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Phenotypic Trait Variation and Adaptation Strategies in Leaves of *Pinus densata* in Southeastern Xizang

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Abstract

To explore the variation in leaf phenotypic traits and environmental adaptation strategies of *Pinus densata* in southeastern Xizang, 15 plots were established across five regions—Gongbujiangda County (GB), Bomi County (BM), Bayi District (BY), Milin City (ML), and Lang County (LX)—and 11 leaf traits were measured, including leaf length (LL), width (LD), area (LA), volume (LV), fresh weight (LFW), dry weight (LDW), tissue density (LTD), specific leaf area (SLA), and leaf greenness index (SPAD). Results showed that all traits except LL varied significantly among regions, with moderate variation overall; SPAD exhibited the highest coefficient of variation, while leaf water content was the most stable. Extensive correlations were detected among traits: leaf size and weight traits were positively intercorrelated and all negatively correlated with LTD, and SLA correlated negatively with LTD but positively with SPAD. Principal component analysis and hierarchical clustering further revealed that phenotypic variation aligned with the leaf economic spectrum and grouped the populations into three strategy types. Specifically, GB populations approached the "slow investment–return" end of the spectrum, BY and BM populations the "fast investment–return" end, while ML and LX occupied intermediate positions (transitional strategies), with ML leaning toward the slow end. These findings demonstrate that *P. densata* in southeastern Xizang has evolved diverse resource use and adaptation strategies through synergistic and trade-off relationships among leaf traits, enabling its persistence in complex high-altitude environments.

Keywords: *P. densata*; leaf phenotypic traits; trait variation; leaf economics spectrum; adaptation strategy; southeastern Xizang

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1. Introduction

Functional traits represent a series of quantifiable, measurable, and relatively stable inherited characteristics. During the long-term evolutionary process, functional traits reflect plants' adaptations to external environments and their strategies for resource utilization [1–5]. These traits are influenced by both genetic factors and environmental conditions. When external factors change, plants can adaptively modify these traits, with their characteristics and variations serving as indicators of survival strategies in different environments. Leaf phenotypic traits are a key component of plant functional traits, typically reflecting leaf size, structure, and photosynthetic capacity. Leaves are essential for material and energy

exchange between plants and their environment, exhibiting significant phenotypic plasticity. Leaf functional traits bridge the connection between plants and their environment, forming the core mechanism for plant responses to environmental changes [6]. Studying these phenotypic traits provides valuable insights into how external environments shape leaf characteristics.

The Qinghai–Xizang Plateau is a crucial region for species formation and adaptive evolution in China. Its biodiversity distribution patterns exhibit remarkable uniqueness, sensitivity to climate change and environmental disturbances, and low ecosystem stability, making it a typical ecologically fragile zone [7]. Influenced by its unique topography and regional weather systems, the plateau exhibits a climatic gradient transitioning from severe cold and aridity in the northwest to warm and humid conditions in the southeast. It also features diverse microclimatic units, most notably the pronounced vertical climatic zonation of its high mountains [8]. These distinctive natural and geographical conditions confer irreplaceable importance to the plateau in ecological research and national regional security strategies. Southeastern Xizang serves as the core forest resource distribution area of Xizang. The moisture corridor formed by the Yarlung Tsangpo River and its tributary valleys acts as a conduit for warm, moist air currents from the northern Indian Ocean. This results in a warm and humid climate in southeastern Xizang, fostering forest vegetation with highly distinctive species composition and community structure [9], which has long attracted significant attention from researchers.

Pinus densata is endemic to western China and constitutes a primary dominant species in the coniferous forests of the Hengduan Mountains, Nyenchen Tanglha Mountains, and the middle reaches of the Yarlung Tsangpo River in southeastern Xizang [10]. It primarily occurs in humid to semi-humid regions at elevations of 2600–3500 m, often growing on sun-exposed slopes and along riverbanks. In Xizang, *P. densata* is mainly distributed in Linzhi City, forming extensive pure stands or mixed forests with Pinus tabulaeformis and Pinus yunnanensis in Bayi District, Bomi County, Milin City, and along the middle and lower reaches of the Yarlung Tsangpo River [11–14]. Its distribution is discontinuous due to topographic and altitudinal barriers, with populations typically exhibiting a uniform spatial pattern [15–17]. Although *P. densata* shows some drought tolerance, its growth is strongly influenced by water availability; under moist conditions, it frequently occupies open sunny slopes, whereas in drier areas, it is confined to valley tributaries and shaded slopes. As a tree species endemic to the Qinghai–Xizang Plateau of China, *P. densata* has been the subject of limited research, and studies on its functional traits remain largely unexplored. This study analyzed 11 leaf phenotypic traits of *P. densata* from 15 sample plots in Nyingchi, southeastern Xizang, and proposed the following hypotheses:

