LEAF FUNCTIONAL TRAITS AND LEAF ECONOMICS SPECTRUM OF *QUERCUS AQUIFOLIOIDES* ACROSS DIFFERENT SLOPE ASPECTS IN NYANG RIVER BASIN, CHINA

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Abstract. To elucidate the adaptive mechanisms and strategies of *Quercus aquifolioides* in different resource environments, we measured 20 leaf functional traits of individuals distributed across slope aspects at 3250 m in the Nyang River Basin, southeastern Xizang, China. Differences in leaf traits between north- and south-facing slopes were analyzed, and leaf economics spectra were constructed for each slope aspect. Results showed that leaves from the north-facing slope had significantly higher leaf area, specific leaf area, chlorophyll, nitrogen, and phosphorus contents, while leaves from the south-facing slope exhibited greater thickness, dry matter content, and carbon concentration. Anatomical traits did not differ significantly between slopes. The leaf economics spectrum indicated that leaves from the north-facing slope represent a fast investment–return growth strategy, whereas leaves from the south-facing slope follow a conservative, slow-return strategy. These findings demonstrate the strong influence of slope aspect on Q. aquifolioides growth strategies, offering insights for ecological restoration and management of alpine evergreen broad-leaved forests.
Keywords: *Quercus aquifolioides, alpine evergreen broad-leaved forest, resource allocation, phenotypic plasticity, principal component analysis, Qinghai-Tibet Plateau*

Introduction

Evergreen broad-leaved forests are a key montane vegetation type along the southeastern Qinghai–Tibet Plateau, distributed primarily in the transition zone of the Himalayas and Hengduan Mountains. These forests play crucial roles in water conservation, soil stabilization, and maintaining ecosystem stability. Due to steep altitudinal gradients and complex thermal regimes, vegetation structure and species composition show pronounced heterogeneity across slope aspects. *Quercus aquifolioides*, a dominant and highly adaptable species, is suitable for studying plant responses to slope-specific habitats.

In the Nyang River Basin, *Quercus aquifolioides* is a common evergreen broad-leaved tree species and an ecological keystone, contributing significantly to biodiversity maintenance, soil and water conservation, and carbon sequestration in the region (Zhang et al., 2025). Plant functional traits reflect adaptive responses to ecological environments and

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provide an important approach for exploring how plants respond and adapt to environmental changes (Violle et al., 2007). As the primary organs directly interacting with the external environment, leaves represent a critical subset of plant functional traits. Their morphological, structural, and physiological characteristics exhibit marked trade-offs in light capture, resource utilization, and stress tolerance strategies (Wright et al., 2004). In alpine ecosystems, slope aspect is a key topographic factor that drives substantial differences in solar radiation, which directly affect environmental variables such as temperature, soil moisture, and nutrient availability (Li et al., 2011). Given that plant adaptive responses to these factors differ (Ahrens et al., 2020), variations in environmental conditions can lead to adaptive divergence in plant functional traits. Elucidating the patterns of trait variation across slope aspects is therefore essential for understanding the ecological strategies and spatial distribution mechanisms of alpine plants.

The leaf economics spectrum (LES) describes a suite of continuous trait combinations shaped by interactions among leaf traits (Wright et al., 2005), reflecting the self-organizing allocation of resources to mitigate environmental constraints. LES theory summarizes two contrasting adaptive strategies under environmental disturbance: at one end of the spectrum, the "fast investment–return" strategy is characterized by short leaf lifespan, high nitrogen and phosphorus content, and strong photosynthetic capacity; at the other end, the "slow investment–return" strategy features long leaf lifespan, low nutrient content, and weak photosynthetic performance (Xun et al., 2020). Since its introduction by Wright et al. (2004), LES theory has been applied across diverse ecosystems and plant functional groups, providing a quantitative framework for evaluating plant resource acquisition, utilization, and trade-off strategies. For example, Reich's global synthesis confirmed the universality of the LES under different environmental conditions and underscored its value in predicting plant responses to climate change (Reich, 2014). Similarly, Díaz et al., drawing on a global plant trait database, demonstrated significant LES trade-offs across tropical, temperate, and arid environments, while also highlighting environment-specific variations in trait expression (Díaz et al., 2016). These studies have laid a solid foundation for the global application of LES and have provided important insights into plant adaptive strategies in specialized habitats.

As a core framework for deciphering the ecological strategies of high-altitude plants, LES offers a valuable lens through which to quantify resource allocation mechanisms in *Quercus aquifolioides* across slope aspects. However, current research on this species has focused primarily on trait responses to elevational gradients (Li et al., 2006) and genomic analyses (Yin et al., 2018), with limited attention to the relationship between leaf functional traits and LES under different slope conditions. In this study, we hypothesize that under similar macroclimatic conditions, *Quercus aquifolioides* will exhibit marked differences in leaf functional traits between slope aspects, with individuals optimizing their resource-use strategies and survival capacities through adjustments in leaf morphology, structure, and physiology. We expect that individuals on north slopes will adopt a fast investment–return adaptive strategy, whereas those on south-facing slopes will display a slow investment–return conservative strategy. To test this hypothesis, we compared leaf functional traits and LES patterns between north and south-facing slopes, aiming to elucidate the growth strategies and adaptive mechanisms of this species under different slope aspects. The findings will contribute to advancing our understanding of alpine plant ecological adaptation and provide a theoretical basis for regional ecological restoration and biodiversity conservation.

