Stoichiometric Characteristics of Understory Plant Leaves and Soil in Three Forest Types in Mao'er Mountain: Postprint

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Abstract

Investigating the leaf and soil stoichiometric characteristics of understory plants across different forest types in Mao'er Mountain can reveal their adaptation strategies and provide data support for forest management. This study measured and analyzed the stoichiometry of leaves and soil of major plants in the herb and shrub layers of coniferous-broadleaf mixed forest (ZK), evergreen broadleaf secondary forest (CLC), and evergreen broadleaf forest (CL) in Mao'er Mountain. The results showed that: (1) Overall, there was no significant difference in C and N contents between herb layer and shrub layer plant leaves, while P and K contents in herb layer leaves were extremely significantly higher than those in shrub layer, and N:P ratio was significantly lower than that in shrub layer. Herb layer plants were more susceptible to N limitation, whereas shrub layer plants were more susceptible to P limitation and exhibited higher N and P use efficiencies. No significant difference was observed in leaf stoichiometry of shrub layer plants among different forest types, whereas N content, C:N and C:P ratios of herb layer leaves showed significant differences, with herb layer plants in coniferous-broadleaf mixed forest demonstrating higher nutrient use efficiency. (2) Soil C and N contents in the three forest types exhibited the trend CL>CLC>ZK, with extremely significant differences among them; coniferous-broadleaf mixed forest soil had the highest P content but the lowest C:P and N:P ratios. (3) Soil in coniferous-broadleaf mixed forest significantly affected some leaf stoichiometric parameters of understory plants, while soil in the other two forest types showed no significant effects. In summary, significant or extremely significant differences existed in soil stoichiometry among different forest types in Mao'er Mountain; plants in different understory layers had distinct nutrient requirements and environmental adaptation strategies. Soil in coniferous-broadleaf mixed forest exerted a strong influence on understory plant leaf stoichiometry, and its low organic matter decomposition efficiency led to N

limitation in soil; therefore, nitrogen management in coniferous-broadleaf mixed forest should be enhanced.

Full Text

Stoichiometric Characteristics of Understory Plant Leaves and Soil in Three Forest Types in Maoershan

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Abstract: Investigating the stoichiometric characteristics of understory plant leaves and soil across different forest types in Maoershan can reveal adaptation strategies of understory vegetation and provide data support for forest management. This study measured and analyzed the leaf and soil stoichiometry of dominant plants in herb and shrub layers across three forest types: coniferous and broad-leaved mixed forest (ZK), evergreen broad-leaved secondary forest (CLC), and evergreen broad-leaved forest (CL). The results showed: (1) Overall, leaf C and N contents did not differ significantly between herb and shrub layers, while P and K contents were extremely significantly higher in the herb layer, and N:P ratio was significantly lower than in the shrub layer. Herb layer plants were more likely limited by N, whereas shrub layer plants were more likely limited by P and exhibited higher N and P use efficiency. Leaf stoichiometry of shrub layer plants showed no significant differences among forest types, but herb layer plants exhibited significant differences in leaf N content, C:N, and C:P among forest types, with higher nutrient use efficiency in the herb layer of coniferous and broad-leaved mixed forest. (2) Soil C and N contents across the three forest types followed the pattern CL > CLC > ZK, with extremely significant differences among them. The coniferous and broad-leaved mixed forest had the highest soil P content but the lowest C:P and N:P ratios. (3) Soil in the coniferous and broad-leaved mixed forest significantly affected some leaf stoichiometric traits of understory plants, while the other two forest types showed no significant effects. In conclusion, significant or extremely significant differences exist in soil stoichiometry among different forest types in Maoershan. Plants in different understory layers have distinct nutrient requirements and environmental adaptation strategies. The soil of coniferous and broad-leaved mixed forest strongly influences understory plant leaf stoichiometry, and its soil is limited by N due to low organic matter decomposition efficiency. Therefore, N management should be strengthened in coniferous and broad-leaved mixed forests.

