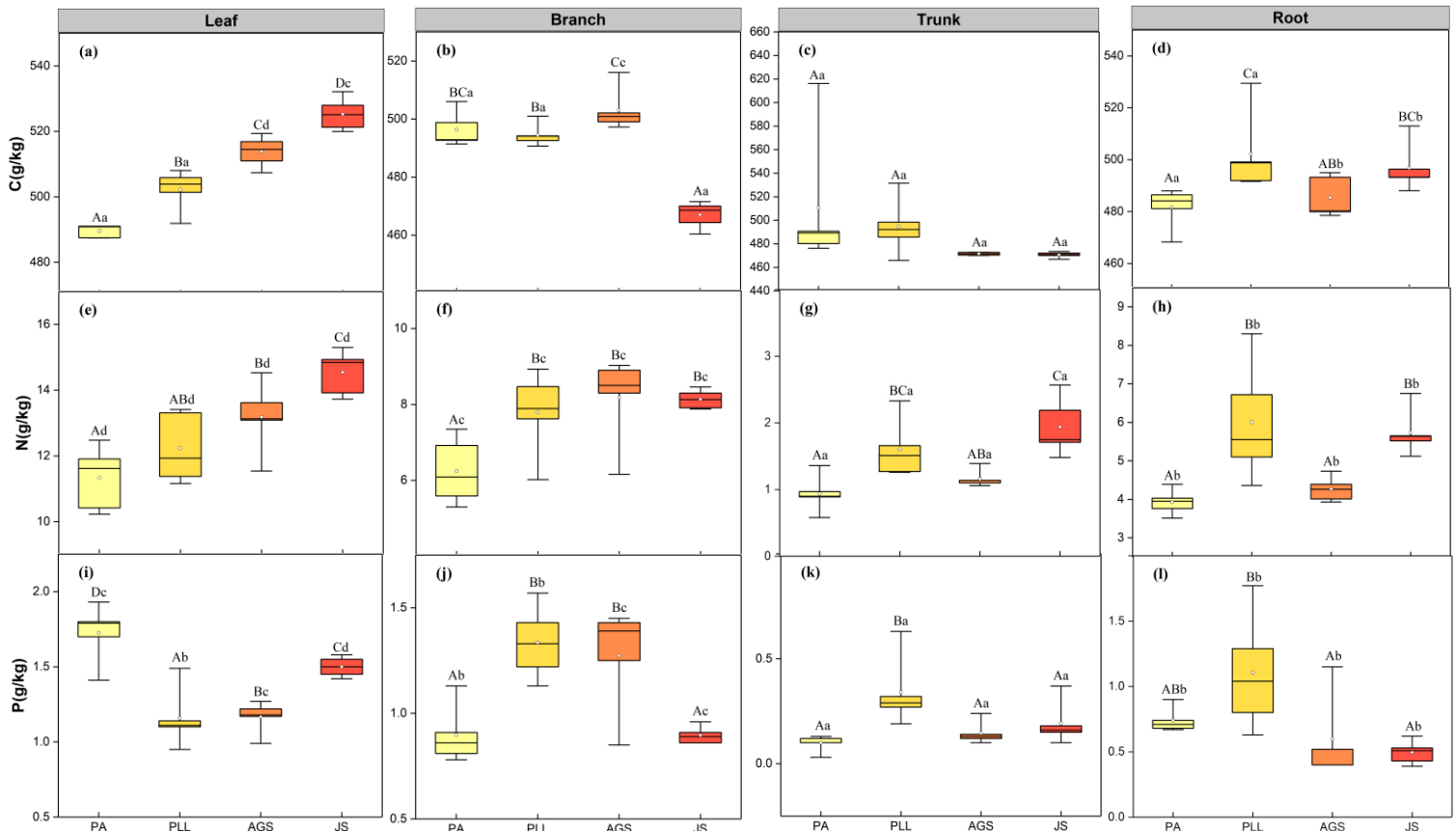
Forest Type	Organ	C	N	P	C/N	C/P	N/P
<i>Pinus armandii</i>	L	0.35	7.67	10.06	7.68	10.89	6.75
	B	1.10	12.44	13.54	11.86	12.07	7.99
	T	10.40	26.53	37.70	40.22	92.12	43.53
	R	1.46	7.44	11.34	6.54	11.33	14.70
	Mean	3.33	13.52	18.16	16.58	31.60	18.24
<i>Picea likiangensis</i> var. <i>linzhiensis</i>	L	1.56	9.54	7.78	9.14	19.26	20.26
	B	0.98	13.33	5.24	18.80	14.93	7.04
	T	5.90	7.89	2.67	25.38	25.34	9.40
	R	3.89	25.56	16.53	27.00	46.15	26.20
	Mean	3.08	14.08	8.06	20.08	26.42	15.72
<i>Abies georgei</i> var. <i>smithii</i>	L	0.83	7.37	8.15	7.57	8.96	3.18
	B	1.33	12.75	17.61	15.02	22.66	9.38
	T	0.25	10.25	33.55	9.16	24.71	17.64
	R	1.48	6.71	47.32	7.10	31.11	30.63
	Mean	0.97	9.27	26.66	9.71	21.86	15.21
<i>Juniperus</i> <i>saltuaria</i>	L	0.85	4.19	4.00	3.64	3.67	3.45
	B	0.87	2.74	3.86	3.58	4.36	3.09
	T	0.47	20.10	48.45	18.99	37.17	22.60
	R	1.72	9.46	16.52	8.66	16.78	9.32
	Mean	0.98	9.12	18.21	8.72	15.49	9.62

