Postprint: Leaf Nitrogen and Phosphorus Resorption Efficiency in Major Forest Types of Northern Mountainous Regions

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Abstract

Nutrient resorption is an important driving force in plant nutrient use strategies, which can reduce nutrient loss, decrease dependence on the environment, and holds significant ecological significance for plant population and community stability, as well as ecosystem nutrient cycling. Based on collected data on nitrogen and phosphorus nutrient contents in mature leaves and litter of various forests (natural forests and plantation forests) in northern mountainous regions (Loess Plateau, Taihang Mountains, and mountainous areas north of Beijing), this study grouped various forest types according to community life forms and management practices, and conducted a comprehensive assessment of their nutrient resorption efficiencies. The results showed that leaf nitrogen and phosphorus resorption efficiencies calculated from nitrogen and phosphorus contents in mature and senesced leaves of various forest vegetation types ranged from 24.5%~71.3% and 18.1%~75.4%, respectively, with mean values of 45.5% and 47.4%. The average nitrogen contents in mature leaves of natural forests and plantation forests in northern mountainous regions were 11.6 g · kg 1 and 21.6 g · kg 1, respectively, with nitrogen content in mature leaves of plantation forests being significantly higher than that of natural forests, indicating that nutrients may be largely in a state of consumption during the growth process of plantation forests. Differences in leaf phosphorus contents between natural forests and plantation forests existed among different regions: phosphorus contents in mature and senesced leaves of natural forests in the Taihang Mountains were significantly higher than those of plantation forests, whereas in mountainous areas north of Beijing, phosphorus content in mature leaves of plantation forests was higher while that in senesced leaves was lower. Nitrogen contents in mature and senesced leaves of shrubs were significantly higher than those of trees, while no significant difference in phosphorus content existed between the two; nitrogen resorption efficiency of shrub leaves was higher than that of trees. Comparison among the three regions revealed that leaf nitrogen and phosphorus

resorption efficiencies of trees in mountainous areas north of Beijing were 62.1% and 67.8%, respectively, higher than those in the other two regions. Correlation analysis indicated that nitrogen content in forest litter in northern mountainous regions was an important factor affecting leaf nitrogen and phosphorus resorption efficiencies. Comparison of nutrient resorption efficiencies among different tree species revealed that coniferous species had higher nutrient resorption efficiencies than broadleaf species, suggesting that coniferous species have higher nutrient resorption efficiencies and are better adapted to nutrient-poor soil environments in mountainous areas. The high nutrient use efficiency of coniferous species should be considered when establishing plantations in mountainous areas.

Full Text

Nitrogen and Phosphorus Resorption Efficiency of Forests in North China

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Abstract

Nutrient cycling is one of the basic functions of forest ecosystems. As two of the main nutrition elements, nitrogen and phosphorus are critical for proper metabolism and growth processes of plants. In order to reduce dependence on external nutrient uptake and minimize nutrient losses, plants can resorb nutrients from senescing leaves prior to abscission and store them in other tissues for reuse. Resorption efficiency, defined as the percent nutrient reduction between live and senescent leaves, quantifies this resorption capacity. Nutrient resorption is a key process in plant nutrient utilization strategy that reduces nutrient loss from ecosystems and lowers environmental dependence, which is crucial for plant population and community stability as well as ecosystem nutrient cycling.

Based on published data from forest ecosystems in the mountainous regions of North China (including the Loess Plateau, Taihang Mountains, and North

Beijing Mountain Area), we compiled and systematized nitrogen and phosphorus contents in mature and senescent leaves across different forest types. Data from 13 sites in these three regions were collected to conduct a comprehensive assessment of nutrient resorption efficiencies. We compared nitrogen and phosphorus resorption efficiencies between trees and shrubs, as well as between natural and plantation forests. To explore the factors regulating nutrient resorption efficiency, we also analyzed relationships between nitrogen and phosphorus contents and resorption efficiency.