Keywords: Maoershan; forest type; soil; herb layer; shrub layer; stoichiometric characteristics

Introduction

Ecological stoichiometry is a theoretical framework and science that analyzes the mass balance of multiple chemical elements and their effects on ecological interactions. Research on stoichiometric characteristics is physiologically significant for revealing species' ecological strategies and adaptations (Li et al., 2023). As the most sensitive organ of plants, leaves are highly responsive to environmental changes with strong plasticity. Their functional traits carry substantial information about environmental variation and are closely related to plant biomass and resource acquisition and utilization (Wright et al., 2004; Niinemets & Kull, 2003). Studying plant environmental adaptability from the perspective of leaf stoichiometry has become a hot topic in ecological research. Mu et al. (2020) suggested that plant leaf functional traits are most closely related to soil. Plants improve soil quality through litter decomposition, while soil quality significantly affects vegetation growth and the speed and direction of community succession. Investigating the response relationship between plant leaf and soil stoichiometry is important for revealing plant ecological adaptation strategies.

Understory plants mainly include shrubs, herbs, vines, and young trees beneath the forest canopy and constitute an important component of forest ecosystems. Different life-form plants occupy different spatial environments (Zhang et al., 2020; Zhu et al., 2014). In recent years, studies on C, N, and P stoichiometry in forest ecosystems have focused primarily on the tree layer or the tree-litter-soil coupling system (Wang et al., 2023; Yu et al., 2023), with relatively few studies on understory plants. However, research has shown that leaf C, N, and P contents and their ratios differ significantly among different life-form plants (Ba et al., 2023), with shrub P content being significantly lower than that of annual and perennial herbs (Liu et al., 2020). As the regeneration and supplement of forests, understory plants play important roles in forest development. Studying leaf stoichiometry of herb and shrub layers in different forest types can help understand the nutrient environment adaptation strategies of understory plants.

The Maoershan National Nature Reserve contains large areas of primary forest vegetation and vertical zonation, especially primary subtropical evergreen broad-leaved forests, which have enormous ecological service value and high scientific research value. However, due to human disturbance, some primary vegetation has degraded into evergreen broad-leaved secondary forests, coniferous and broad-leaved mixed forests, shrublands, and grasslands, causing significant impacts on forest ecosystem functions. Holl (2017) noted that primary forest degradation threatens biodiversity and ecological security. Currently, most studies on forest plants and soil responses in Maoershan focus on dominant upper-layer plants, with few studies on understory plant responses to soil factors (Zhu et al., 2004; Huang & Jiang, 2002). Therefore, combining the current forest status in Maoershan, this study selected three different forest types—coniferous and broad-leaved mixed forest (ZK), evergreen broad-leaved secondary forest (CLC), and evergreen broad-leaved forest (CL)—as research objects. We measured chemical element contents in plant leaves and soil, analyzed their stoichiometric characteristics and internal relationships, aiming to explore: (1) differences in leaf stoichiometry between the same understory layer (herb and shrub layers) across different forest types, and between different understory layers within the same forest type; (2) differences in soil stoichiometry among different forest types in Maoershan; and (3) correlations between leaf and soil stoichiometric characteristics of herb and shrub layer plants across different forest types. The goal is to reveal the ecological adaptation strategies of understory plants in different forest types in this region and provide basic data for forest management in Maoershan.

1.1 Study Area Overview

Maoershan National Nature Reserve is located in northeastern Guangxi, with geographical coordinates of 110°20'–110°35' E, 25°48'–25°58' N. The total area is 17,008.5 hm^2, with the main peak at 2,141.5 m altitude. Maoershan has a mid-subtropical mountain climate, with an average annual temperature of 7 °C at the summit (maximum 23 °C, minimum -1.9 °C) and 16–18 °C at the foot. The annual accumulated temperature above 10 °C is approximately 6,000 °C, and annual precipitation exceeds 2,500 mm. The evergreen broad-leaved forest and evergreen coniferous-broadleaved mixed forest zones are distributed between 300–1,200 m altitude (Zhu et al., 2004; Huang & Jiang, 2002). This study selected three different forest types within this zone (coniferous and broad-leaved mixed forest, evergreen broad-leaved secondary forest, and evergreen broad-leaved forest) to analyze and compare leaf and soil stoichiometric characteristics of understory herb and shrub layers.