(1) There are significant differences in leaf phenotypic traits of *P. densata* among different regions in southeastern Xizang, and these differences arise from adaptive adjustments of *P. densata* to local environmental conditions.
(2) The adaptation strategies of leaf phenotypic traits of *P. densata* in different regions of southeastern Xizang align with the leaf economics spectrum, with each region exhibiting its respective strategy.

2. Materials and Methods

2.1. Study Area and Sampling

The study area is located in Linzhi City, southeastern Xizang Autonomous Region (29°33′–30°40′ N, 93°27′–95°17′ E), at the junction of the Nyenchen Tanglha Mountains and Hengduan Mountains. With a mean elevation of approximately 3100 m, the region exhibits a humid subtropical–plateau transitional climate [18]. The mean annual temperature ranges from 8.5 to 10.2 °C. Influenced by the monsoon system and warm air masses from the

Indian Ocean, precipitation is concentrated in the warm season. Annual precipitation ranges from 650 to 2200 mm, with June and July accounting for approximately 40% of the total, making the area a major precipitation center of the Qinghai–Xizang Plateau [19,20]. Southeastern Xizang represents the primary forested region of the plateau. The tree layer is dominated by *P. densata*, *Abies georgei* var. *smithii*, and *Picea likiangensis* var. *linzhiensis*. The shrub layer commonly includes *Rhododendron*, *Berberis*, *Rosa omeiensis*, and *Sophora*.

Field sampling was conducted in August 2024 in Linzhi City, southeastern Xizang, including Bayi District (BY), Milin City (ML), Bomi County (BM), Gongbujiangda County (GB), and Lang County (LA), where *P. densata* samples were surveyed and collected. In each region, three 20 m × 20 m plots were established at least 5 km apart within representative pure stands of *P. densata*. Within each plot, three healthy *P. densata* individuals were selected as standard trees. From each standard tree, three to five branch bundles were collected from the eastern, southern, western, and northern aspects of the mid-canopy and placed in sterile, sealed, light-protected bags (Table 1).

Table 1. Location of sampling point.

Area	Plot	Longitude	Latitude
Bayi District	BY1	94°47′56.20″ E	29°56′45.65″ N
	BY2	94°22′27.36″ E	29°39′20.61″ N
	BY3	94°12′45.37″ E	29°45′39.73″ N
Milin City	ML1	94°43′19.60″ E	29°26′19.57″ N
	ML2	94°1′15.12″ E	29°11′25.95″ N
	ML3	94°14′43.59″ E	29°14′9.48″ N
Bomi County	BM1	95°25′19.97″ E	29°55′14.79″ N
	BM2	95°43′44.44″ E	29°52′19.42″ N
	BM3	95°47′18.41″ E	29°48′46.70″ N
Gongbujiangda County	GB1	93°25′22.89″ E	29°52′58.24″ N
	GB2	93°41′12.66″ E	29°58′29.13″ N
	GB3	93°53′41.62″ E	29°59′54.19″ N
Lang County	LX1	93°5′39.81″ E	29°6′11.46″ N
	LX2	93°8′12.07″ E	29°8′2.80″ N
	LX3	93°26′57.20″ E	29°6′12.18″ N

