Ecological Stoichiometric Characteristics of Broad-Leaved Korean Pine Forests and Their Responses to Latitudinal Gradients: Postprint

Authors: Li Xixia, Du Tianyu, Wei Yawei, Zhou Yongbin

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Abstract

To investigate the spatial distribution and influencing factors of nutrient and ecological stoichiometric characteristics of Korean pine (Pinus koraiensis) needles, typical old-growth broadleaf-Korean pine forests were selected along a latitudinal gradient in three regions based on the distribution patterns of temperate broadleaf-Korean pine forests in China: Changbai Mountain (42°27' N), Zhangguangcai Range (44°16' N), and Lesser Khingan Range (48°05' N). The contents of carbon (C), nitrogen (N), and phosphorus (P) in Korean pine needles, as well as organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP) in surface soil (0-15 cm) and mid-layer soil (15-30 cm) were measured, and their distribution characteristics and interrelationships were analyzed. The results showed that: 1) The C, N, and P contents in Korean pine needles were significantly higher than those in soils. The ranges of C, N, and P contents in surface soil were 27.6-87.4 mg/g, 2.0-7.2 mg/g, and 0.26-0.92 mg/g, respectively; those in mid-layer soil were 8.1-59.7 mg/g, 0.7-4.6 mg/g, and 0.2-0.82 mg/g, respectively; while those in needles were 495.5-507.4 mg/g, 12.7-172.5 mg/g, and 1.1-2.1 mg/g, respectively. 2) SOC, C/N, and C/P in soils increased extremely significantly with increasing latitude, whereas the stoichiometric characteristics of elements in needles did not change significantly with latitude. 3) The N and P contents in needles were significantly positively correlated with soil N and P contents, respectively; meanwhile, needle N was significantly correlated with soil C/N, and needle P with soil N/P. In comparison, the N and P contents in Korean pine needles were relatively low, which may indicate insufficient soil N and P supply in broadleaf-Korean pine forests, and the needle N/P ratio was only 9.9, suggesting that N limitation is more pronounced in the temperate broadleaf-Korean pine forests of Northeast China. This study provides a foundation for elucidating the nutrient supply status and limiting factors in temperate broadleaf-Korean pine forests of Northeast China, and for

proposing management measures to enhance Korean pine productivity in these forest regions.

Full Text

Preamble

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Characteristics of Ecological Stoichiometry in Broad-Leaved Korean Pine Mixed Forest and Its Response to Latitude Gradient in Northeast China

LI Xixia, DU Tianyu, WEI Yawei, ZHOU Yongbin
College of Science, Shenyang Agricultural University; College of Forestry, Shenyang Agricultural University; Liaoning Liaohe Plain Forest Ecosystem Research Station, Chinese Forest Ecosystem Research Network, Changtu 112500, China

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Abstract

This study investigated the spatial distribution patterns and influencing factors of nutrient contents and ecological stoichiometric characteristics in Korean pine (*Pinus koraiensis* Sieb. et Zucc.) leaves across the temperate broad-leaved Korean pine mixed forest distribution range in Northeast China. Based on the distribution characteristics of these forests, we selected three typical old-growth broad-leaved Korean pine mixed forest sites along a latitudinal gradient: Changbai Mountain (42°27 N), Zhangguangcai Mountain (44°16 N), and Xiaoxing' anling Mountain (48°05 N). We measured carbon (C), nitrogen (N), and phosphorus (P) contents in surface soil (0–15 cm), subsurface soil (15–30 cm), and Korean pine leaves, and analyzed their spatial variation patterns along the latitude gradient and the relationships between leaf and soil nutrients.