### Changes in Element Content and Stoichiometric Ratio of Various Organs in Different Forest Types

Figure 2 shows that the C content in various organs of different forest types of tree plants was 490 to 525, 467 to 503, 471 to 511, and 482 to 502 g/kg, respectively. Except for trunk organs, there were significant differences ( $p < 0.05$ ). The C content in the leaves of the *Juniperus saltuaria* forest was significantly higher than that of the other three forest types, while the branches and trunk organs were the opposite in the *Juniperus saltuaria* forest, with the lowest C content (467, 471 g/kg). The C content in the roots of the *Picea likiangensis* var. *linzhiensis* forest was the highest (502 g/kg). There was no significant difference ( $p > 0.05$ ) in the C content of different organs in the same forest type, *Pinus armandii* forest and *Picea likiangensis* var. *linzhiensis* forest. On the contrary, there was a significant difference ( $p < 0.05$ ) in the C content of different organs in *Abies georgei* var. *smithii* forest and *Juniperus saltuaria* forest. The C content in the trunk organs of *Pinus armandii* forest was significantly higher than that of the other three, while that of *Picea likiangensis* var. *linzhiensis* forest, *Abies georgei* var. *smithii* forest, and *Juniperus saltuaria* forest was the highest.

The characteristics of plant nutrient changes in the same organ and different forest types had a mean of 12.8, 7.59, 1.41, and 4.98 g/kg among different organs, with significant differences ( $p < 0.05$ ). Among them, the N content in the leaves of *Juniperus saltuaria* forest was significantly higher than that of the other three forest types, with a mean of 14.5 g/kg; In terms of P content, except for leaf organs, the ranking of branches, trunks, and root organs among various forest types is that *Picea likiangensis* var. *linzhiensis* forest had the highest content, and there was no obvious similarity with other forest types. The N content of leaves in different organs of the same forest type was significantly higher than that of other organs, with the lowest trunk content (0.94, 1.16, 1.61, 1.94 g/kg). There were significant differences among different organs ( $p < 0.05$ ), and the distribution order was consistent as leaf > branch > root > trunk; The distribution pattern of P content among

various organs of the four forest types was relatively similar to that of N content, with the lowest content being trunk, 0.10, 0.14, 0.19, 0.34 g/kg, followed by root organs (0.50 to 1.11 g/kg). Overall, the average C, N, and P content of each organ was consistently arranged in the order of leaf>branch>root>trunk. There were significant differences in the distribution characteristics of nutrient elements in different forest types and plant organs ( $p<0.05$ ).