2.2. Measurements

Samples were transported to the laboratory for processing and trait measurements. Leaves from perennial twigs were detached, pooled, and thoroughly mixed. Uniform subsampling was performed using the quartering method. For each plot, 15 leaves were selected and divided into three groups of five leaves each. Fresh leaf weight (LFW, g) was measured using an electronic balance with a precision of 0.001 g. Leaf length (L, mm), leaf width (LD, mm), and leaf thickness (LT, mm) were measured using a digital vernier caliper with a precision of 0.01 mm. Leaf greenness index (SPAD) was determined using an SPAD-502Plus chlorophyll meter (Konica Minolta, Tokyo, Japan). After fresh weight measurement, samples were oven-dried at 80 °C to constant mass to determine leaf dry weight (LDW, g). Leaf area (LA, cm^2), specific leaf area (SLA, cm^2/g), leaf water content (LWC), leaf volume (LV, cm^3), and leaf tissue density (LTD, g/cm^3) were calculated based on the measured parameters. Calculations were performed using the formulas specified in the forestry industry standard LY/T 2812-2017 "Methodology for functional traits measurement of woody plants in forests" [21]. The calculation formulas were as follows:

$$LA = \frac{\pi \times LD \times L}{2} \quad (1)$$

$$SLA = \frac{LA}{LDW} \quad (2)$$

$$LWC = \frac{LFW - LDW}{LFW} \quad (3)$$

$$LV = LT \times LA \quad (4)$$

$$LTD = \frac{LDW}{LV} \quad (5)$$

2.3. Statistical Analysis

Descriptive statistics (mean, standard deviation, and coefficient of variation) were calculated for each trait within each region using Microsoft Excel 2016. All statistical analyses were performed using SPSS 27.0.1 (IBM, Armonk, NY, USA). The normality of data distribution was assessed using the Shapiro–Wilk test, and homogeneity of variances was examined using Levene's test (based on medians). Since all traits met the assumptions of normality ($p > 0.05$) and homogeneity of variances ($p > 0.05$), one-way analysis of variance (ANOVA) was employed to test for significant differences in leaf phenotypic traits among the five regions. When ANOVA indicated significant differences ($p < 0.05$), post hoc multiple comparisons were conducted using Tukey's honestly significant difference (HSD) test to identify specific differences between regions. Results are presented as mean ± standard deviation, with different lowercase letters indicating significant differences at $p < 0.05$. Pearson correlation analysis was used to examine relationships among traits, and principal component analysis (PCA) was performed to explore overall variation patterns and adaptation strategies. Principal component analysis was performed on standardized trait data using the correlation matrix to ensure equal weighting of variables. The resulting biplot applies symmetric scaling to simultaneously display trait loadings and sample scores, with vector lengths proportional to trait contributions. Hierarchical cluster analysis was performed to explore the natural grouping of the 15 samples based on the 11 leaf traits. Euclidean distance was used as the dissimilarity measure, and Ward's method was applied as the linkage rule. Prior to clustering, all variables were standardized to Z-scores (mean = 0, standard deviation = 1) to eliminate the influence of different measurement scales. All figures were generated using OriginPro 2021 (OriginLab, Northampton, MA, USA).

2.4. AI Tool Usage

During the preparation of this manuscript, the authors used ChatGPT 4.0 (OpenAI, San Francisco, CA, USA) for language polishing and proofreading. The authors have reviewed and edited the output and take full responsibility for the content of this publication.

3. Results

3.1. Characterization of Leaf Phenotypic Traits in Southeast Xizang

One-way ANOVA based on a total of 15 plots ($n = 3$ per region) showed that, except for leaf length (LL), the other 10 leaf traits differed significantly among the five regions ($p < 0.05$). Post hoc comparisons with Tukey's HSD test revealed the following patterns of regional differences for each trait (Table 2, Figure 1).

Leaf length (LL): No significant differences among regions ($F_{4, 10} = 2.15$, $p = 0.419$). Leaf width (LD): Significant regional differences ($F_{4, 10} = 13.41$, $p < 0.001$). BM had the lowest LD, significantly lower than all other regions. BY was significantly lower than ML, LX, and GB, but not significantly different from BM. No significant differences were found among ML, LX, and GB, and all were significantly higher than BY and BM. Leaf thickness (LT): Significant regional differences ($F_{4, 10} = 10.93$, $p = 0.001$). BM and BY were significantly

lower than ML, LX, and GB, with no significant differences between BM and BY or among ML, LX, and GB.

Table 2. Comparison of leaf phenotypic traits.

