Postprint: Altitudinal Variation in Twig Stoichiometry of Xinjiang Wild Apple

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Abstract

To reveal the variability in nutrient stoichiometry characteristics of Xinjiang wild apple (Malus sieversii) across different altitudes, a valley was selected as a fixed study area, and continuous investigations and sampling were conducted for 3 years (2016–2018) at four altitude gradients (1300 m, 1400 m, 1500 m, and 1600 m) to comparatively analyze the spatiotemporal variation characteristics of N, P, and K stoichiometry in one-year-old branches and their relationships with environmental factors. The results showed that most stoichiometric indices in branches of Xinjiang wild apple exhibited moderate or weak variation across different altitudes and years, with P showing the weakest variation and N:K the strongest. Year had significant effects on five stoichiometric indices except P:K, whereas altitude only had significant effects on N:P. Branch N, N:P, and N:K were also influenced by the interaction between year and altitude. Branch P (except in 2017), K, and P:K showed no significant differences among different altitudes, but all exhibited obvious interannual variation. Branch N, N:P, and N:K simultaneously displayed significant interannual and altitudinal variability with divergent trends. Correlation analysis and NMDS analysis indicated that the intrinsic growth status of wild apple (dead branch rate, projected canopy coverage, pest and disease severity, and fruit yield), annual precipitation, and soil factors all exerted certain influences on branch stoichiometric characteristics, though different stoichiometric indices showed distinct response patterns. Overall, better plant growth was associated with lower nutrient content in branches. These findings demonstrate that branch stoichiometric characteristics of wild apple exhibit obvious variability across altitude gradients and interannually, with relatively complex influencing factors.

Full Text

Variation in One-Year-Old Branch Stoichiometry of Malus sieversii at Different Altitudes and the Influencing Factors in Tianshan Mountains, China

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Abstract

To reveal the variability in nutrient stoichiometric characteristics of Xinjiang wild apple (*Malus sieversii*) at different altitudes, we selected a valley as a fixed study area and conducted investigation and sampling at four altitude gradients (1300 m, 1400 m, 1500 m, and 1600 m) over three consecutive years (2016–2018). We analyzed the spatio-temporal variation characteristics of nitrogen (N), phosphorus (P), and potassium (K) stoichiometry in one-year-old branches of *M. sieversii* and their relationships with environmental variables. The results showed that branch stoichiometric indexes of wild apple trees tended to exhibit moderate and weak variations across different altitudes and years, with P showing the weakest variability and N:K showing the strongest. Year significantly affected five stoichiometric indexes (except P:K), whereas altitude only had a significant effect on N:P. Branch N, N:P, and N:K were also influenced by the interaction between year and altitude. There were no significant differences in branch P (except in 2017), K, and P:K across altitudes, although all displayed significant interannual variations. Branch N, N:P, and N:K showed both significant temporal and spatial variability, with divergent changing trends. Correlation analysis and non-metric multidimensional scaling (NMDS) analysis demonstrated that the trees' own growth status (dead branch rate, projective coverage, degree of disease and insect pests, and fruit amount), annual precipitation, and soil factors all affected branch stoichiometric characteristics to varying degrees, with different stoichiometric indexes showing distinct response patterns. Overall, better plant growth corresponded to lower nutrient contents in one-year-old branches. These findings indicate that branch stoichiometric characteristics of wild apple trees exhibit obvious variability across different altitude gradients and interannual scales, with complex influencing factors.

Keywords: *Malus sieversii*; one-year-old branch; stoichiometry; inter-annual variation; altitude; environmental factor

Introduction

Malus sieversii is a precious and endangered wild fruit tree species relict from the Tertiary period, primarily distributed across the Tianshan Mountains in the Ili River Valley region of Xinjiang, China, as well as in Kazakhstan and Kyrgyzstan. Wild apples from the Ili region of Xinjiang are considered the ancestors of modern cultivated apples, reflecting their extremely important germplasm resource value. However, in recent decades, the survival of *M. sieversii* has been severely impacted by strong disturbances from the apple borer (*Agrilus mali*), grazing, human logging, and climate change, resulting in large-scale withering and death, with the population facing severe degradation. Therefore, it is urgent to identify the causes of degradation and mortality from multiple perspectives to carry out targeted conservation and restoration efforts.