1.2 Sampling Methods

A 20 m × 20 m temporary plot was established in each forest type (Table 1). Using the grid method, five 5 m × 5 m quadrats were set up at the four corners and center of each plot. Plants with high coverage or abundance in the herb and shrub layers that met sampling requirements were selected as leaf collection targets. The herb layer included herbs and herbaceous vines, while the shrub layer included shrubs, woody vines, and young trees no taller than 5 m (Table 2). Mature leaves with normal shape and color and without pests or diseases were collected. Plants that appeared repeatedly in the five quadrats were sampled separately and then mixed into one sample. Fresh leaf samples weighed at least 100 g per plant species. Leaves were brought back to the laboratory, killed at 120 °C for 30 minutes in an oven, then dried at 80 °C to constant weight, ground, and passed through a 100-mesh sieve for leaf nutrient content determination.

In each of the five quadrats across forest types, soil was collected from 0–20 cm depth using a soil auger. Soil samples were labeled and brought back to the laboratory for air-drying. After removing stones and fine roots, soils were ground and passed through a 100-mesh sieve for analysis.

Table 1 Basic conditions of sample plots | Forest type | Longitude | Latitude |

			Altitude (m)	Slope (°)	Canopy density
Coniferous and broad-leaved mixed forest	110°29 37 E	25°51 46 N	[data]	[data]	[data]
Evergreen broad-leaved secondary forest	110°29 16 E	25°53 06 N	[data]	[data]	[data]
Evergreen broad-leaved forest	110°29 11 E	25°52 50 N	[data]	[data]	[data]

Table 2 Dominant understory plants in different forest types

Layer	Dominant plant species
Herb layer of coniferous and broad-leaved mixed forest	*Lophatherum gracile*, *Miscanthus sinensis*, *Alpinia japonica*
Shrub layer of coniferous and broad-leaved mixed forest	*Castanopsis fargesii*, *Dalbergia hupeana*, *Adinandra millettii*, *Litsea pseudoelongata*, *Viburnum fordiae*, *Clerodendrum cyrtophyllum*, *Glochidion puberum*, *Ardisia crenata*, *Melastoma dodecandrum*, *Sarcandra glabra*, *Rubus amphidasys*, *Kadsura longipedunculata*
Herb layer of evergreen broad-leaved secondary forest	*Notoseris macilenta*, *Artemisia lactiflora*, *Smilax riparia*, *Dioscorea japonica*, *Impatiens siculifer*
Shrub layer of evergreen broad-leaved secondary forest	*Phoebe bournei*, *Eurya loquaiana*, *Cornus hongkongensis*, *Rhododendron orbiculare*, *R. fortunei*, *Oreocnide frutescens*, *Rubus kwangsiensis*, *Hedera nepalensis*
Herb layer of evergreen broad-leaved forest	*Fordiophyton faberi*, *Pellionia radicans*, *Tripterospermum chinense*
Shrub layer of evergreen broad-leaved forest	*Litsea elongata*, *Symplocos anomala*, *S. sumuntia*, *S. ramosissima*, *Ficus heteromorpha*, *Dichroa febrifuga*, *Rubus buergeri*

1.3 Sample Analysis

Leaf element measurements included carbon (LC), nitrogen (LN), phosphorus (LP), and potassium (LK) contents, with calculations of carbon-to-nitrogen ratio (LC:LN), carbon-to-phosphorus ratio (LC:LP), nitrogen-to-phosphorus ratio (LN:LP), and potassium-to-phosphorus ratio (LK:LP). Soil element measurements included carbon (SC), nitrogen (SN), and phosphorus (SP) contents, with calculations of SC:SN, SC:SP, and SN:SP ratios.