Trait	LX	BY	ML	BM	GB
LL	141.76 ± 12.05 a	154.07 ± 12.64 a	148.28 ± 12.74 a	156.01 ± 7.22 a	165.7 ± 6.2 a
LD	0.824 ± 0.032 a	0.678 ± 0.102 b	0.799 ± 0.033 a	0.616 ± 0.039 c	0.897 ± 0.021 a
LT	0.529 ± 0.021 a	0.440 ± 0.026 b	0.522 ± 0.043 a	0.423 ± 0.035 b	0.627 ± 0.07 a
LA	1.832 ± 0.111 b	1.629 ± 0.172 b	1.863 ± 0.194 b	1.512 ± 0.135 b	2.337 ± 0.12 a
LV	0.097 ± 0.01b	0.072 ± 0.012 b	0.097 ± 0.005 b	0.064 ± 0.011 c	0.146 ± 0.01 a
LFW	0.149 ± 0.016 b	0.178 ± 0.026 b	0.195 ± 0.034 b	0.159 ± 0.021 b	0.276 ± 0.035 a
LDW	0.077 ± 0.003 c	0.072 ± 0.005 c	0.095 ± 0.016 b	0.063 ± 0.009 c	0.112 ± 0.006 a
LWC	0.481 ± 0.036 b	0.590 ± 0.038 a	0.511 ± 0.004 b	0.604 ± 0.011 a	0.587 ± 0.069 a
LTD	0.799 ± 0.062 ab	1.015 ± 0.1 a	0.986 ± 0.147 ab	0.992 ± 0.031 ab	0.772 ± 0.014 b
SLA	23.913 ± 0.91 a	22.554 ± 0.83 ab	19.806 ± 1.48 b	24.432 ± 1.22 a	20.865 ± 1.97 b
SPAD	28.778 ± 4.8 b	37.056 ± 4.07 ab	30.589 ± 6.06 ab	40.200 ± 1.69 a	31.589 ± 2.63 ab

Data are presented as mean ± standard deviation. Different lowercase letters within the same row indicate significant differences at $p < 0.05$. Abbreviations of leaf traits are as follows: leaf length (LL, mm), leaf width (LD, mm), leaf thickness (LT, mm), leaf area (LA, mm^2), leaf volume (LV, mm^3), leaf fresh weight (LFW, g), leaf dry weight (LDW, g), leaf tissue density (LTD, g/cm^3), specific leaf area (SLA, cm^2/g), leaf water content (LWC), and leaf greenness index (SPAD). Regional abbreviations: LX = Lang County, BY = Bayi District, ML = Milin City, BM = Bomi County, GB = Gongbujiangda County.