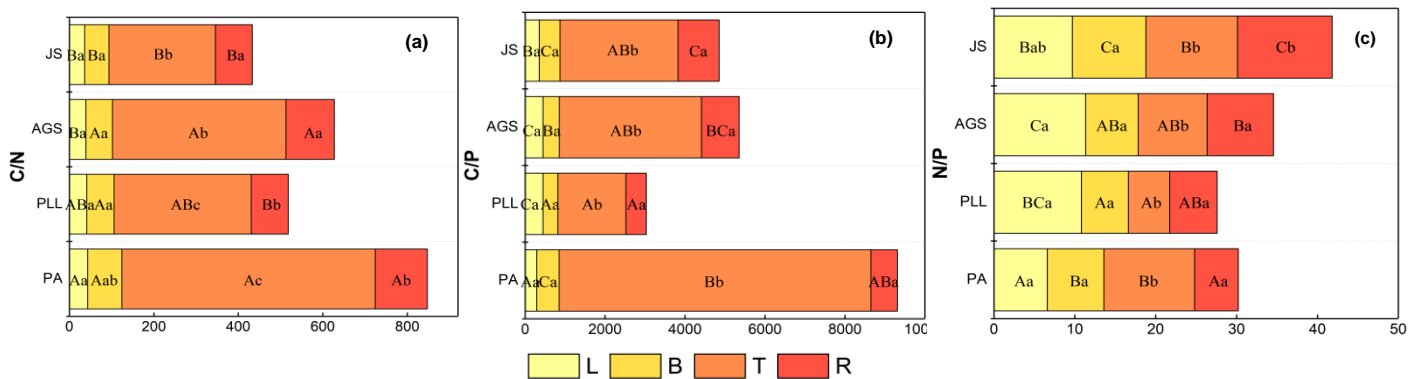


**Fig. 2.** Characteristics of changes in nutrient C, N, and P contents of various organs in four forest stands. PA : *Pinus armandii* forest; PLL : *Picea likiangensis* var. *linzhiensis* forest; AGS : *Abies georgei* var. *smithii* forest; JS: *Juniperus saltuaria* forest. (a-l) indicates the variation of C, N and P nutrient contents of different organs in different forest types. Different capital letters indicate significant differences between different forest types for the same organ, and different lowercase letters indicate significant differences between different organs for the same forest type ( $p<0.05$ ).

The stoichiometric ratio can reflect the ecological strategies adopted by plants during their growth and development in different habitats. One can obtain relevant information on plant growth status from it. Figure 3 shows that the stoichiometric changes in C/N, C/P, and N/P ratios varied depending on different forest types and organs. The average C/N, C/P, and N/P ratios of each organ in the four forest types were 36.2 to 600, 287 to 7800, and 5.10 to 11.70, respectively. Overall, the C/N and C/P ratios of the leaves in the four forest types were relatively low, while the C/N and C/P ratios of the trunk organs were relatively high. However, the N/P ratio of the leaves in the four forest types was the highest. There was no significant difference ( $p>0.05$ ) in the C/N ratio among the leaves, branches, and root organs of *Pinus armandii* forest and *Picea likiangensis* var. *linzhiensis* forest with different organs of the same forest type, and the order was consistently stem > root > branch > leaf. In the C/P ratio, the overall trend from *Pinus armandii* forest to