Following the methods of Wu et al. (2023), LC, LN, and SN were determined using an elemental analyzer (Elementar Vario Macro cube, Germany). LP, LK, SC, and SP were determined using the molybdenum-antimony anti-colorimetric method, flame photometry, potassium dichromate volumetry-external heating method, and sodium hydroxide fusion-molybdenum-antimony anti-colorimetric method, respectively.

1.4 Data Analysis

Data were organized using Excel. To meet normality and ANOVA assumptions, all data were natural log-transformed using ln(x+1). SPSS 23.0 was used for t-tests and one-way ANOVA, with Duncan's method for significance testing ($\alpha = 0.05$). Pearson correlation coefficients were used to analyze relationships between understory plant leaf stoichiometry and soil factors.

Results

2.1 Leaf Stoichiometric Characteristics of Understory Plants in Different Forest Types

Analysis of leaf stoichiometry in herb and shrub layers across three forest types (Table 3) revealed that overall, LP, LK, LC:LP, and LN:LP differed extremely significantly between the two layers. LP and LK in the herb layer were extremely significantly higher than in the shrub layer, while LC:LP and LN:LP were extremely significantly lower. LC:LN was significantly lower in the herb layer, with no significant differences in LN, LC, LK:LP, or LN:LK between layers.

Comparing the same layer across different forest types, LN in the herb layer of evergreen broad-leaved secondary forest was significantly higher than in coniferous and broad-leaved mixed forest, but not significantly different from evergreen broad-leaved forest. LC:LN in the herb layer of coniferous and broad-leaved mixed forest (21.953) was significantly higher than in the other two forest types. LC:LP in the herb layer of evergreen broad-leaved forest and coniferous and broad-leaved mixed forest was significantly higher than in evergreen broad-leaved secondary forest. No significant differences in leaf stoichiometry were found among shrub layers across the three forest types.

Within the same forest type, all indices showed no significant differences between layers in evergreen broad-leaved forest. In evergreen broad-leaved secondary forest, LN, LP, and LK in the herb layer were significantly or extremely significantly higher than in the shrub layer, while LC:LN, LC:LP, LN:LP, and LN:LK were significantly or extremely significantly lower. LC and LK:LP showed no significant differences between layers. In coniferous and broad-leaved mixed forest, only LN:LP in the shrub layer was significantly higher than in the herb layer, with no significant differences in other indices.

Table 3 Variation in leaf stoichiometry of forest understory plants

Trait	Herb layer (overall)	Shrub layer (overall)	ZK herb	ZK shrub	CLC herb	CLC shrub	CL herb	CL shrub
LC ($g \cdot kg^{-1}$)	411.067±24.597	417.817±20.703	403.110±23.720	393.937±22.576	395.716±28.049	424.620±21.110	419.858±19	
kg^{-1})	22.650±1.193	20.703±2.990	18.373±1.881	21.800±1.100	24.314±1.489	21.341±1.100	17.010±2.423	17.106±5.025
LP ($g \cdot kg^{-1}$)	1.371±0.732**	1.100±0.369**	1.205±0.794**	1.100±0.361**	1.489±1.024*	1.100±0.361**	1.772±0.361**	1.100±0.361**
LK ($g \cdot kg^{-1}$)	17.492±15.676**	10.466±4.853 **	17.492±17.492 *	10.532±4.595 *	30.199±11.750 *	12.271±4.595 *	13.273±10.281 *	8.335±4.595 *
LC : LN	18.373±4.068 *	21.800±6.609*	21.953±0.869b	18.373±1.772*b	17.010±6.237*	21.341±4.488a	24.314±4.068*	21.800±6.609*
LC : LP	272.509±74.651**	419.338±130.071**	308.629±25.281a	447.376±65.237**b	179.359±16.968 **	381.564±29.486a	240.019±13.909 *	419.338±130.071 **
LN : LP	16.017±2.923 **	19.451±3.784 **	14.405±3.229 *	18.781±2.728 *	12.347±10.281 *	17.997±3.784 *	22.164±2.399 *	19.451±3.784 **
LK : LP	11.107±1.092	12.089±1.855±	10.786±0.386 *	10.552±1.910±	12.089±2.283 *	11.107±2.698 *	6.999±2.399 *	12.089±1.092 *
LN :								

LK	1.371±0.369	1.100±0.386*	1.205±0.361**	1.100±0.361**	1.489±1.024*	1.100±0.361**	1.772±0.361**	1.100±0.361**

Note: * indicates significant differences between herb and shrub layers within the same forest type (P<0.05); ** indicates extremely significant differences between herb and shrub layers within the same forest type (P<0.01). Different lowercase letters indicate significant differences among forest types within the same layer (P<0.05); no letters indicate no significant differences (P>0.05).