The results showed that nitrogen and phosphorus resorption efficiencies for forests ranged from 24.5%-71.3% and 18.1%-75.4%, respectively, with averages of 45.5% and 47.4%, both slightly lower than global averages. Average nitrogen content in mature leaves of plantation forests was 21.6 $g \cdot kg^{1}$, significantly higher than that of natural forests (11.6 $g \cdot kg^{1}$), indicating excessive nutrient consumption during plantation growth. In the Taihang Mountains, nitrogen content in mature and senescent leaves and nitrogen resorption efficiency for shrubs were significantly higher than those for trees, while phosphorus resorption efficiency was relatively lower, demonstrating that plant growth in this region is primarily limited by nitrogen supply.

Comparisons among different areas showed that nitrogen and phosphorus resorption efficiencies in the North Beijing Mountain Area were higher than those in the Loess Plateau and Taihang Mountains. Correlation analysis revealed that both nitrogen and phosphorus resorption efficiencies were significantly correlated with nitrogen content in senescent leaves, indicating that the nitrogen content of senescent forest leaves (also called nutrient resorption proficiency) in North China is the main limiting factor for nitrogen and phosphorus resorption efficiencies. Based on comparisons of nutrient resorption efficiencies among different vegetation species, coniferous forests exhibited greater nutrient resorption efficiencies than broad-leaved species, suggesting that in nutrient-poor mountain soils, coniferous forests have more efficient nutrient resorption and are likely more adaptable to such barren environments. In the development of artificial plantations in mountain regions, the high nutrient use efficiency of coniferous forests should be considered.

Keywords: Mountain regions in North China; Forest type; Life form; Management pattern; Nitrogen and phosphorus content; Nutrient resorption efficiency

Introduction

Nutrient cycling is a fundamental function of ecosystems. In ecosystem nutrient cycling, nitrogen and phosphorus occupy crucial positions and are often the key elements limiting plant growth in natural ecosystems. To minimize dependence on current-season nutrient uptake and reduce nutrient losses, plants resorb mineral elements from senescing leaves for reuse in subsequent growing seasons. Nutrient resorption at the end of the growing season represents an

internal nutrient cycling process in plants. Resorption efficiency (RE) is defined as the ratio of the difference in element content between mature and senescent leaves to the content in mature leaves, and this metric quantifies a plant' s capacity to recycle nutrients. As an important driver of plant nutrient use strategy, nutrient resorption reduces nutrient loss and environmental dependence, significantly influencing the chemical characteristics and decomposition processes of litter, and thus holds important ecological significance for plant population and community stability as well as ecosystem nutrient cycling.

Plant nutrient resorption represents an adaptive strategy to external environmental conditions, primarily influenced by soil nutrient availability, environmental factors, and genetic characteristics. Studies in the Dongling Mountain region on *Quercus wutaishansea* Mary forests found that nitrogen resorption efficiency in deciduous plants is strongly affected by nutrient content in mature leaves, which is itself controlled by soil nutrient supply. However, Aerts noted that while nutrient resorption is an important nutrient conservation mechanism at the species level, resorption efficiency is not particularly sensitive to improved soil nutrient availability at the interspecific level. Forest type also significantly affects nutrient resorption efficiency. Comparative studies of coniferous and broad-leaved forests in the Taihang Mountains revealed substantial differences in nutrient resorption between evergreen coniferous and deciduous broad-leaved forests. Deciduous species such as *Robinia pseudoacacia* Linn. can resorb 34%–53% of nitrogen and 28%–56% of phosphorus from leaves, whereas *Platycladus orientalis* (L.) Franco showed no obvious nutrient resorption, with significant differences also observed in litter nutrient content and decomposition characteristics between these forest types. Global-scale meta-analyses have confirmed these patterns, with Kobe et al. demonstrating that variability in nutrient resorption within species is not entirely determined by external nutrient supply levels, while variation among species tends to be more strongly driven by soil nutrient resources.