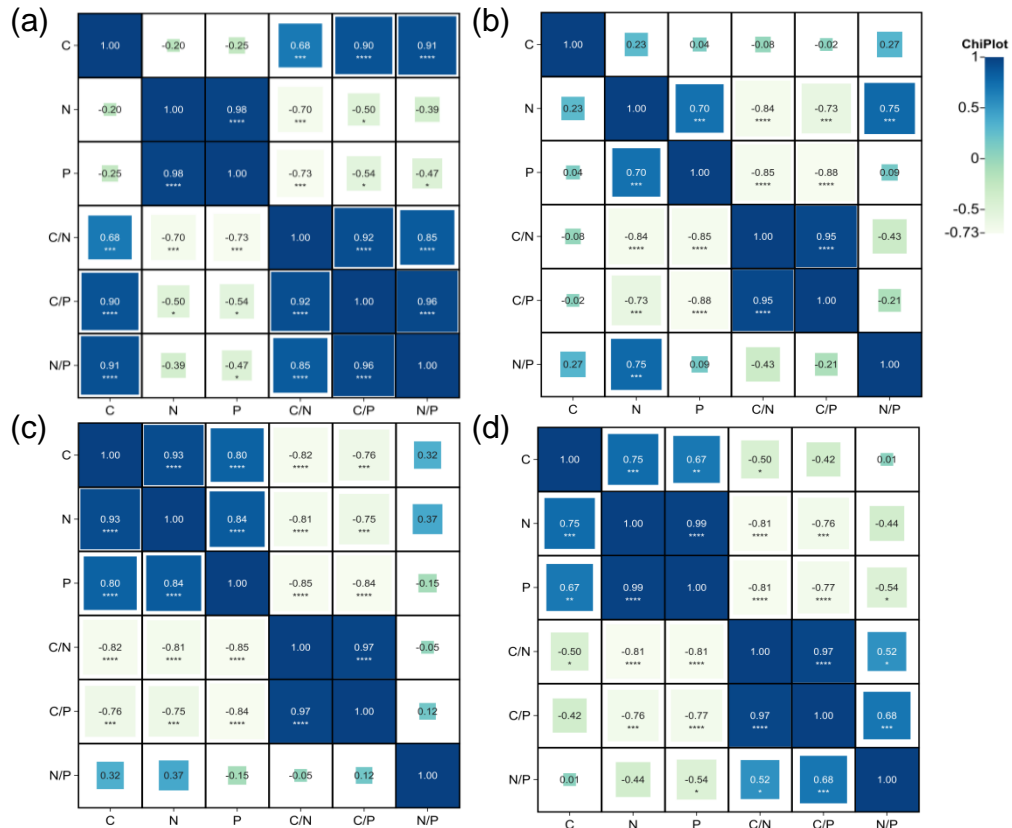
*Juniperus saltuaria* forest is decreasing, with some forest types showing an increase. Except for the stem organs, there was no significant difference in other organs. The average N/P ratios were 9.60, 7.11, 9.04, and 7.79, respectively. Unlike the C/N and C/P ratios, the N/P ratio ranked among organs as leaf > stem > root > branch, and the difference was significant ( $p < 0.05$ ). The C/N ratio of leaf organs in different forest types with the same organ was significantly lower than that of other organs in all forest types, and the C/N ratio of branch organs in *Pinus armandii* forest was significantly higher than that in the other three forest types. There was no significant difference among leaves, trunks and roots ( $p > 0.05$ ), and the C/N ratio showed a downward trend from *Pinus armandii* forest to *Juniperus saltuaria* forest. The order of C/P ratio among organs in *Pinus armandii* forest and *Juniperus saltuaria* forest was the same: trunk > root > branch > leaf, and that in *Picea likiangensis* var. *linzhiensis* forest and *Abies georgei* var. *smithii* forest was the same: trunk > root > leaf > branch. The N/P ratio was highest in all organs except for the leaf organs, with *Juniperus saltuaria* forest as the highest value, and the difference was significant ( $p < 0.05$ ).



**Fig. 3.** L: leaf, B: branch, T: trunk, R: root PA: *Pinus armandii* forest; PLL: *Picea likiangensis* var. *linzhiensis* forest; AGS: *Abies georgei* var. *smithii* forest; JS: *Juniperus saltuaria* forest. (a-c) represents the variation characteristics of the ecological stoichiometric ratios of various organs in different forest types. Different capital letters represent significant differences between different forest types in the same organ, and different Minusculer represent significant differences between different organs in the same forest type ( $p < 0.05$ ).