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Materials and methods

Study area

The study area is located in the middle reaches of the Nyang River (29°45′–30°15′N, 93°20′–94°10′E), encompassing the gorge section from the northern part of Bayi District to the southern part of Gongbo'gyamda County, Nyingchi City (river kilometer 98–217), on the southeastern Qinghai-Tibet Plateau, China. Elevations range from 2800 m to 4200 m, with a vertical relief of 1400 m, representing the core distribution zone of *Quercus aquifolioides* (concentrated between 3100 m and 3800 m). The mean annual temperature ranges from 5.2°C to 10.8°C, and annual precipitation is 531–782 mm, with approximately 70% falling between June and September. The growing season (≥5°C) lasts for 145–198 days. The dominant soil types are brown earth (3100–3600 m) and subalpine meadow soil (3600–4000 m). Other major vegetation in the area includes *Pinus densata*, *Betula utilis*, and *Picea likiangensis var. Linzhiensis* (Zou et al., 2025).

Methods

Sample plot setting and data collection

In late June 2024, during the peak growing season, sampling was conducted in the typical distribution zone of *Quercus aquifolioides* in the middle reaches of the Nyang River, Tibet Autonomous Region. At an elevation of 3250 m, north-facing and south-facing slopes were selected on opposite sides of the valley. The south-facing slope was located at 94.151°E, 29.754°N, and the north-facing slope was located at 94.099°E, 29.718°N (*Fig. 1*). These coordinates represent the approximate central positions of the sampled plots on each slope. Five 20 m × 20 m plots were established on each slope, with slope position and inclination kept approximately consistent, retaining slope aspect as the primary variable. The plots were spaced 50 m apart. Each 20 m × 20 m plot was subdivided into four 10 m ×10 m subplots. In some subplots, *Quercus aquifolioides* individuals were sparse or absent; thus, three subplots per plot containing the species were selected for leaf collection.

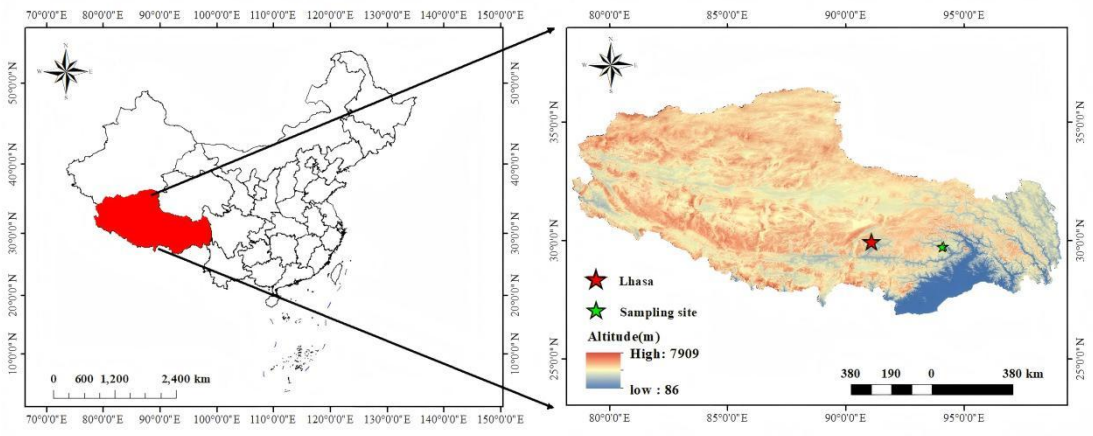

Figure 1. *Sampling diagram of study area*

From each plot, two upright, healthy individuals with a diameter at breast height (DBH) of 20–30 cm were chosen. To ensure the representativeness of the leaf samples, we collected

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mature, sun-exposed leaves from the current-year branches in all four cardinal directions (east, south, west, and north) of each tree crown. For morphological trait measurements, 50 mature, sun-exposed leaves from current-year branches were collected from each individual. For anatomical trait analysis, three mature, sun-exposed leaves from current-year branches per individual were fixed in FAA solution (5 ml 38% formaldehyde +5 ml acetic acid + 90 ml 75% alcohol). For physiological trait measurements, another three mature, sun-exposed leaves were immediately frozen in liquid nitrogen. In addition, three soil samples (0–10 cm depth) were collected from each subplot and pooled for soil property analysis. All samples were collected between 10:30 and 11:30 a.m. Climatic data were obtained from WorldClim, and plot information was recorded using a handheld GPS device.

Leaf traits determination

Freshly collected leaves were transported to the laboratory, where they were weighed using an electronic balance with a precision of 0.001 g (model: FA2204Pro, precision: 0.0001 g, Changzhou Xingyun Instrument Co., China). The leaves were then scanned using a flatbed scanner (model: Epson Perfection V39II, Seiko Epson Corp., Japan), and the resulting images were processed in FAMeLeS to measure leaf length (LL, cm), leaf width (LW, cm), and leaf area (LA, cm^2), and to calculate the length-to-width ratio (LL/LW) (Montès et al., 2024). The leaves were subsequently oven-treated at 100°C for 20 min to halt metabolic activity, then dried at 80°C to a constant weight. The dry mass was recorded, and specific leaf area (SLA, cm^2/g, *Eq. 1*) and leaf dry matter content (LDMC, *Eq. 2*) were calculated.

$$\text{Specific leaf area (SLA)} = \frac{\text{Leaf area (LA)}}{\text{Leaf dry weight}} \quad \text{(Eq.1)}$$

$$\text{Leaf dry matter content (LDMC)} = \frac{\text{Leaf dry weight}}{\text{Saturated fresh weight}} \quad \text{(Eq.2)}$$