The results showed that: (1) Leaf C, N, and P contents were significantly higher than those in soil. In surface soil (0–15 cm), C, N, and P ranged from 27.6–87.4 mg/g, 0.26–0.92 mg/g, and 2.0–7.2 mg/g, respectively; in subsurface soil (15–30 cm), they ranged from 8.1–59.7 mg/g, 0.7–4.6 mg/g, and 0.2–0.82 mg/g, respectively; while in leaves, they ranged from 495.5–507.4 mg/g, 12.7–17.3 mg/g, and 1.1–2.1 mg/g, respectively. (2) Soil organic carbon (SOC) and C/N and C/P ratios increased significantly with increasing latitude, whereas leaf element stoichiometric characteristics showed no significant latitudinal variation. (3) Leaf N and P contents were significantly positively correlated with total N and P in surface soil, respectively; additionally, leaf N was significantly correlated with C/N in surface soil, and leaf P was correlated with N/P in surface soil. (4) Compared with natural forest ecosystems along the North-South Transect of Eastern

China, Korean pine leaves had lower N and P contents, suggesting insufficient nutrient supply for Korean pine growth. Furthermore, the low leaf N/P ratio (9.9) indicated stronger N limitation than P limitation in broad-leaved Korean pine forests. These results clarify the nutrient supply conditions and limiting factors in Northeast China' s temperate broad-leaved Korean pine forests and provide a foundation for developing management strategies to enhance Korean pine productivity.

Keywords: ecological stoichiometry characteristics; latitude gradient; Korean pine; broad-leaved Korean pine forest; Northeast China

Introduction

Ecological stoichiometry is the science that integrates biological, chemical, and physical principles to study the balance of energy and multiple chemical elements in biological systems. It has become a hot topic in ecological research, attracting widespread attention from scholars worldwide. Most studies have focused on vegetation and soil ecological stoichiometric characteristics across different ecosystems, examining patterns at various scales from global and regional to ecosystem and individual levels.

Research along vertical altitude gradients has shown that soil organic carbon and total nitrogen contents increase linearly with altitude or show an initial increase followed by a decrease. Plant and soil C/N, C/P, and N/P ratios are related to temperature, altitude, and soil constraints. Along latitudinal gradients, studies have found that plant leaf nitrogen and phosphorus contents increase significantly with latitude, while N/P ratios decrease. For example, Reich and Oleksyn' s global-scale study of plant leaf nutrients found that N/P ratios decrease with increasing latitude. However, regional studies in China have primarily focused on arid regions such as the Loess Plateau, with limited research on forest ecosystems, particularly broad-leaved Korean pine forests—the zonal climax vegetation in the eastern mountainous regions of Northeast China.

Although previous studies have reported on soil physicochemical properties, fine root stoichiometry, and soil enzyme activities in broad-leaved Korean pine forests, research from an ecological stoichiometry perspective on soil and leaf characteristics along latitudinal gradients remains lacking. This study addresses this gap by comparing changes in ecological stoichiometric characteristics of soil and Korean pine leaves across different latitudes to explore the nutrient allocation patterns and adaptation mechanisms of Korean pine under varying latitudinal conditions.

1. Sample Plot Selection and Study Area Overview

We selected three representative sites across the typical distribution area of natural broad-leaved Korean pine forests in China, arranged from south to north along a latitudinal gradient: Lushuihe in Changbai Mountains, Muling in Zhangguangcai Mountains, and Wuying in Xiaoxing' anling. All three study areas feature a temperate continental climate with mean annual precipitation of 550–700 mm. The soil type is dark brown forest soil. Dominant tree species include Korean pine (*Pinus koraiensis*), Manchurian ash (*Fraxinus mandshurica*), Mongolian oak (*Quercus mongolica*), and Manchurian walnut (*Juglans mandshurica*). In Muling and Xiaoxing' anling, coniferous trees also include small amounts of spruce (*Picea* spp.) and fir (*Abies nephrolepis*). Korean pine is the most abundant coniferous species, accounting for 23%–46% of stand volume. Detailed geographic and climatic information for each site is provided in .