2.2 Soil Stoichiometric Characteristics in Different Forest Types

Soil stoichiometric analysis (Table 4) showed that SN and SC in the three forest types followed the pattern CL > CLC > ZK. SN differed extremely significantly among all types. SC in evergreen broad-leaved forest was extremely significantly higher than in coniferous and broad-leaved mixed forest, but not significantly different from evergreen broad-leaved secondary forest. SP in coniferous and broad-leaved mixed forest was extremely significantly higher than in the other two forest types. SC:SP and SN:SP were both extremely significantly lower in coniferous and broad-leaved mixed forest. SC:SN showed no significant differences among the three forest types.

Table 4 Variation in soil stoichiometric characteristics across forest types

Trait	ZK	CLC	CL
SN ($g \cdot kg^{-1}$)	2.693±0.892C	3.758±0.437B	5.163±0.747A
SP ($g \cdot kg^{-1}$)	0.358±0.089A	0.131±0.031B	0.185±0.041B
SC ($g \cdot kg^{-1}$)	73.112±15.193B	99.671±19.955AB	126.545±18.006A
SC:SN	29.888±14.276	26.659±5.350	24.890±4.778
SP	212.702±65.655B	779.617±148.603A	711.858±176.914A
SN:SP	7.489±1.270B	29.427±3.733A	28.332± A

Note: Different uppercase letters in the same row indicate extremely significant differences among forest types (P<0.01); unmarked letters indicate no significant differences (P>0.05).

2.3 Correlations Between Leaf and Soil Stoichiometric Characteristics

As shown in Table 5 , correlations between herb layer leaf and soil stoichiometry were not significant in evergreen broad-leaved secondary forest or evergreen broad-leaved forest. In coniferous and broad-leaved mixed forest, LP was significantly negatively correlated with SP, while LC:LN was significantly correlated with SN:SP.

Table 5 Correlation analysis between leaf and soil stoichiometric characteristics in herb layer

Trait	SC:SN	SC:SP	SN:SP
LC:LN	-0.999*	0.998*	
LC:LP			
LN:LP			
LK:LP			
LN:LK			

Note: * indicates significant correlation at the 0.05 level (two-tailed). The same below.

According to Table 6 , LN:LK in shrub layer plants of coniferous and broad-leaved mixed forest was significantly negatively correlated with SN but significantly positively correlated with SC:SP, while LK:LP was significantly negatively correlated with SC:SN. In evergreen broad-leaved forest, SN in shrub layer plants was significantly positively correlated with LK:LP.

Table 6 Correlation analysis between leaf and soil stoichiometric characteristics in shrub layer | Trait | SC:SN | SC:SP | SN:SP | |——-|——-|——-|——-| | LC:LN | | | | | LC:LP | | | | | LN:LP | | | | | LK:LP | -0.998* | -0.999* | 1.000** | | LN:LK | 0.892* | | |

Note: ** indicates significant correlation at the 0.01 level (two-tailed).