Paraffin sectioning was employed to prepare transverse sections of leaves, which were then used to measure and calculate leaf thickness (LT, μm), upper epidermis thickness (UET, μm), lower epidermis thickness (LET, μm), palisade tissue thickness (PTT, μm), spongy tissue thickness (STT, μm), compactness of the leaf tissue (CTR, *Eq. 3*), sponginess ratio (SR, *Eq. 4*), and the palisade ratio (CP, *Eq. 5*). Specifically, fixed leaves were trimmed with a blade into 1 cm^2 segments, followed by graded ethanol dehydration (30%, 50%, 70%, 85%, 95%, 100%). After dehydration, the samples were cleared with xylene, infiltrated with paraffin, and embedded. Sections were cut to a thickness of 10 μm using a rotary microtome (model: LEICA RM2235, Leica Microsystems, Germany), double-stained with safranin and fast green, and mounted with neutral balsam. Microscopic observation and imaging were performed with an optical microscope (model: Olympus CX21, Olympus Corporation, Japan) at 20× magnification. Measurements were taken using ImageJ software (version 6.0; National Institutes of Health, Bethesda, MD, USA), with ten randomly selected fields of view per sample, and the mean values were calculated to reduce measurement error.

$$\text{Leaf tightness (CTR)} = \frac{\text{Palisade tissue thickness (PTT)}}{\text{Leaf thickness (LT)}} \quad \text{(Eq.3)}$$

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$$\text{Spongy ratio (SR)} = \frac{\text{Sponge tissue thickness STT)}}{\text{Leaf thickness (LT)}} \quad \text{(Eq.4)}$$

$$\text{Coefficient of palisade (CP)} = \frac{\text{Palisade tissue thickness (PTT)}}{\text{Sponge tissue thickness (STT)}} \quad \text{(Eq.5)}$$

After processing, the collected leaves were analyzed for chlorophyll content, carbon (C), nitrogen (N), and phosphorus (P) concentrations, as well as the carbon-to-nitrogen ratio (C\:N) and nitrogen-to-phosphorus ratio (N\:P). Chlorophyll content was determined following the spectrophotometric method described by Wang and Huang (2014). The determinations of C, N, and P followed the procedures of Bao (2007): C content was measured using the $K_2Cr_2O_7$–H_2SO_4 external heating method, N content was determined by the Kjeldahl method, and P content was measured using the molybdenum–antimony anti-colorimetric method. For each subplot, leaves were ground and homogenized, and each measurement was repeated three times, with the mean value recorded.

Soil factors determination

After air-drying and sieving, the collected soil samples were analyzed for pH, soil water content (SWC), carbon (C), nitrogen (N), phosphorus (P), and potassium (K) concentrations, and the C\:N and N\:P ratios were calculated, following the methods of Bao (2007). Soil pH was determined using the glass electrode method, SWC was measured by the oven-drying method, C, N, and P were determined using the same methods as for leaf samples, and K content was measured using flame photometry. For each subplot, soil samples were homogenized, and each parameter was measured in triplicate, with the mean value recorded.

Data processing

The raw data were first processed in Excel to compute the mean and standard deviation for each trait. The degree of variation was quantified using the coefficient of variation (CV = [standard deviation (SD) / mean (M)] × 100%) (Fan et al., 2022). Descriptive statistics for the 20 leaf functional traits and 8 environmental factors were performed in SPSS 23. Differences between north and south-facing slopes were tested using independent-samples t-tests with a significance threshold of 0.05, and results are presented in summary tables. Trait–trait correlations were visualized as a heatmap generated in Origin 2021. Principal component analysis (PCA) was then conducted to extract major axes of variation and to elucidate the response strategies of *Quercus aquifolioides*.

Results

Leaf functional traits among different slope aspects

Leaf functional traits of *Quercus aquifolioides* from north and south-facing slopes were measured to assess inter-aspect differences. Several traits exhibited significant variation between slope aspects. As shown in *Table 1,* in terms of morphological traits, LL, LW, LL/LW, LA, and SLA were all significantly higher on the north slope than on the south-facing slope ($p < 0.01$), whereas LDMC was significantly lower on the north

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slope ($p < 0.01$). For anatomical traits, LT on the south-facing slope was significantly greater than that on the north slope, while other anatomical parameters—including UET, LET, PTT, STT, CTR, SR, and CP—showed no significant differences between slopes ($p > 0.05$). In terms of physiological traits, all variables except N content differed significantly between aspects: Chl and P content were significantly higher on the north slope, whereas C, C\:N, and N\:P were significantly higher on the south-facing slope. Regarding the coefficient of variation (CV), all morphological traits except LL/LW had higher CV values on the north slope. For anatomical traits, UET, LET, CTR, and CP had lower CV values on the north slope, whereas the remaining anatomical traits showed the opposite trend. For physiological traits, all parameters except Chl had lower CV values on the north slope than on the south-facing slope.