Nutrient elements are important components of ecological stoichiometry research, and nutrient ecological stoichiometry serves as a key tool for addressing ecosystem nutrient cycling, determining limiting elements, and understanding material and energy flow-related ecological problems. For instance, plant N:P ratios can reflect plant nutrient use efficiency and serve as a primary indicator for identifying plant limiting elements (i.e., N limitation when $N:P < 14$, P limitation when $N:P > 16$, and co-limitation or no limitation when $14 \leq N:P \leq 16$). Consequently, studying nutrient elements in wild apple trees and their relationships with individual growth and environmental factors can help reveal nutrient utilization strategies and provide a basis for analyzing degradation causes.

Altitude is a comprehensive environmental factor that influences plant stoichiometric characteristics by altering topography, light, temperature, soil, and other environmental factors. Previous studies have shown inconsistent patterns in how plant leaf stoichiometric characteristics change with altitude. For example, the leaf N content of *Leontopodium alpinum* showed a decreasing then increasing trend with altitude, while N:P showed an increasing then decreasing then increasing pattern. Research on plants in the arid regions of the central Tianshan Mountains found that leaf N decreased with altitude while N:P gradually increased and P showed significant changes. These varying responses are related to plant species, functional groups, and geographic regions.

In addition to altitude, plant stoichiometric characteristics typically show significant interannual variation. Different years have distinct environmental characteristics, particularly climatic features (annual precipitation, mean temperature, sunshine duration, etc.), which may be key drivers of interannual variation in plant stoichiometry. Studies on rubber trees (*Hevea brasiliensis*) in Hainan found that N:P showed an "N" -shaped change across years, while N:K showed wave-like changes, indicating that different nutrient elements have significantly different interannual fluctuation patterns. Similarly, grassland plants on the Qinghai-Tibet Plateau showed clear interannual changes in leaf N:P, with different indexes following different patterns.

Given these knowledge gaps, this study investigated one-year-old branches of *M.*

sieversii across different altitude gradients to analyze the variability of N, P, K, and their ratios across years and altitudes, as well as the relationships between stoichiometric characteristics and meteorological factors and tree growth status. The objectives were to understand the effects of altitude on the stoichiometric characteristics of *M. sieversii* and identify the main influencing factors to provide a scientific basis for ecological conservation of this species.

1. Study Area and Methods

1.1 Study Area Overview The study area is located at the Yeguolin Improvement Farm, Guoshan Team 3, Ergou, Xinyuan County, Ili Prefecture, Xinjiang (83.589°E, 43.377°N), on the northern foothills of the Nalati Mountains in the western Tianshan Mountains. Xinyuan County has a continental semi-arid climate with warm winters and cool summers, and distinct mountain climate characteristics. The mean annual precipitation is 400–500 mm, the frost-free period is 140–180 days, the snow cover period is about 150 days, the mean annual temperature is 6–9.3°C, and annual sunshine duration is 2500 h. A temperature inversion layer exists between 1200–1600 m in the Ili River Valley region, where temperature increases with altitude (typically 0.1–0.3°C per 100 m) or remains relatively stable. Within the inversion layer, the mean January temperature can be as low as -10°C, while the monthly mean temperature is 2–3°C higher than in the plain area below. The inversion layer also receives higher annual precipitation than the plain area, creating stable climatic conditions with abundant spring precipitation and vigorous plant growth, supporting high biodiversity.

The soil under wild apple forests is primarily developed from carbonate-rich loess parent material, with thick humus layers, dark brown color, moderate texture, good structure, loose and porous composition, rich in carbonates and base substances, and high fertility. Wild apple trees typically form pure stands or mixed forests with *Armeniaca sibirica*, *Juglans regia*, and other species.

1.2 Methods

1.2.1 Wild Apple Branch Sampling Based on the actual upper and lower distribution limits of wild apple trees in the study area, we established four altitude gradients: 1300 m, 1400 m, 1500 m, and 1600 m. Each altitude gradient included survey plots on both east- and west-facing slopes, with each plot measuring 30 m × 30 m. Within each plot, 15 medium-sized wild apple trees were marked as permanent sample trees (30 trees per altitude gradient). Investigations and sampling were conducted continuously from 2016 to 2018. During sampling, four uniformly growing one-year-old vegetative branches were collected from the middle of the canopy in each of the four cardinal directions (east, south, west, north). Branch length ranged from 15–20 cm, with smooth bark and moderate lignification, and basal diameter between 2.5–3.5 mm. A total of 16 branches were collected from each tree, mixed to form one composite sample per tree, placed in labeled envelopes, and stored in foam incubators with ice packs.