Discussion

3.1 Differences in Leaf Stoichiometric Characteristics Among Different Layers and Forest Types

C, N, P, and K elements jointly affect plant growth and influence each other. The dynamic balance of element contents and their stoichiometric characteristics are direct influencing factors of plant productivity and soil fertility (Dong et al., 2019; Yu et al., 2014). In this study, leaf C content of understory plants was 411.067 $g \cdot kg^{-1}$, lower than the global average (464 $mg \cdot g^{-1}$) and the average leaf C content in Yunnan's monsoon evergreen broad-leaved forest (470.3 $g \cdot kg^{-1}$) (Liu et al., 2010; He et al., 2000). This may be because our research focused on understory plants, where upper-layer dominant plants have competitive advantages that limit resource acquisition and utilization by understory plants, resulting in weaker C storage capacity. Since understory herb and shrub layer plants are mostly fast-growing species, leaf N content in this study (22.650 $g \cdot kg^{-1}$) was slightly higher than the global average N content (20.10 $mg \cdot g^{-1}$). Research indicates that leaf P content in Chinese plants is lower than the global scale (Ren et al., 2007), consistent with our results. Plant C:N and C:P ratios typically reflect plant N and P use efficiency and can help determine N and P nutrient supply conditions for plant growth (Wang & Yu, 2008). In this study, leaf C:N was lower than the global average of 22.5 and lower than that in Zhejiang Tiantong's evergreen broad-leaved forest (39.9) and evergreen coniferous forest (48.1). Leaf C:P was slightly higher than the global average of 232 but lower than that in Zhejiang Tiantong's evergreen broad-leaved forest (758.0) and evergreen coniferous forest (677.9), indicating lower N and P use efficiency in understory plants in our study area (Yan et al., 2010; Elser et al., 2000). Since N:P threshold values vary with ecosystem type and plant species composition, a single N:P threshold cannot be used alone to determine limiting elements across different ecosystems. However, lower N:P ratios generally indicate greater N limitation, while higher N:P ratios indicate greater P limitation (Jiang et al., 2019). In this study, the N:P ratio in the herb layer was lower than in the shrub layer, indicating that herb layer plants were more N-limited while shrub layer plants were more P-limited.

In comparisons between different layers within the same forest type, overall understory plants and evergreen broad-leaved secondary forest plants showed similar patterns of leaf stoichiometric changes. Leaf C content did not differ significantly between layers, while leaf P and K contents were significantly or extremely significantly higher in the herb layer, possibly because herbaceous plants have short lifespans and fast growth rates, requiring more N and P for growth and reproduction (Liu et al., 2020; Zhang et al., 2019). Between different layers, almost all stoichiometric differences were non-significant in evergreen broad-leaved forest and coniferous and broad-leaved mixed forest, while most stoichiometric differences were significant or extremely significant in evergreen broad-leaved secondary forest. Whether this represents an adaptive response to human disturbance requires further study. Since C content variation in plants is relatively small, changes in P content affect C:P variation, resulting in significant or extremely significant differences between herb and shrub layers, consistent with previous research (Reich et al., 2004; Hedin, 2004). The growth rate hypothesis suggests that plants with higher C:N and C:P ratios have slower growth rates (Zhang et al., 2016). In this study, C:N and C:P ratios were higher in the shrub layer than in the herb layer, with significant or extremely significant differences in overall and evergreen broad-leaved secondary forest comparisons (Table 3), indicating higher N and P use efficiency but slower growth in shrub layer plants. This suggests that different understory layers adopt different nutrient utilization strategies in the same habitat. In evergreen broad-leaved forest and coniferous and broad-leaved mixed forest, differences in leaf stoichiometry between layers were not significant, while most leaf stoichiometric traits differed significantly or extremely significantly between herb and shrub layers in evergreen broad-leaved secondary forest. This may be because human disturbance altered understory space and light resources, causing changes in dominant understory species and consequently changes in nutrient utilization strategies.

In analyses of understory leaf stoichiometry within the same layer across different forest types, no significant differences were found among shrub layers of the three forest types, indicating relatively stable nutrient utilization among shrub layer plants across forest types. Overall, understory plants in evergreen broad-leaved secondary forest showed higher N, P, and K contents, possibly because after human disturbance and logging of upper vegetation in secondary forests, understory plants could access more resources, facilitating rapid growth and exhibiting higher N, P, and K contents. Leaf C:N and C:P ratios can reflect plant nutrient use efficiency to some extent (Ba et al., 2023; Yuan et al., 2019). Xing et al. (2000) suggested that plants show higher or lower nutrient use efficiency under conditions of nutrient deficiency or excess. In this study, leaf C:N and C:P ratios in both layers of coniferous and broad-leaved mixed forest were higher than in the other two forest types, indicating higher nutrient use efficiency in understory plants of this forest type. Combined with soil analysis, this may be due to N limitation in the soil, leading to higher nutrient use efficiency in understory plants.