Table 1. *Comparison of leaf traits between north slope and south-facing slope*

Factor	Units	North-facing slopes (mean ± SD)	South-facing slopes (mean ± SD)	p
LL	mm	*49.339 ± 10.887(22.066)*	*43.539 ± 7.943(18.243)*	< 0.01
LW	mm	35.698 ± 6.973(19.533)	34.079 ± 5.715(16.770)	> 0.05
LL/LW		*1.380 ± 0.122(8.841)*	*1.278 ± 0.101(7.903)*	< 0.01
LA	cm^2	*12.089 ± 2.951(24.411)*	*10.980 ± 2.548(23.206)*	< 0.01
SLA	cm^2/g	*72.986 ± 8.249(11.302)*	*68.857 ± 6.303(9.153)*	< 0.01
LDMC		*0.439 ± 0.004(1.258)*	*0.451 ± 0.006(1.019)*	< 0.01
LT	μm	*749.128 ± 35.141(4.691)*	*761.561 ± 31.492(4.135)*	< 0.05
UET	μm	72.192 ± 4.242(5.877)	72.526 ± 4.822(6.649)	> 0.05
LET	μm	19.525 ± 2.062(10.260)	19.681 ± 2.113(10.739)	> 0.05
PTT	μm	340.360 ± 25.500(7.492)	342.223 ± 23.646(6.910)	> 0.05
STT	μm	286.609 ± 21.743(7.586)	287.051 ± 16.255(5.663)	> 0.05
CTR		0.454 ± 0.013(2.918)	0.450 ± 0.035(7.728)	> 0.05
SR		0.383 ± 0.023(6.128)	0.377 ± 0.016(4.336)	> 0.05
CP		1.887 ± 0.053(4.437)	1.197 ± 0.119(9.953)	> 0.05
Chl	μg/g	*1197.362 ± 34.513(4.068)*	*1136.234 ± 46.219(2.882)*	< 0.001
C	mg/g	*439.046 ± 10.321(11.917)*	*455.112 ± 11.235(16.796)*	< 0.05
N	mg/g	*13.914 ± 0.942(1.674)*	*13.103 ± 0.960(9.617)*	< 0.05
P	mg/g	*1.477 ± 0.147(4.960)*	*1.136 ± 0.099(4.227)*	< 0.01
C:N		*31.708 ± 2.371(12.203)*	*34.901 ± 2.440(8.074)*	< 0.01
N:P		*9.452 ± 0.387(5.251)*	*11.768 ± 1.483(6.000)*	< 0.01

LL: Leaf length; LW: Leaf width: LL/LW: Leaf length/Leaf width; LA: Leaf area; SLA: Specific leaf area; LDMC: Leaf dry matter content; LT: Leaf thickness; UET: Upper epidermis thickness; LET: Lower epidermis thickness; PTT: Palisade tissue thickness; STT: Sponge tissue thickness; CTR: Leaf tightness; SR: Spongy ratio; CP: Coefficient of palisade; Chl: Chlorophyll. Data in parentheses was the coefficient of variation. Italic values indicate significant differences between north and south-facing slopes at $p < 0.05$. The same below

Correlations among leaf functional traits of Quercus aquifolioides on different slope aspects

The correlation patterns among leaf functional traits of Quercus aquifolioides on north and south-facing slopes are visualized in *Figure 2*. As shown in *Figure 2,* LL, LW, LL/LW, and LA exhibited mostly significant positive correlations with one another. SLA

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and LDMC showed relatively weak correlations with other traits. Among anatomical traits, most parameters were significantly correlated. For physiological traits, Chl displayed significant correlations with certain morphological and anatomical traits; N and P contents were significantly positively correlated, whereas C\:N and N\:P ratios were significantly negatively correlated with N and P contents. The strength of these trait–trait correlations varied between slope aspects.

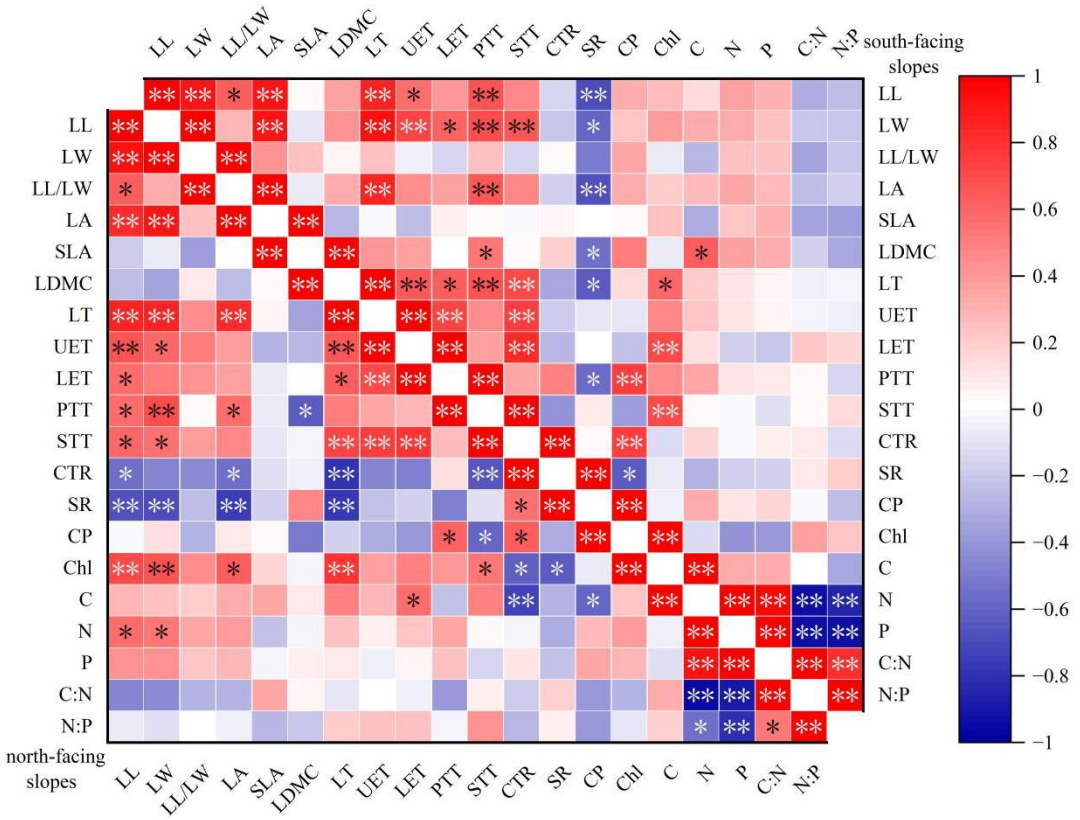

Figure 2. *Correlation heatmap of leaf functional traits on north and south-facing slopes*