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1. Sample Collection and Processing

At each site, we established 20 m × 20 m sample plots in old-growth forests with minimal human disturbance. Within each plot, we selected five healthy, similarly-growing Korean pine individuals. During the peak growing season in August, we collected mature leaves from upper, middle, and lower canopy positions and different aspects. Leaves from the same tree were mixed to form one sample. Soil samples were collected from the center and four corners of each plot at two depths: surface (0–15 cm) and subsurface (15–30 cm). Soils from the same layer within a plot were mixed to form composite samples.

All samples were placed in labeled self-sealing bags and transported to the laboratory. Leaf and soil organic carbon (SOC) were determined using the potassium dichromate external heating method [25]. Total nitrogen (TN) was measured by the Kjeldahl method [26], and total phosphorus (TP) by the molybdenum-antimony colorimetric method [27]. Soil samples were air-dried and ground to pass through a sieve before analysis.

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2. Data Processing

We used one-way ANOVA and multiple comparisons to analyze differences in stoichiometric characteristics of Korean pine soil and leaves across latitudes. Pearson correlation analysis was employed to examine relationships between leaf C, N, P and their ratios with latitude and soil nutrients.

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2. Results and Analysis

1. Soil Ecological Stoichiometry

Soil organic carbon (SOC) content in surface soil (0–15 cm) ranged from 27.6–87.4 mg/g, with a mean of 45.95 mg/g. Total nitrogen (TN) ranged from 2.0–7.2 mg/g (mean: 56.01 mg/g), and total phosphorus (TP) ranged from 0.26–0.92 mg/g (mean: 77.00 mg/g). SOC and TN contents showed significant positive correlations with latitude ($p < 0.01$), with the highest and lowest values both occurring at the Muling site. The C/N, C/P, and N/P ratios ranged from 11.49–15.88, 55.36–174.53, and 4.04–11.93, respectively, all increasing significantly with latitude.

In subsurface soil (15–30 cm), SOC ranged from 8.1–59.7 mg/g (mean: 32.51 mg/g), TN from 0.8–4.6 mg/g (mean: 14.71 mg/g), and TP from 0.2–0.82 mg/g (mean: 30.95 mg/g). SOC content was extremely significantly positively correlated with latitude ($p < 0.01$). The C/N, C/P, and N/P ratios ranged from 9.22–15.01, 35.27–112.73, and 3.67–8.48, respectively, also showing clear increasing trends with latitude. Overall, soil element variation was greatest in the Muling region [Figure 1: see original paper].

2. Korean Pine Leaf Ecological Stoichiometry Along the Latitude Gradient

Korean pine leaf organic carbon content ranged from 495.5–507.4 mg/g, with mean values of 500.48, 503.96, and 501.79 mg/g at Lushuihe, Muling, and Wuying, respectively. Leaf nitrogen content ranged from 12.7–17.3 mg/g (means: 14.99, 14.11, and 14.17 mg/g), and leaf phosphorus content ranged from 1.1–2.1 mg/g (means: 1.57, 1.50, and 1.44 mg/g). None of the leaf C, N, or P contents showed significant changes with latitude. Similarly, leaf C/N (26.37–28.75), C/P (235.14–350.1), and N/P (8.13–13.76) ratios exhibited no significant latitudinal trends [Figure 2: see original paper].

3. Relationships Between Leaf Chemical Stoichiometry and Soil Nutrients

Leaf N and P contents were significantly positively correlated with total N and P contents in surface soil, respectively. Leaf N content was also significantly correlated with C/N ratio in surface soil, while leaf P content was correlated with N/P ratio in surface soil. Leaf C/P and N/P ratios showed significant positive correlations with soil C/P and N/P ratios in both surface and subsurface layers. Leaf C/N ratio was significantly negatively correlated with soil C/N ratio. These relationships indicate that soil nutrient content influences plant nutrition primarily through stoichiometric ratios .