1.2.2 Branch Sample Processing and Index Determination All branch samples (one composite sample per tree) were transported to the laboratory and oven-dried at 65°C to constant weight. The dried branches were ground into powder using a disc vibration mill (RS200, Retsch, Germany) and stored in sealed bags in a dark, dry place. Carbon and nitrogen contents were determined using a carbon-nitrogen analyzer (Multi N/C 3100, Analytik Jena, Germany). Phosphorus content was measured using the molybdenum-antimony anti-colorimetric method, and potassium content was determined by flame photometry. All results are expressed as mass contents ($mg \cdot g^{-1}$), and branch stoichiometric ratios (C:N, C:P, C:K, N:P, N:K, P:K) were calculated.

1.2.3 Investigation of Individual Tree Growth Status The basal diameter (measured at 10 cm above ground level, converted from basal circumference) and height (from trunk base to canopy top) of each sample tree were measured using a diameter tape and height pole. Subsequently, comprehensive assessments of dead branch rate (DBR), degree of disease and insect pests (DIP), projective coverage (Cov), and fruit amount (FA) were conducted through visual estimation according to established standards. DBR (%) was calculated as the percentage of dead branches relative to total branches per tree, with higher values indicating lower proportions of living branches. DIP was rated on a scale of 1–5, with higher values indicating more severe pest and disease damage, evaluated based on leaf spot numbers, diseased leaf counts on branches, and overall diseased leaf numbers. FA was comprehensively evaluated based on fruit size, quantity, and tree size, rated on a scale of 0–5 (0 = no fruit, higher values = more fruit). For trees of similar size, larger and more numerous fruits received higher ratings. Projective coverage (%) was calculated as the crown area (derived from canopy length and width measured with a tape) minus gaps, with gap fraction estimated visually.

1.2.4 Soil Sample Collection and Analysis Based on the number and distribution of sample trees within each plot, composite soil samples were collected from 0–10 cm depth at 1–2 m north and south of each tree. A total of 30 soil samples were mixed per plot, with 60 samples per altitude gradient. Each year, 180 soil samples were collected across all altitudes. Soil samples were air-dried and sieved, then analyzed following standard methods in *Soil Agrochemical Analysis* for soil organic carbon, total N, available N, available P, available K, and electrical conductivity.

1.2.5 Acquisition of Geographic and Meteorological Factors During field investigations, geographic and topographic parameters including latitude, longitude, altitude, slope, aspect, and slope position were recorded for each plot using a GPS. Mean annual precipitation (MAP) data were obtained from the

Xinyuan County Meteorological Bureau. Due to the presence of a temperature inversion layer, mean annual temperature and temperature differences across altitudes were not considered as factors affecting branch stoichiometry in this study.

1.2.6 Data Processing Methods Descriptive statistical analysis was performed on branch stoichiometric parameters across years and altitudes, with variability compared using coefficient of variation (Cv: 0–25% = weak variation, 25–75% = moderate variation, >75% = strong variation). General linear two-way ANOVA was used to analyze the effects of year and altitude on branch stoichiometric characteristics and their interactions. Duncan' s multiple comparison method ($\alpha = 0.05$) was used to compare differences among altitudes and years. Pearson correlation analysis was used to examine relationships between branch stoichiometric characteristics and individual growth parameters, altitude, precipitation, and soil physicochemical properties. Non-metric multidimensional scaling (NMDS) was employed to explore multivariate relationships between stoichiometric characteristics and environmental factors, revealing the main influencing factors for branch stoichiometry at different altitudes. SPSS 19.0 software was used for descriptive statistics, correlation analysis, and ANOVA; ORD V5.0 software was used for NMDS analysis; Excel 2013 was used for conventional data analysis; and Origin 8.5 was used for figure preparation.