Contribution level of functional traits of leaves to environmental adaptation

As shown in the *Figure 3* and *Tables 2* and *3*, the first five principal components of *Quercus aquifolioides* leaf traits across slope aspects explained a total of 87.789% of the variance, capturing the majority of the information from the 20 measured indicators. The principal component composite scores for north-slope leaves were mainly distributed in the first and fourth quadrants, indicating that loadings in these directions had strong influences on north-slope leaf traits. In contrast, the composite scores for south-slope leaves were primarily concentrated in the second and third quadrants.

The first principal component (PC1) accounted for 35.0% of the variance in leaf traits, and the second principal component (PC2) accounted for 26.3%. The factor loadings of each trait on the principal components for north and south slopes are detailed in *Tables 2* and *3*, respectively. Among the 20 traits, LL, P, LL/LW, and N\:P had relatively large absolute projections on PC1 and were therefore strongly associated with this axis, whereas LT, LET, UET, and STT were more strongly associated with PC2. Analysis of trait loadings across PC1–PC5 showed that, on north slopes, LL, CP, LDMC, SLA, and LET made

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substantial contributions, whereas on south-facing slopes, LW, P, CP, LL/LW, and SLA were the dominant contributors. These traits can serve as key indicators for assessing the adaptive strategies of *Quercus aquifolioides* leaves to different slope-aspect environments.

Discussion

Differences in leaf functional traits among different slope aspects

Plant functional traits are closely linked to resource acquisition and utilization, and they also reflect plant adaptability to external environmental conditions (Meng et al., 2007). As shown in *Table A1* in the *Appendix*, significant differences in soil properties (e.g., soil water content, nutrient availability) were observed between the north and south-facing slopes. Leaves on south-facing slopes had higher dry matter content and greater thickness than those on north slopes, likely because they accumulated more biomass to enhance structural stability (Wang et al., 2019). In contrast, north-slope leaves had higher chlorophyll content, indicative of greater photosynthetic efficiency and stronger resource acquisition capacity. The shorter average daily light duration on north slopes may drive leaves to maximize resource acquisition efficiency under limited light conditions. On south-facing slopes, in response to water stress, plants increased LT and reduced SLA to enhance dry matter content and structural robustness, thereby maintaining survival even under resource-limited conditions.