### Correlation Analysis of Plant Element Content and Stoichiometric Ratios

Figure 4 shows that the C content of *Abies georgei* var. *smithii* forest and *Juniperus saltuaria* forest was highly significantly positively correlated with N and P content ( $p < 0.001$ ), while the C content of *Pinus armandii* forest was negatively correlated with N and P content. The N content and P content of different forest types were all highly significantly positively correlated ( $p < 0.001$ ). The changes in C/P and N/P ratios of *Picea likiangensis* var. *linzhiensis* forest and *Juniperus saltuaria* forest were insignificantly correlated with the changes in C content ( $p > 0.05$ ), while *Pinus armandii* forest and *Abies georgei* var. *smithii* forest had a very significant positive correlation with C content ( $p < 0.001$ ), and N and P content had a very significant negative correlation with C/N and C/P ratios ( $p < 0.001$ ). The N/P ratio and N content showed a highly significant positive correlation in the *Picea likiangensis* var. *linzhiensis* forest, but no significant correlation in the other three forest types. The N/P ratio and P content showed a significant negative correlation in the *Pinus armandii* forest and *Juniperus saltuaria* forest ( $p < 0.05$ ).



**Fig. 4.** Correlation analysis of elemental content and stoichiometric ratios of plants in different forest types.  $p < 0.05^{**}$ ;  $p < 0.01^{***}$ ;  $p < 0.001$ . (a-d) sequentially represents the correlation between the elemental content and stoichiometry of various organs in different forest types, including (a) *Pinus armandii* forest, (b) *Picea likiangensis* var. *linzhiensis* forest, (c) *Abies georgei* var. *smithii* forest, and (d) *Juniperus saltuaria* forest.

### Characteristics of C, N, and P Contents of Various Plant Organs among Different Forest Types

The content of C, N, and P, as important life elements in plants, can reflect the ability of plants to absorb and store nutrients in different living environments (Yu *et al.* 2014; Xu *et al.* 2016). In this study, the C content of four forest types of trees ranged from 490 to 525 g/kg, which was higher than the results of Chen *et al.* (2021), who studied different forest stands on Hainan Island. The present results also were higher than for Chinese terrestrial coniferous forests (Tang *et al.* 2018) and Bi *et al.* (2017) for different forest types in the Liaodong Mountain area. These differences are probably related to their stand conditions, and the Sygera Mountains are mountainous forests with large altitude differences. It can be seen that the vegetation in the Sygera Mountains in this study area has a high C accumulation capacity. Among different forest types, the C content of leaves of trees of all four forest types was higher than the global (Elser *et al.* 2000) plant leaf C content of 464 g/kg, and higher than the 458 g/kg of monsoonal evergreen broad-leaved forest in Yunnan Pu'er (Huang *et al.* 2016) and the 450.00 g/kg of plant leaf C of 32 species (Yan *et al.* 2010) in Zhejiang Tiantong. This was probably because C content is the material basis and energy source for the growth and development of plant leaf organs. The higher leaf C content helps to improve the plant's ability to adapt to stressful environments. The branch organs play a secondary role as the closest nutrient transport site to the leaves, accumulating some nutrients while the leaves photosynthesize. The nutrient content

obtained by the leaves from the branches is consumed and converted into organic matter, which is transported from the branch organs to other organs, resulting in a relatively higher C content in their branches than in the roots and trunk organs. As the main body of plant accumulated nutrients, the nutrient content of trunk organs was the minimum (Fig. 2), and the C content was 471 to 511 g/kg, which is similar to the research results of Zhang *et al.* (2021). This may be because the trunk organs, as the main organs of plant transportation, are related to the xylem with poor response to the surrounding environment (Meinzer *et al.* 2009), so the trunk content is relatively low. This research result differed from the conclusion of Liu *et al.* (2016), which was possibly due to differences in the distribution of C content among different organs due to differences in species.