Although numerous studies have examined nutrient utilization, most have focused on nutrient cycling in specific forest types, with few comprehensive comparisons across different regional forest types and even fewer syntheses comparing nutrient cycling between natural and plantation forests. The mountainous regions of North China, extending from west to east across the Loess Plateau, Taihang Mountains, and North Beijing Mountain Area, represent important components of China' s forest resources. These forests play crucial roles in windbreak and sand fixation, water source conservation, soil erosion control, and atmospheric purification for northern China, particularly the Beijing-Tianjin region. However, due to natural environmental changes and human activities, vegetation in these mountainous areas has been severely degraded, with increasingly deteriorating ecological conditions, particularly prominent environmental problems such as soil erosion and water resource shortages. In recent decades, the Chinese government has implemented ecological restoration projects in these regions, including the Grain for Green program, artificial afforestation, and the Three-North Shelter Forest Program, aimed at restoring natural vegetation.

Nevertheless, due to uneven spatiotemporal distribution of rainfall and poor soil nutrient conditions, vegetation restoration faces numerous challenges that seriously affect the development of agricultural and forest ecosystems. In particular, low productivity of planted communities and deteriorating site conditions further impede vegetation restoration processes.

This study collected and compiled published data on leaf nitrogen and phosphorus contents in major forest types across the Loess Plateau, Taihang Mountains, and the stony mountainous area north of Beijing (referred to as the "North Beijing Mountain Area") to comprehensively evaluate nutrient resorption efficiencies across different forest types. The findings will provide theoretical foundations for forest management in North China' s mountainous regions and have profound implications for nutrient balance and ecosystem stability.

1.1 Study Area Overview

This study focused on mountainous regions of North China, extending from west to east across the Loess Plateau, Taihang Mountains, and North Beijing Mountain Area. The Loess Plateau is located in the middle reaches of the Yellow River and upper reaches of the Haihe River in north-central China, within the transitional zone between temperate arid and semi-arid climates, with mean annual temperatures of 4.3–14.3°C and mean annual precipitation of 200–750 mm. Vegetation types show a zonal distribution from southeast to northwest, including forest vegetation zones, forest-steppe zones, typical steppe zones, desert steppe zones, and steppe desert zones. Due to natural environmental changes and human activities, vegetation on the Loess Plateau has been almost completely destroyed, with increasingly deteriorating ecological conditions, making it one of the most severely soil-eroded regions in China and worldwide.

The Taihang Mountains have a semi-arid, semi-humid continental monsoon climate, with dry winters and hot, rainy summers, mean annual temperatures of 5–13°C, and mean annual precipitation of 400–600 mm. Rainfall distribution is extremely uneven, with the rainy season (July–September) accounting for approximately 70% of annual precipitation. Soils are cinnamon soils developed from coarse skeletal weathering materials, characterized by poor fertility and high gravel content. The vegetation belongs to the north warm-temperate deciduous broad-leaved forest subzone, with secondary shrub-grass communities and artificial vegetation developing after broad-leaved forest destruction in low hilly areas. The Taihang Mountains represent one of the ecologically fragile regions where water resource shortages severely constrain agricultural and forestry systems.

The North Beijing Mountain Area constitutes an important component of the North China stony mountainous region and serves as a critical natural ecological barrier between Beijing and the North China Plain. The climate is warm-temperate, semi-humid monsoon, with multi-year mean temperatures of 8–10°C and mean annual precipitation of 500–700 mm. The original zonal vegetation

was warm-temperate deciduous broad-leaved forest, while current forest vegetation consists primarily of plantations established after 1958. Zonal soils are mainly mountain cinnamon soils, brown forest soils, and mountain meadow soils. The region currently experiences drought conditions and severe water shortages.

1.2 Data Collection

Based on data from published articles (including journal papers and dissertations) available online, we collected and compiled nitrogen and phosphorus content data in mature and senescent leaves of major forest community types across the Loess Plateau, Taihang Mountains, and North Beijing Mountain Area (13 study sites total). Nutrient resorption efficiencies were calculated based on these data. Information on geographic coordinates, altitude, vegetation types, climate characteristics, and soil properties for each study site is presented in .