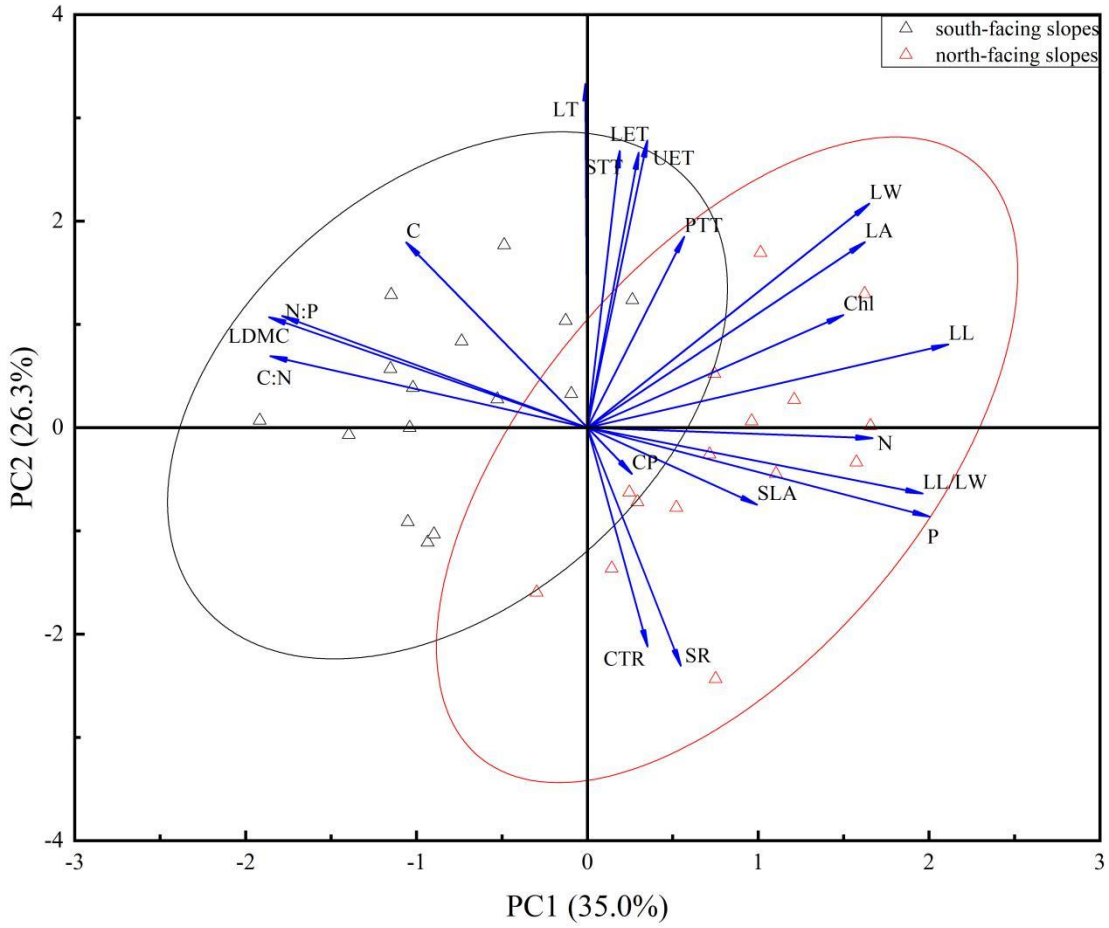

Figure 3. *Principal component analysis of leaf functional traits on different slope aspects*

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Table 2. *Loadings of principal component analysis for leaf functional traits on north-facing slopes*

Factor	PC1	PC2	PC3	PC4	PC5
LL	0.344	-0.066	0.031	0.067	-0.083
LW	0.330	-0.102	-0.091	-0.009	0.077
LL/LW	0.201	0.040	0.283	0.210	-0.394
LA	0.303	-0.055	-0.115	-0.136	-0.077
SLA	-0.027	0.050	-0.111	-0.611	0.366
LDMC	-0.097	0.095	0.501	-0.123	0.050
LT	0.339	0.094	-0.122	-0.082	-0.073
UET	0.247	0.152	-0.019	0.311	0.168
LET	0.246	0.169	0.116	0.141	0.444
PTT	0.200	-0.211	-0.356	0.161	0.297
STT	0.251	0.252	0.054	0.169	0.304
CTR	-0.244	-0.262	-0.103	0.219	0.291
SR	-0.253	0.089	0.240	0.277	0.377
CP	-0.036	-0.382	-0.339	-0.010	-0.012
Chl	0.284	-0.013	0.042	-0.177	-0.040
C	0.152	0.277	0.114	-0.312	0.106
N	0.179	-0.328	0.273	0.030	0.045
P	0.121	-0.371	0.297	-0.101	0.108
C:N	-0.127	0.379	-0.231	-0.141	-0.003
N:P	0.007	0.334	-0.249	0.287	-0.157
Variance contribution rate/%	38.948	22.413	12.011	9.603	4.788
Variance contribution rate/%	38.948	61.360	73.371	82.974	87.762

Table 3. *Loadings of principal component analysis for leaf functional traits on south-facing slopes*

Factor	PC1	PC2	PC3	PC4	PC5
LL	0.354	-0.001	-0.017	-0.192	-0.144
LW	0.367	0.078	-0.041	0.020	-0.083
LL/LW	0.145	-0.150	0.038	-0.510	-0.182
LA	0.339	0.010	0.010	-0.104	-0.201
SLA	0.008	-0.106	-0.188	-0.386	0.489
LDMC	0.214	-0.128	0.213	0.328	-0.076
LT	0.343	0.161	-0.025	-0.063	-0.083
UET	0.253	0.189	-0.127	0.240	0.060
LET	0.193	0.313	-0.150	0.088	0.229
PTT	0.297	0.024	0.292	-0.026	0.274
STT	0.211	0.295	-0.256	0.093	0.138
CTR	-0.028	-0.158	0.398	0.036	0.451
SR	-0.254	0.091	-0.252	0.186	0.265
CP	0.146	-0.186	0.469	-0.095	0.170
Chl	0.139	0.327	-0.015	-0.136	0.368
C	0.146	-0.098	0.159	0.508	-0.005
N	0.163	-0.354	-0.254	0.125	0.024
P	0.143	-0.380	-0.232	0.099	0.101
C:N	-0.118	0.340	0.330	0.045	-0.032
N:P	-0.136	0.356	0.177	-0.095	-0.219
Variance contribution rate/%	34.508	23.191	14.141	9.959	7.503
Variance contribution rate/%	34.508	57.699	71.840	81.799	89.302

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The coefficient of variation (CV) is an effective measure of leaf trait plasticity. In this study, morphological indicators such as leaf length, leaf width, and leaf area exhibited higher CV values on north slopes compared with south-facing slopes. This suggests that north-slope leaves are more responsive in morphology to environmental fluctuations, readily adjusting to microhabitat changes and thus displaying greater phenotypic plasticity. In contrast, the lower plasticity of south-slope leaves may result not only from their relatively stable morphological structure but also from stronger environmental stress and lower N and P contents, which could constrain growth and development and reduce plasticity. Structurally, leaf thickness was significantly greater on south-facing slopes. As reported by Wei et al., thicker leaves can provide greater structural support, effectively resisting environmental stresses such as drought. Increased thickness can also raise stomatal density, optimize gas exchange, and improve water-use efficiency, thereby enhancing plant adaptability to adverse conditions (Wei et al., 2025). However, other anatomical traits showed no significant differences between slope aspects, which may be attributable to species-specific genetic constraints (Wu et al., 2016). Physiologically, south-slope leaves of *Quercus aquifolioides* had significantly higher C content but lower N and P contents compared with north-slope leaves. This pattern indicates that under stronger light and temperature stress, south-slope leaves tend to increase C storage and stress resistance at the expense of N and P investment, thereby enhancing tolerance to unfavorable environmental conditions.