3.2 Differences in Soil Stoichiometric Characteristics Among Different Forest Types

C, N, and P are the main components of soil nutrients and significantly affect ecosystem productivity (Song et al., 2019). In this study, SN and SC in the three forest types showed the pattern CL > CLC > ZK. Soil C and N contents in evergreen broad-leaved forest were 1.7 and 1.9 times higher than in coniferous and broad-leaved mixed forest, mainly because soil C and N contents primarily originate from decomposition and accumulation of surface forest litter. The understory soil in evergreen broad-leaved forest is moist, with abundant broadleaf litter that decomposes quickly, enhancing soil nutrients. In contrast, coniferous species in mixed forests adopt conservative ecological strategies, returning fewer nutrients to the soil, and pine needle litter decomposes slowly with slower nutrient release (Zhang et al., 2019; Ouyang et al., 2007). Soil P content was extremely significantly higher in coniferous and broad-leaved mixed forest than in the other two forest types, mainly because soil P primarily originates from rock weathering and is influenced by parent material, with only a small portion derived from plant return.

Soil C:N:P stoichiometric ratios reflect the ability of soils to release N and P elements and are often used to predict and measure soil organic matter composition and decomposition rates (Tian et al., 2010). Soil C:N reflects the balance of soil C and N nutrition and the mineralization capacity of soil N (Wang et al., 2013). In this study, SC:SN ranged from 24.890 to 29.888 across the three forest types, with no significant differences, indicating that the soil C:N ratio remains relatively stable during soil nutrient input and output processes. SC:SN showed the pattern ZK > CLC > CL, all higher than the global average (12.4), indicating slow soil mineralization rates in all three forest types, with the slowest organic matter decomposition efficiency in coniferous and broad-leaved mixed forest. Soil C:P is an important indicator of soil microbial nutrient release and P absorption capacity from the soil environment, and is inversely proportional to soil P mineralization rate (Li et al., 2018; Zhu et al., 2013). SC:SP showed the pattern CLC > CL > ZK, indicating that coniferous and broad-leaved mixed forest had the highest soil P mineralization efficiency, which may be one reason for its higher SP content (Table 4). Soil N:P can reflect N and P mineralization rates and nutrient pool capacity, thereby determining community nutrient limitation levels (Zhang et al., 2019). Bui and Henderson (2013) found that soil N:P < 10 indicates N limitation. In this study, soil N:P in coniferous and broad-leaved mixed forest was 7.489, lower than the threshold of 10 from Bui and Henderson (2013) and lower than the national average N:P of 8 from Tian et al. (2010), indicating relatively low soil N content and N limitation on plant growth. Management practices could supplement nitrogen fertilizer to improve soil nutrients and promote plant growth.

3.3 Relationships Between Leaf and Soil Stoichiometric Characteristics

Research shows that chemical element contents in plants are closely related to those in soil (Ba et al., 2023; Jiang et al., 2019). In this study, correlations between leaf and soil stoichiometry differed among layers within the same forest type. The correlation patterns between leaf and soil stoichiometry in herb and shrub layers were similar across the three forest types: soil effects on understory plant leaf stoichiometry were strongest in coniferous and broad-leaved mixed forest, while effects were not significant in evergreen broad-leaved secondary forest and evergreen broad-leaved forest. This may be because soil C and N contents in coniferous and broad-leaved mixed forest were significantly lower than in the other two forest types, and insufficient soil nutrients more strongly affected understory plant growth. In contrast, relatively abundant nutrients in evergreen broad-leaved secondary forest and evergreen broad-leaved forest could provide required growth conditions for plants, thus having smaller effects on understory herb and shrub layer plants.

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