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2. Results

2.1 Variability and Sources of Variation in Branch N, P, and K Stoichiometry of *M. sieversii* at Different Altitudes The coefficient of variation showed that wild apple branch stoichiometric indexes mostly exhibited moderate and weak variation across different spatio-temporal scales, with maximum Cv values of 42.9% (Table 1). P showed the weakest variability, with maximum Cv values of only 15.1%, demonstrating strong stability. Two-way ANOVA results (Table 2) indicated that year significantly affected all stoichiometric indexes except P:K ($P < 0.05$), while altitude only significantly affected N:P ($P < 0.01$). The interaction between year and altitude also significantly affected N, N:P, and N:K ($P < 0.05$). Overall, the branch stoichiometric characteristics of *M. sieversii* showed moderate to weak variability, with differences across altitudes and years.

2.2 Differences in Branch Stoichiometric Characteristics Across Altitudes and Years ANOVA results (Figure 1) revealed that branch N content showed fluctuating decreasing trends with altitude in 2016 and 2018, while 2017 showed the opposite pattern. N:P and N:K showed decreasing trends with altitude in 2016 and 2018, but irregular changes in 2017. Branch P content decreased with altitude in 2016, but showed no regular pattern in other years. Branch K content showed no significant differences across altitudes in any year, but displayed significant interannual differences. P:K showed no significant altitudinal gradient differences in any year, but exhibited significant interannual variation. Overall, the variability of N, N:P, and N:K with altitude was lower than that of P and K, and branch stoichiometric characteristics mostly showed significant interannual variation.

2.3 Correlations Between Branch Stoichiometric Characteristics and Individual Growth and Environmental Factors Correlation analysis (Table 3) showed that branch N, N:P, and N:K were all significantly negatively correlated with projective coverage and fruit amount ($P < 0.01$), while N and N:K were significantly positively correlated with DBR and DIP. P was significantly negatively correlated with coverage and significantly positively correlated with DBR. None of the three stoichiometric ratios showed significant correlations with individual growth parameters. Overall, better growth status (higher coverage and fruit amount, lower DBR) corresponded to lower branch N content, while poorer growth corresponded to higher N content. This may be because pest and disease stress causes partial or extensive branch death, triggering plant stress responses that increase N content to enhance protective substances.

Altitude showed no significant correlation with branch stoichiometric characteristics, while N:K was significantly negatively correlated with annual precipitation. Among soil physicochemical factors, soil total N had the weakest correlation with branch stoichiometric indexes (only significantly negatively correlated with N:K), while other soil factors showed stronger correlations, mostly reaching significant or highly significant levels. Branch N content was significantly positively correlated with soil total N and significantly correlated with electrical conductivity. Branch stoichiometric ratios showed weak correlations with soil factors, with only N:P significantly correlated with available P and N:K significantly correlated with available K. In contrast, individual growth parameters and environmental factors showed stronger correlations with N, P, and K, but weaker correlations with stoichiometric ratios.

2.4 Multivariate Analysis of Influencing Factors on Branch Stoichiometric Characteristics NMDS analysis showed that the first two axes cumulatively explained 97.3% of the variance, indicating good ordination results (Table 4). All stoichiometric indexes except P:K were significantly positively correlated with Axis 1, while N:P and N:K were significantly negatively correlated with Axis 2. Among all biotic and abiotic factors, 11 showed significant or highly significant correlations ($P < 0.01$) with the ordination axes, except for altitude, DIP, and soil total P. Annual precipitation, projective coverage, and fruit amount were significantly negatively correlated with both axes, while DBR was significantly positively correlated with Axis 1. Annual precipitation was also significantly positively correlated with Axis 2. Among the seven soil factors significantly correlated with the axes, all except electrical conductivity were positively correlated with their respective axes.

The ordination plot (Figure 2) showed that branch N, P, and K were clearly separated into upper and lower groups, with stoichiometric indexes within each group also showing separation trends along Axis 1. Based on correlation coefficients, the main influencing factors on branch stoichiometric characteristics were annual precipitation, projective coverage, DBR, fruit amount, soil total N, and electrical conductivity (Table 4). Thus, branch N, P, and K of wild apple trees are influenced by the combined effects of multiple factors, showing different environmental response characteristics.

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3. Discussion

Branches support leaves and play important roles in plant photosynthesis, nutrient transport, and water conduction. Their nutrient status directly affects leaf growth and photosynthetic physiology. Compared with branches, leaves require higher nutrient concentrations to maintain photosynthetic functions, so leaf nutrient contents are typically higher than branch contents. Plant nutrient stoichiometric characteristics generally show certain interannual and altitudinal variations, but these patterns differ among plant functional groups or species.