4. Comparison with Other Regions

Compared with forest ecosystems along the North-South Transect of Eastern China (NSTEC), Chinese terrestrial plants, and global terrestrial plants, Korean pine leaves in our study area had higher carbon content (502.2 mg/g, 8.8% higher than NSTEC forests) but lower nitrogen (20.1 mg/g, 21.3% lower than NSTEC forests) and phosphorus (1.50 mg/g, 17.7% lower than global terrestrial plants). The leaf N/P ratio (9.9) was significantly lower than that of Chinese terrestrial plants (20.2 mg/g), indicating stronger nitrogen limitation .

Soil C/N, C/P, and N/P ratios in the 0–15 cm layer were higher than global grassland soils and Chinese terrestrial soils but lower than global forest soils. The 15–30 cm layer showed similar patterns, with C/N significantly higher than Chinese terrestrial soils but C/P and N/P lower than Chinese and global terrestrial soils .

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1. Leaf and Soil Nutrient Stoichiometry Characteristics

The high leaf carbon content in broad-leaved Korean pine forests suggests strong carbon sequestration capacity. The relatively low leaf N and P contents may be attributed to the region' s low temperatures, which affect plant metabolic processes and soil microbial activity. According to the temperature-biogeochemistry hypothesis proposed by Reich and Oleksyn, low temperatures reduce soil microbial and enzyme activity, slowing nitrogen mineralization and leading to lower soil N availability. The low leaf N/P ratio (9.9) indicates nitrogen limitation, consistent with findings for temperate and boreal forests.

Soil C/N, C/P, and N/P ratios were higher than those of Chinese terrestrial soils and global grassland soils, likely due to accumulation of organic carbon in the surface layer. The subsurface soil had lower organic carbon but relatively stable N and P contents, resulting in different stoichiometric ratios compared to the surface layer.

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2. Latitudinal Patterns of Stoichiometric Characteristics in Broad-Leaved Korean Pine Forests

Soil SOC, TN, and TP contents in both surface and subsurface layers showed similar patterns, with SOC and TN significantly positively correlated with latitude. This contrasts with studies on the Loess Plateau that found exponential decreases in these elements with latitude, likely due to differences in climate (more humid conditions in our study area) and soil properties. The latitudinal increase in soil elements may be driven by temperature effects on decomposition rates and microbial activity.

In contrast, leaf C, N, and P contents and their ratios showed no significant latitudinal trends. This may be because Korean pine' s distribution gradient is relatively small, and the sample size was limited. Additionally, the narrow latitudinal range may not capture sufficient environmental variation to produce clear patterns. The lack of significant trends warrants further research with expanded sampling.

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3. Relationships Between Soil Nutrient Characteristics and Plant Leaf Stoichiometry

The correlation patterns between leaf and soil elements were consistent across soil layers. Leaf N and P contents correlated with their respective soil total N and P contents, while leaf stoichiometric ratios (C/N, C/P, N/P) correlated more strongly with soil ratios than with individual element contents. This suggests that soil nutrient availability influences plant nutrient use efficiency through stoichiometric balance rather than absolute quantities.

The significant positive correlations between leaf C/P, N/P and soil C/P, N/P indicate that soil nutrient ratios strongly regulate plant nutrient utilization. The negative correlation between leaf C/N and soil C/N further demonstrates this regulatory relationship. These findings align with studies in other ecosystems showing that plant nutrient status reflects soil stoichiometric characteristics.

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4. Conclusion

Our study revealed that soil organic carbon in broad-leaved Korean pine forests increases significantly with latitude, while leaf nutrient stoichiometry shows no significant latitudinal patterns. The low leaf N/P ratio (9.9) indicates stronger nitrogen than phosphorus limitation in this ecosystem. Leaf nutrient contents and stoichiometric ratios are more strongly influenced by soil nutrient status than by latitude, with soil stoichiometric ratios serving as key regulators of plant nutrient use efficiency. These findings provide fundamental data for understanding nutrient cycling and developing management strategies to enhance productivity in Northeast China' s temperate broad-leaved Korean pine forests.

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