1.3 Data Analysis

Resorption efficiency (RE) was defined as the ratio of the difference in nutrient content between mature and senescent leaves to the content in mature leaves, which quantifies a plant' s capacity to recycle nutrients. Nitrogen resorption efficiency was calculated as:

$$RE = (N_{mature} - N_{senesced})/N_{mature} \times 100\% \quad (1)$$

where N_{mature} is nitrogen content in mature leaves and $N_{senesced}$ is nitrogen content in senescent leaves. Phosphorus resorption efficiency was calculated using the same formula. Since data on nutrient content of truly senescent leaves were generally unavailable, nutrient content data from undecomposed litter were used as a substitute.

All collected data on nitrogen and phosphorus contents in mature and senescent leaves and nutrient resorption efficiencies were statistically analyzed and frequency distribution maps were generated. Forest vegetation in the three mountainous regions of North China was then categorized by trees versus shrubs and natural versus plantation forests to compare differences in nutrient contents and resorption efficiencies among vegetation types. Linear regression analysis was used to examine relationships between nitrogen and phosphorus contents in mature and senescent leaves and resorption efficiency, while differences in nutrient resorption efficiency among tree species were also compared. All statistical analyses were performed using SPSS 16.0, all figures were created using Origin Pro 8.0, and the significance level was set at $P < 0.05$.

2.1 Distribution Characteristics of Leaf Nutrient Content and Resorption Efficiency

Based on the compiled published data, nitrogen and phosphorus contents in mature leaves of forests in North China' s mountainous regions ranged from 5.0–

58.7 g · kg ¹ and 0.77–9.4 g · kg ¹, respectively, with mean values of 22.1 g · kg ¹ and 2.20 g · kg ¹. Frequency distributions of nitrogen and phosphorus contents in mature leaves are shown in Figure 1: see original paper, both exhibiting skewed distributions with peaks at 18.2 g · kg ¹ and 1.68 g · kg ¹, respectively.

Nitrogen and phosphorus contents in senescent leaves ranged from 3.2–24.3 g · kg ¹ and 0.4–3.1 g · kg ¹, respectively, with mean values of 12.0 g · kg ¹ and 1.03 g · kg ¹. Frequency distributions of nitrogen and phosphorus contents in senescent leaves are shown in Figure 1: see original paper, also exhibiting skewed distributions with peaks at 7.5 g · kg ¹ and 0.85 g · kg ¹, respectively.

Based on nitrogen and phosphorus contents in mature and senescent leaves, calculated nitrogen and phosphorus resorption efficiencies ranged from 24.5%–71.3% and 18.1%–75.4%, respectively, with mean values of 45.5% and 47.4%, as shown in the frequency distributions in Figure 1: see original paper.

2.2 Comparison of Leaf Nutrient Content and Resorption Efficiency Among Different Vegetation Types

Due to limited shrub data available only for the Taihang Mountains, analysis results are presented in [Figure 2: see original paper]. Nitrogen contents in mature and senescent leaves of shrubs were significantly higher than those of trees, while phosphorus contents showed no significant differences between the two groups. Comparison of resorption efficiencies revealed that nitrogen resorption efficiency was higher in shrubs than in trees, whereas phosphorus resorption efficiency was lower.

Comparisons of tree leaf nutrients across the three regions showed that mature leaf nitrogen and phosphorus contents in the Loess Plateau (29.8 g · kg ¹ and 3.6 g · kg ¹, respectively) were significantly higher than those in the Taihang Mountains and North Beijing Mountain Area (nitrogen: $P = 0.017$; phosphorus: $P = 0.035$). Senescent leaf nitrogen content in the Loess Plateau (18.4 g · kg ¹) was also significantly higher than in the other two regions ($P = 0.016$), while no significant differences in senescent leaf phosphorus content were observed among regions ($P = 0.361$). Nitrogen and phosphorus resorption efficiencies in the North Beijing Mountain Area (62.1% and 67.8%, respectively) were significantly higher than those in the other two regions ([Figure 2: see original paper]E-F; nitrogen: $P = 0.013$; phosphorus: $P = 0.034$).