The mean N and P contents of the four forest type trees were 6.70 and 0.85 g/kg, respectively, which were significantly lower than the national (Liu *et al.* 2005) mean scale N contents (20.20 and 1.46 g/kg), and also lower than the results of different regional studies on salt quinoa in Hulunbuir (Su *et al.* 2022) and globally (Reich and Oleksyn 2004), indicating that the overall low N and P contents of plant leaves in this region may be related to the high precipitation related. The biogeochemistry hypothesis suggests that in areas with high precipitation, soil leaching is severe, and the effective nutrient content is reduced. This affects the changes in nutrient content in plants, resulting in relatively low plant N and P content. On the other hand, it may be due to differences in soils, where part of the nutrients absorbed by the plant body originate from the soil, and its N and P content in the plant is related to the availability of N and P nutrient elements in the soil (Yu *et al.* 2017). Figure 2 shows that there were significant differences in the nutrient contents of plant organs in different stand types, and the highest N and P contents were found in leaf organs, which is consistent with the results of Zhang *et al.* (2021). This is probably because leaf organs, as the most important functional organs, play an important role in the synthesis of many compounds such as photosynthesis, proteins, and nucleic acids, and are essential elements in biochemical processes, so the N and P contents of leaf organs are relatively high. At the same time, this study also found that the N content of *Pinus armandii* forest plants at low altitudes in leaves, branches, roots, and stems was significantly lower than that of *Juniperus saltuaria* forest plants at high altitudes. The N content of various organs (leaves, branches, roots, and stems) in *Pinus armandii* forest was the minimum, significantly lower than that of *Picea likiangensis* var. *linzhiensis* forest, *Abies georgei* var. *smithii* forest, and *Juniperus saltuaria* forest in higher altitude regions. These differences in nutrient allocation among plants can be attributed to differences in environmental conditions along altitude gradients, which means that the efficiency of plant N absorption in low altitude areas is lower. Compared with global or national scale studies, the N content of plant leaf organs shows an upward trend with increasing altitude (Reich and Oleksyn 2004; Han *et al.* 2005; Bi *et al.* 2017), which clearly confirms this viewpoint. In different organs of the same forest type, the order of N content of each organ in the four forest types is leaf > branch > root > trunk. The P content in *Pinus armandii* forest and *Juniperus saltuaria* forest was leaf > branch > root > trunk. In addition, *Picea likiangensis* var. *linzhiensis* forest and *Abies georgei* var. *smithii* forest were branch > leaf > root > trunk. This indicates that at the same research scale, under the influence of environmental factors such as climate and soil, the nutrient content of each organ exhibited similar changes, similar to the N content in this study, but its own genetic factors dominate. This feature was highlighted in the P content, indicating that different species had differences in the absorption and distribution of elements, which is consistent with previous research conclusions (Liu *et al.* 2015). Overall, for the C, N, and P contents of different organs in

the four forest types, the order of their mean values was consistent as follows: leaf > branch > root > trunk.