In the process of environmental adaptation, plant leaves tend to develop an optimized combination of functional traits that are mutually coordinated (Long et al., 2023). Among the morphological indicators, leaf area was significantly positively correlated with leaf length, leaf width, and leaf thickness, likely because at high elevations, leaves allocate more biomass to support tissues within larger laminae, thereby expanding leaf area to maximize light interception and carbon gain (Pan et al., 2013). Nitrogen and phosphorus contents in leaves were also positively correlated. Both elements are essential for plant growth: N is indispensable for protein synthesis, and P is crucial for cell division and energy metabolism, resulting in a strong synergistic relationship. In this study, north-slope leaves contained significantly higher N and P but lower C than south-slope leaves. Under weaker light conditions, lower photosynthetic rates on north slopes may be compensated for by increasing N and P content in leaves, thereby maintaining relatively stable photosynthetic capacity. Conversely, drought stress on south-facing slopes may drive the translocation of N from leaves to roots or storage organs such as stems to enhance water absorption capacity, resulting in reduced foliar N. Similarly, because P is also involved in water uptake, drought may induce P translocation from leaves to roots. Environmental stress on south-facing slopes may also lead plants to allocate more C to leaves to sustain photosynthetic function or to increase structural C (e.g., lignin in cell walls) to enhance stress resistance. In addition, lower soil pH may increase the availability of N and P, facilitating their uptake and leading to relatively high N and P accumulation in north-slope leaves during growth. Leaf dry matter content (LDMC) on south-facing slopes was more closely related to morphological traits than on north slopes. In this study, specific leaf area (SLA) was significantly lower on south-facing slopes, indicating that, compared with north-slope leaves, south-slope leaves require greater dry mass investment per unit leaf area. The larger leaf size of north-slope individuals, coupled with their structural stability, may also reflect an adaptive strategy to their respective environments.

The results of the principal component analysis (PCA) indicate that the first five principal components captured the integrated information of *Quercus aquifolioides* leaf

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functional traits across slope aspects, effectively representing the major differences in morphological, anatomical, and physiological characteristics between north and south-facing slopes. In north-slope plots, PC1 was dominated by expansive morphological traits such as leaf length (LL), leaf width (LW), leaf area (LA), and compactness (CTR), while PC2 was driven primarily by structural traits, including upper and lower epidermis thickness (UET, LET) and spongy tissue thickness (STT). Individuals with high PC1 scores exhibited stronger leaf expansion capacity, reflecting a strategy of increasing photosynthetic surface area to enhance resource acquisition under low-light conditions. Along the PC2 axis, greater tissue thickness indicated a tendency toward structural protection, likely serving to cope with long-term moist but low-energy environmental stress. This combination can be summarized as a "high-expansion–moderately conservative" intermediate strategy, balancing photosynthetic needs with structural stability. In south-slope plots, PC1 was also dominated by leaf area–related traits, but PC2 placed greater weight on structural tissue parameters (LET, STT, UET), underscoring adaptations for defense against high light intensity and water availability fluctuations. Chlorophyll (Chl) and structural traits were coupled along PC2 and PC3, suggesting that south-slope plants reinforce structural integrity while simultaneously adjusting photosynthetic capacity to maintain physiological function. This indicates a more typical "high structural investment–strong defense" strategy in south-slope environments, tailored to cope with intense radiation, high evaporative demand, and pronounced diurnal temperature variation. Taken together, the PCA results reveal that north-slope leaves are positioned more toward the morphological expansion and functional acquisition end of the spectrum in PC1 and PC2 space, exhibiting "high investment–high return" fast-growth characteristics. In contrast, south-slope leaves show a marked tendency toward structural enhancement along PC2, emphasizing a "low risk–high maintenance" resource-conservation strategy. This ecological functional shift parallels patterns observed in the functional trait transitions between current-year and older leaves: as environmental stress intensifies, leaf resource allocation shifts toward structural investment, with survival strategies transitioning from acquisition-oriented to defense-oriented modes.

Leaf economics spectrum of Quercus aquifolioides under different slope aspects

Within the framework of the leaf economics spectrum (LES), the fast investment–return strategy is generally characterized by thinner leaves, larger specific leaf area (SLA), lower tissue density, higher leaf dry matter content, and stronger photosynthetic capacity, whereas the slow investment–return strategy exhibits the opposite trait profile. The integrated analysis of our multi-dimensional trait set clearly demonstrates that north-facing slope leaves adopted a fast investment–return, acquisition-oriented strategy, enabling rapid morphological expansion to capture more sunlight, thereby enhancing photosynthetic rates and accelerating biomass accumulation. By contrast, south-facing slope leaves tended toward a slow investment–return, conservative strategy, which prioritizes structural stability and durability, allowing them to maintain function and survive under conditions of higher environmental stress.

Compared with *Quercus wutaishanica* studied by Chen (2020), *Quercus aquifolioides* in the Nyang River Basin exhibited greater leaf thickness and lower specific leaf area (SLA). Relative to the findings of Li Yi et al. for *Quercus mongolica*, both chlorophyll (Chl) and soluble sugar (SS) contents were lower in *Quercus aquifolioides* (Li et al., 2024). These comparisons suggest that, within the leaf economics spectrum of several Quercus species, *Quercus aquifolioides* in the Nyang River Basin is generally biased

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toward a slow investment–return strategy. This tendency is likely attributable to the higher elevation and greater environmental pressures of the Nyang River Basin, where long-term exposure to complex and variable habitat conditions favors the adoption of more conservative strategies that enhance stress resistance and environmental tolerance.