2.3 Comparison Between Natural and Plantation Forests

In the North Beijing Mountain Area, nitrogen contents in mature and senescent leaves of plantation forests (33.5 g · kg ¹ and 8.3 g · kg ¹, respectively) were significantly higher than those in natural forests, though nitrogen resorption efficiency showed no significant difference between the two forest types ([Figure 3: see original paper]A, C, E). In the Taihang Mountains, phosphorus contents in mature and senescent leaves of natural forests (2.7 g · kg ¹ and 1.3 g · kg ¹, respectively) were significantly higher than those in plantation forests. In the

North Beijing Mountain Area, plantation forests had higher phosphorus content in mature leaves but lower phosphorus content in senescent leaves, resulting in higher phosphorus resorption efficiency ([Figure 3: see original paper]B, D, F).

Comparisons of plantation forest leaf nutrient contents and resorption efficiencies across the three regions revealed the following ranking for mature leaf nitrogen and phosphorus contents: North Beijing Mountain Area > Loess Plateau > Taihang Mountains. Nitrogen and phosphorus resorption efficiencies showed the same pattern, while senescent leaf nutrient contents did not show consistent trends.

2.4 Relationships Between Leaf Nutrient Content and Resorption Efficiency

Correlation analysis revealed that nitrogen resorption efficiency in North China' s forests was significantly correlated with nitrogen content in senescent leaves ([Figure 4: see original paper]B, $P = 0.031$) but not with nitrogen content in mature leaves ([Figure 4: see original paper]A). Nitrogen resorption efficiency was also not affected by leaf phosphorus content ([Figure 4: see original paper]G, H). Phosphorus resorption efficiency was significantly correlated with nitrogen content in senescent leaves ([Figure 4: see original paper]F, $P = 0.012$) but not with nitrogen or phosphorus contents in mature leaves. These results indicate that nitrogen content in senescent leaves is a key factor influencing both nitrogen and phosphorus resorption efficiencies in North China' s forests.

2.5 Comparison of Nutrient Resorption Efficiency Among Different Forest Types

As shown in , comparisons of nutrient resorption efficiencies among different tree species revealed that *Larix principis-rupprechtii* in natural forests had the highest phosphorus resorption efficiency (62.6%). In plantation forests, *Larix kaempferi* exhibited the highest nitrogen and phosphorus resorption efficiencies, reaching 64.7% and 72.5%, respectively. These results demonstrate that from a nutrient utilization perspective, coniferous species in the nutrient-poor Taihang Mountains have higher nutrient resorption efficiencies and are better adapted to such barren soil conditions.

Discussion and Conclusion

3.1 Comparison of Forest Nutrient Content and Resorption Efficiency in North China Mountain Regions

In this study, mean nitrogen and phosphorus contents in mature leaves of forests in North China' s mountainous regions were 22.5 $g \cdot kg^{1}$ and 2.17 $g \cdot kg^{1}$, respectively. Compared with global averages (mean nitrogen content of 28.6 $g \cdot kg^{1}$ and mean phosphorus content of 1.77 $g \cdot kg^{1}$), nitrogen content was lower while phosphorus content was higher, resulting in a lower N:P ratio that suggests

forest growth in North China' s mountainous regions is more strongly limited by nitrogen. Since most forests in this region are located in stony mountainous areas with poor, low-nutrient soils, plant growth is severely nitrogen-limited, necessitating scientific forest management.

Nitrogen and phosphorus play important roles in plant metabolism during ecosystem nutrient cycling. Plant nutrient resorption involves recycling mineral elements from senescing leaves and storing them in relevant organs to reduce nitrogen loss and environmental dependence. In this study, nitrogen and phosphorus resorption efficiencies for forests in North China' s mountainous regions averaged 45.5% and 47.4%, respectively, slightly lower than global averages for plants (mean nitrogen resorption efficiency of 50% and mean phosphorus resorption efficiency of 52%). Approximately 50% of nutrients can be reused through resorption, though interspecific differences in nutrient resorption can range from 5% to 80%. During senescence, plants extend nutrient residence time within tissues through translocation from senescing to living tissues, thereby increasing nutrient use efficiency.