### Characteristics of Ecological Stoichiometric Ratios of Plant Organs Between Different Forest Types

In plant communities, if the stoichiometric ratios of C, N, and P are not suitably matched in the natural environment, it will affect the cycling pathways of nutrient elements. The scarcity or excess of any element will lead to the accumulation or consumption of the other two elements (Cai *et al.* 2021). Among them, C reserves are to some extent controlled by the availability of N and P nutrient elements. N and P scarcity will indicate a relative excess of C content, while N and P abundance will indicate a relative deficiency of C content (Güsewell 2004). Therefore, the stoichiometric ratios of plant bodies can be used to indicate patterns of C accumulation and N and P nutrient limitation in the ecosystems in which they are found. In this study, the mean C/N and C/P ratios of the four forest type trees were significantly higher than those of plants within the global (Elser *et al.* 2000) scale C/N (22.50) and C/P (232.00), which may be due to the adaptive mechanisms of woody plants in the region to nutrient stress. The C/N and C/P ratios can reflect the utilization efficiency of plant N and P content and the assimilation ability of C. The higher the value, the higher the utilization efficiency. Among the four forest types, the minimum value of C/N ratio of each organ appeared in the *Juniperus saltuaria* forest, and the maximum value was *Pinus armandii* forest. Except for the C/P ratio of leaf organs in the *Pinus armandii* forest, the C/P ratios of branch, trunk, and root organs all showed the lowest values in the *Picea likiangensis* var. *linzhiensis* forest. This means that *Pinus armandii* forest had a higher N utilization efficiency than *Juniperus saltuaria* forest. Among various organs, the C/N ratio showed a pattern of trunk > root > branch > leaf in different forest types. In the C/P ratio, except for *Picea likiangensis* var. *linzhiensis* forest and *Abies georgei* var. *smithii* forest, which showed trunk > root > leaf > branch, the C/P ratio of the other two forest types was consistent with the results of C/N ratio, showing trunk > root > branch > leaf. The results of the study were more similar to Liu *et al.* (2016), which may be due to the fact that leaves, as functional organs, need sufficient N and P nutrient elements to synthesize various enzymes for biochemical reactions under photosynthesis, thus making the C/N and C/P ratios of leaves small.

The differences in living areas, developmental stages, and plant species can all affect the changes in the critical value of the N/P ratio. However, there is no accurate definition of the threshold for the N/P ratio. In aquatic ecosystems, when the N/P ratio is greater than 16, it indicates that its growth is mainly limited by P, when the ratio is less than 14, it is limited by N, and when the ratio is between 14 and 16, it is jointly limited by N and P elements (Zhang *et al.* 2023). In the study of nutrient limitation in terrestrial ecosystems, Güsewell (2004) proposed that the plant growth process is N limited when  $N/P < 10$ , and P limited when  $N/P > 20$ . When the ratio is between the two, the relationship is insignificant, that is, it is considered to be jointly restricted by N and P. The study area belongs to forest ecosystem, so the threshold value of terrestrial ecosystem is used for analysis. In this study, among the four forest types of tree plants, except for *Juniperus saltuaria* forest with an N/P ratio of 10 to 20, which is jointly limited by both, the N/P ratios of the other three forest types are all less than 10. The growth of tree plants is mainly limited by N, indicating that there are different nutrient limiting conditions among different forest types (Fig. 3). The research results are consistent with those of Niu *et al.* (2013). Due to the differences between different forest types, their elements have specificity in

absorption and utilization. Therefore, each organ of the four forest types of tree plants has different responses to the limitation of N and P content. Except for the N/P ratio of leaf organs, all other organs showed higher N/P ratios in *Abies georgei* var. *smithii* forest than the other three forest types, which is similar to the C/N comparison above, indicating that *Abies georgei* var. *smithii* forest and *Juniperus saltuaria* forest have stronger absorption ability of nutrient element N and P content in each organ at higher altitudes, and better adaptability to harsh environments. Among different organs, there are differences in N/P ratios among the four forest types, which may be due to differences in nutrient absorption, distribution, and utilization efficiency among plant organs in different conditions.