The leaf economics spectrum (LES) describes how plants adjust their resource allocation strategies under specific environmental conditions, reflecting the coordination and balance among leaf morphological construction, elemental composition, and physiological activity (Wright and Sutton-Grier, 2012). While our trait set comprehensively covers morphological and physio-chemical axes, we acknowledge that incorporating direct physiological measurements (e.g., stomatal density, photosynthetic rates) would provide even deeper mechanistic insights into the resource-use strategies. This represents a valuable direction for future research. In this study, leaf area, specific leaf area (SLA), leaf thickness, and water-use efficiency emerged as the core traits shaping the LES. On north slopes, leaves sought to gain a competitive advantage in light acquisition by rapidly expanding leaf area and sustaining efficient photosynthesis, thus adopting a fast investment–return, growth-oriented strategy. This approach enables the rapid accumulation of energy through high photosynthetic capacity, providing the necessary energy and nutrient support for both vegetative and reproductive growth. In contrast, south-slope leaves tended to develop thicker laminae and smaller SLA to reduce water loss and maintain survival under resource-limited conditions. Although their photosynthetic efficiency and growth rate were lower than those of north-slope leaves, their more developed structural morphology and higher structural material content allowed them to maintain structural stability in the complex high-elevation environment. This enhanced structural investment also improves resistance to heat and high-radiation damage, providing long-term protection and stability for the plant (Reich et al., 1998).

The unique growth strategies of *Quercus aquifolioides* across different slope aspects at high elevations, as revealed in this study, are the outcome of the long-term combined influence of multiple habitat factors. Situated on the plateau, the Nyang River Basin subjects *Quercus aquifolioides* to intense solar radiation and high irradiance, placing the species under persistent environmental stress. At the same time, low soil water content and nutrient availability constrain nutrient uptake by the roots, compelling the plants to compensate through enhanced nutrient acquisition via the leaves. The capacity for adaptive adjustment along the leaf economics spectrum is one of the key mechanisms enabling *Quercus aquifolioides* to cope with such conditions. Furthermore, the highly heterogeneous environment of the Nyang River Basin has, over time, selected for a "dual-strategy coordination" mechanism in leaf traits across slope aspects—allowing individuals to survive under variable and resource-limited conditions. Through prolonged adaptive evolution, these dual strategies have become genetically fixed, ultimately enhancing the species' ecological competitiveness in the region. This mechanism not only explains the distinctive survival strategies of Quercus aquifolioides but also provides a more comprehensive theoretical basis for understanding the ecological adaptability of alpine plants.

Conclusion

Quercus aquifolioides leaves exhibited pronounced functional trait differences between slope aspects. South-slope leaves possessed more developed structural morphology and lower biochemical activity, whereas north-slope leaves displayed greater

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growth vigor. These differences indicate that north-slope leaves adopt a fast investment–return, acquisition-oriented strategy, characterized by rapid growth and high photosynthetic efficiency to facilitate swift biomass accumulation. In contrast, south-slope leaves follow a slow investment–return, conservative strategy, prioritizing stability and durability to persist under harsh environmental conditions. Overall, *Quercus aquifolioides* has evolved two distinct growth strategies to cope with the environmental challenges associated with different slope aspects. This differentiation not only enhances the species' capacity for survival and reproduction in the complex, high-elevation montane ecosystems but also reflects a finely tuned internal coordination and trade-off mechanism between strategies. Through this mechanism, *Quercus aquifolioides* can simultaneously promote growth and enhance resistance to multiple stresses, including intense radiation, drought, and wind exposure.

Nevertheless, this study has certain limitations. The habitat conditions faced by tree species in the Nyang River Basin are highly specific and complex, and our investigation was restricted to the adaptability of *Quercus aquifolioides* at a single elevation and within a single geographic area. Future research should expand to encompass multiple elevations and regions to improve the generality of the conclusions. Moreover, this study focused primarily on leaf functional traits and did not include other potentially influential traits, such as stomatal density or physiological parameters related to photosynthesis. Incorporating these factors in future analyses would allow for a more comprehensive understanding of plant adaptive mechanisms under varying environmental conditions. Future studies could explore *Quercus aquifolioides* adaptive strategies from multiple perspectives, particularly in the context of global climate change, examining shifts in growth patterns across slope aspects, climatic regimes, and varying levels of environmental stress. Additionally, integrating genomic analyses with functional trait data could yield deeper insights into the genetic basis of adaptability. Ultimately, such research will provide a stronger theoretical foundation for the conservation and ecological restoration of alpine plant species.

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APPENDIX

Table A1. *Comparison and coefficient of variation (CV) of soil factors between north and south-facing slopes*

Factor	North-facing slopes (mean ± SD)	South-facing slopes (mean ± SD)	P	North-facing CV	South-facing CV
ph	5.01 ± 0.40	5.13 ± 0.29	>0.05	7.90	5.57
SWC	*10.339 ± 0.629*	*9.457 ± 0.387*	<0.01	6.088	4.097
C	*58.060 ± 6.919*	*27.332 ± 4.591*	<0.01	11.917	16.796
N	*3.975 ± 0.067*	*1.757 ± 0.169*	<0.01	1.674	9.617
P	0.412 ± 0.020	0.406 ± 0. 017	>0.05	4.960	4.227
K	*1.046 ± 0.024*	*1.223 ± 0.029*	<0.01	2.292	2.349
C:N	14.609 ± 1.783	15.455 ± 1.248	>0.05	12.203	8.074
N:P	*9.673 ± 0.508*	*4.323 ± 0.259*	<0.01	5.251	6.000

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