This study found that branch N, P, and K of wild apple trees showed different changing trends across years and altitudes, similar to patterns observed in alpine oak (*Quercus aquifolioides*). The mean branch N content (4.95 $mg \cdot g^{-1}$) was slightly lower than that of oil tea in Changshan, Zhejiang (5.62 $mg \cdot g^{-1}$), but higher than that of alpine oak shrubs (1.21–1.25 $mg \cdot g^{-1}$). The mean P content (1.25 $mg \cdot g^{-1}$) was lower than that of alpine oak shrubs (1.81 $mg \cdot g^{-1}$) but higher than that of evergreen shrubs in central Guizhou karst regions (0.71 $mg \cdot g^{-1}$). These differences reflect interspecific and regional heterogeneity in plant stoichiometric characteristics.

The balance among nutrients often affects plant growth more than absolute nutrient concentrations. Plant N:P ratios reflect both individual functional attributes and plant-environment interactions, as element or energy supply imbalances can alter interspecific interactions and community structure. The N:P ratio of *M. sieversii* varied across years and altitudes, with N:P decreasing then increasing with altitude in 2016 and 2018, similar to trends in *Sabina przewalskii* leaves in the central Qilian Mountains. In 2017, N:P was significantly lower at 1600 m than at other altitudes, while other years showed no significant altitudinal differences. This may be because the low precipitation in 2017 reduced soil weathering rates and plant-available P, causing significant differences among altitudes.

Two-way ANOVA indicated that year significantly affected branch stoichiometric characteristics, while altitude did not. This contrasts with the "nutrient limitation" hypothesis, which suggests that low soil temperature at high altitudes limits root activity and nutrient uptake, causing nutrient limitation. The lack of significant altitudinal effects on branch N, P, and K may be because the stable climate of the temperature inversion layer makes soil parent material composition and properties similar across altitudes. Additionally, the temperature inversion effect may enhance plant resistance maintenance capacity, preventing significant nutrient decreases with altitude.

Precipitation did not significantly affect N content but significantly promoted N:K, suggesting that moderate precipitation increases enhance plant resistance. Soil factors, especially soil nutrients, often significantly correlate with plant stoichiometric characteristics. In this study, soil N content increases helped raise branch N content, and soil electrical conductivity promoted K content increases, consistent with results from the Loess Plateau hilly region. Soil pH was near neutral (6.8-7.2), resulting in weaker overall correlations between soil factors and branch chemical elements.

In terms of influencing factors, projective coverage and fruit amount showed significant negative correlations with branch N, N:P, and N:K, while DBR showed significant positive correlations, indicating that better growth (higher coverage and fruit amount, lower DBR) corresponded to lower branch N content. This may be because fruit development demands more nutrients from leaves, reducing element concentrations in branches. Similar patterns have been observed in *Quercus wutaishansea* on the Loess Plateau, where nutrient contents decreased significantly during the fruiting period.

Overall, the factors influencing branch stoichiometric characteristics of *M. sieversii* at different altitudes are complex, involving both internal physiological reasons and external environmental factors, with different stoichiometric indexes showing inconsistent response patterns.

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4. Conclusions

1) The branch stoichiometric characteristics of *M. sieversii* showed moderate to weak variation overall. Year was the main factor causing stoichiometric variation, while the interaction between year and altitude also had significant effects. Branch P, K, and P:K showed low variability across altitudes but significant interannual variation. Branch N, N:P, and N:K showed both significant interannual and altitudinal variability.

2) Four individual growth parameters (dead branch rate, projective coverage, degree of disease and insect pests, and fruit amount) significantly affected branch N, P, and K stoichiometry, with better growth corresponding to lower nutrient contents. Abiotic environmental factors including annual precipitation and multiple soil physicochemical factors (soil total N, available N, available P, available K, and electrical conductivity) also substantially influenced branch stoichiometric characteristics.

3) NMDS analysis revealed that branch N, P, and K formed different stoichiometric index groups with distinct environmental response characteristics.

The stable climate effect of the temperature inversion layer prevented significant decreases in branch N, P, and K with altitude, indicating that *M. sieversii* branches have strong capacity to maintain internal stability.

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