### Relationships between Plant Element Content and Ratios

Different forest types are external expressions of biochemical adaptations to the external environment, and there is a relatively consistent internal link between the C, N and P contents of plants in their physiological and biochemical processes, reflecting a convergence of adaptation and evolution to the external environment (Sun *et al.* 1993; (Niu *et al.* 2013). Because different forest type arbors and plants have different adaptability to habitat conditions, their resource utilization efficiency has distribution differences, which may be reflected in the chemometric characteristics of C, N, and P (Wang and Zheng 2020). Correlation analysis showed that the contents of N and P in the four forest types were positively correlated (Fig. 4). This result reflects the synergy of changes in two nutrient elements in plants, which is a powerful guarantee for the stable growth and development of plants and is also one of the most basic characteristics of plants. This is similar to the research results of Wu *et al.* (2010) and Wang *et al.* (2014), which further verifies the general rule of the stoichiometric relationship of higher terrestrial plants, namely a “dilution effect.” The law is to compare the content of C in plants to the solvent in the solution, and the content of N and P to the solute in the solution, that is, C has a certain dilution effect on N and P, and it also reflects the balance of nutrient utilization efficiency of plants during C fixation (He *et al.* 2017). In each forest type, N and P content showed a highly significant negative correlation with C/N and C/P ratio. N content and N/P ratio showed a highly significant positive correlation in *Picea likiangensis* var. *linzhiensis* forest, and P content showed a significant negative correlation in *Pinus armandii* forests and *Juniperus saltuaria* forest. This is similar to the research results of Tao *et al.* (2016) but differed from the research results of Li *et al.* (2012), indicating that the differences in the stoichiometric characteristics of plant organs may be influenced by different species and regional scales. The correlation between the changes in C/P, N/P ratios and C content in *Picea likiangensis* var. *linzhiensis* forest and *Juniperus saltuaria* forest was insignificant, while the correlation between the changes in C/N, C/P ratios and C content in *Pinus armandii* forest and *Abies georgei* var. *smithii* forest was highly significant and positively correlated, indicating that different tree types have different strategies for balancing the efficiency of N and P content utilization during the C fixation process. The coefficient of variation of stoichiometric characteristics was as follows: C/P (24%) > N/P (15%) > C/N (14%) (Table 3).

When plants are affected by different factors during their growth process, their C, N, and P contents will also change accordingly. In this study, the interaction between forest types and organs had the greatest impact on C content and N/P ratio, with organs being the least affected. Organs had the greatest impact on N, P content and C/N, C/P ratio, while forest types were the least affected. However, their impact also reached a significant level (Table 2), which is similar to the research results of Zhang *et al.* (2019). During the process



of plant species differentiation, there were certain differences in the storage and accumulation of organic matter among different plants due to their own genetic characteristics. Even under the influence of the same climatic environment, this inherent plant difference still dominated. As an essential element of the plant body, the distribution of N and P content among plant organs depends on their structural and functional differences. Among them, plant leaf organs, as the main organs of photosynthesis, showed relatively higher N and P content compared to other organs, smaller overall coefficient of variation, and relatively high stability. This is consistent with the research results of Liu *et al.* (2015) and Xu *et al.* (2018), reflecting the “conservative” strategy between element content and its ratio during the evolution of life organisms, in line with the “Stable Leaf Nutrient Content Hypothesis” (Elser *et al.* 2000). Therefore, the influence of N and P content and C/N, C/P ratio among organs was significant. In addition, plant-apoptotic matter-soil is a complete nutrient cycle system; this study only made a systematic analysis for plant nutrients but did not study the characteristics of apoptotic matter and soil nutrients; so, the C, N, P, and K in the nutrient cycle system cannot be better reflected. Future research should pay attention to the integrity of the nutrient cycle system research.

## CONCLUSIONS

1. Influenced by the standing conditions and other factors, the N/P ratio of square-branched Berlin was in the range of 10 to 20, and the growth was limited by the common limitation of the two, while the N/P ratios of the remaining three forest types were all less than 10, which shifted from N- and P-co-restricted to N-restricted, suggesting that there were different nutrient limitation types among the different forest types.
2. Under the condition of different environmental gradients, a strong domestication reaction was found between N and P contents, which further verifies the universal law of stoichiometry of higher terrestrial plants (“dilution effect”) and carries out the “optimal allocation principle” in the process of nutrient allocation to various organs of plants.
3. The variation source N, P content and C/P, C/N ratio were mainly affected by organs, but the influence of forest type also reached a significant degree, indicating that plant types and the distribution of nutrient elements in organs should be comprehensively considered when studying phytochemistry metrological characteristics.
4. Interestingly, leaf organs showed the highest stability among various contents, which supports our previous hypothesis that more active organs have a higher ability to maintain relatively stable element content and proportion, reflecting the “conservation” strategy between element content and its ratio during the evolution of living organisms.

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