3.2 Differences in Leaf Nutrient Efficiency Among Different Forest Types

Due to climate and human factors, original natural forest vegetation in North China has been largely destroyed, resulting in fragile regional ecological conditions. Vegetation restoration projects such as the Grain for Green program have improved regional ecological conditions and enhanced ecosystem productivity. However, plantation development faces numerous challenges, with landscape characteristics showing signs of degradation, making it necessary to compare nutrient cycling between natural and plantation forests.

In this study, mean nitrogen and phosphorus contents in mature leaves of natural forests in North China' s mountainous regions were 11.6 $g \cdot kg^{1}$ and 2.57 $g \cdot kg^{1}$, respectively, compared to 21.6 $g \cdot kg^{1}$ and 2.35 $g \cdot kg^{1}$ in plantation forests. Natural forests had higher phosphorus but lower nitrogen contents. Plantation forests generally have higher nutrient contents during early growth stages because nutrients are essentially in a state of consumption. Plantation forests typically have relatively simple structure, poorly developed shrub and herb layers, and especially those with short rotation periods experience frequent human disturbance and prolonged nutrient overconsumption with insufficient return, leading to significantly decreased soil fertility and degraded site nutrient conditions. Therefore, long-term plantation cultivation is not conducive to nutrient maintenance and sustainable ecosystem development, requiring good site conditions combined with artificial fertilization and management to ensure sustainable productivity.

Mean nitrogen and phosphorus resorption efficiencies were 47.1% and 54.8% in natural forests and 47.7% and 53.0% in plantation forests, respectively, showing essentially no difference between forest types. Nutrient consumption in planta-

tion forests leads to reduced soil nutrients and declining site productivity, and plants adapt to these changes by recycling most nutrients. Comparisons across the three regions showed the same ranking for mature leaf nitrogen and phosphorus contents and resorption efficiencies: North Beijing Mountain Area > Loess Plateau > Taihang Mountains. However, we cannot conclude that plants in the North Beijing Mountain Area adapt to nutrient-poor environments through higher nutrient resorption efficiency, as changes in resorption efficiency result from species distribution across large spatial scales, and higher resorption efficiency merely reflects nutrient scarcity in the local environment.

Comparisons among tree species revealed that *Larix principis-rupprechtii* in natural forests had the highest phosphorus resorption efficiency, while *Larix kaempferi* in plantation forests had the highest nitrogen and phosphorus resorption efficiencies (64.7% and 72.5%, respectively), significantly higher than global averages. These findings are consistent with research in the Changbai Mountains, where coniferous species showed higher nutrient resorption efficiencies than broad-leaved species. From a nutrient utilization perspective, coniferous species in nutrient-poor mountainous regions have higher nutrient resorption efficiencies and are better adapted to such environments. The high nutrient use efficiency of coniferous species should be considered in artificial afforestation programs in mountainous areas.

Conclusion

Based on compiled data from natural and plantation forests in North China' s mountainous regions (Loess Plateau, Taihang Mountains, and North Beijing Mountain Area), this study comprehensively evaluated nutrient resorption efficiencies across forest types. Mean nitrogen and phosphorus resorption efficiencies were 45.5% and 47.4%, respectively, approaching global averages for plant leaves. Comparisons between natural and plantation forests revealed that mature leaf nitrogen content in plantation forests was significantly higher than in natural forests, suggesting that nutrients are essentially in a state of consumption during plantation growth. Prolonged excessive nutrient consumption with insufficient return leads to significantly decreased soil fertility and degraded site conditions, requiring proper management and tending measures to ensure sustainable productivity in plantation forests. Comparisons among tree species demonstrated that coniferous forests had higher leaf nutrient resorption efficiencies than broad-leaved species, indicating that coniferous species are better adapted to the poor soil conditions of North China' s mountainous regions from a nutrient recycling perspective.

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