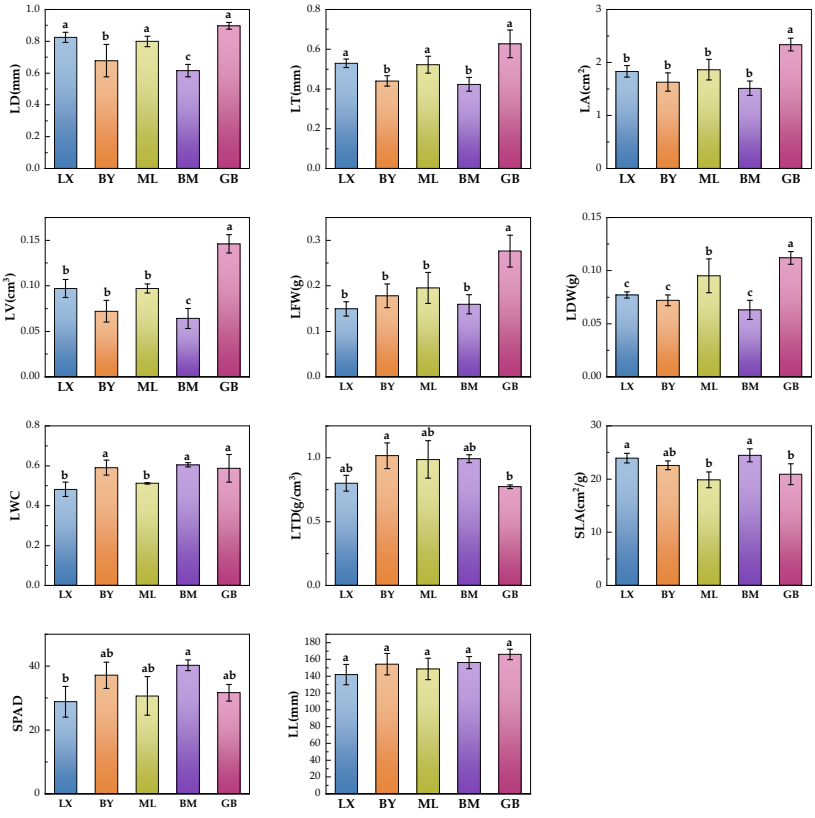


Figure 1. Comparison of 11 leaf phenotypic traits of *Pinus densata* across five regions in southeastern Xizang. Bars represent mean ± SD (n = 3 plots per region). Different letters above bars indicate significant differences among regions within each trait (Tukey HSD, $p < 0.05$). Abbreviations of leaf traits are as follows: leaf length (LL, mm), leaf width (LD, mm), leaf thickness (LT, mm), leaf area (LA, mm^2), leaf volume (LV, mm^3), leaf fresh weight (LFW, g), leaf dry weight (LDW, g), leaf tissue density (LTD, g/cm^3), specific leaf area (SLA, cm^2/g), leaf water content (LWC), and leaf greenness index (SPAD). Regional abbreviations: LX = Lang County, BY = Bayi District, ML = Milin City, BM = Bomi County, GB = Gongbujiangda County.

Leaf area (LA): Significant regional differences ($F_{4, 10} = 13.35$, $p < 0.001$). No significant differences were observed among BM, BY, LX, and ML, and all were significantly lower than GB. Leaf volume (LV): Significant regional differences ($F_{4, 10} = 31.82$, $p < 0.001$). BM was significantly lower than BY, ML, and LX, while no significant differences existed among BY, ML, and LX. GB was significantly higher than all other regions.

Leaf fresh weight (LFW): Significant regional differences ($F_{4, 10} = 10.32$, $p = 0.001$). No significant differences were found among LX, BM, BY, and ML, and all were significantly lower than GB. Leaf dry weight (LDW): Significant regional differences ($F_{4, 10} = 14.49$, $p < 0.001$). No significant differences were observed among BM, BY, and LX. ML was significantly higher than BM but not significantly different from BY or LX. GB was significantly higher than all other regions.

Leaf water content (LWC): Significant regional differences ($F_{4, 10} = 5.97$, $p = 0.010$). LX and ML were significantly lower than GB, BY, and BM, with no significant differences between LX and ML or among GB, BY, and BM.

Leaf tissue density (LTD): Significant regional differences ($F_{4, 10} = 5.61$, $p = 0.012$). BY was significantly higher than GB ($p < 0.05$), with no other significant differences among regions.

Specific leaf area (SLA): Significant regional differences ($F_{4, 10} = 6.41$, $p = 0.008$). ML was significantly lower than LX and BM ($p < 0.05$), with no other significant differences among regions (LX, BM, BY, GB).

Leaf greenness index (SPAD): Significant regional differences ($F_{4, 10} = 4.00$, $p = 0.034$). BM was significantly higher than LX ($p < 0.05$), with no other significant differences among regions.

3.2. Variation in Leaf Phenotypic Traits

As shown in Figure 2, the coefficient of variation (CV) for *P. densata* needle phenotypic traits across counties and districts in southeastern Xizang ranged from 2.27% to 22.05%. Among the traits, Milin City exhibited the highest CV for SPAD (22.05%), with relatively high CVs for LFW, LDW, and LTD, whereas LWC had the lowest CV (2.27%). In Bomi County, LDW showed the highest CV (21.31%), followed by LFW and LV, while LWC had the lowest CV (3.32%). In Linzhi County, SPAD exhibited the highest CV (18.67%), whereas other traits showed lower variability, with LTD being the lowest (3.68%). In Bayi District, SPAD had the highest CV (18.47%), while SLA had the lowest (4.54%). In Lang County, SPAD showed the highest CV (17.33%), LD the lowest (4.56%), and LV and LFW had relatively higher CVs.

3.3. Correlations Among Leaf Phenotypic Traits

Functional traits are key indicators of plant survival strategies, reflecting adaptations to environmental change and trade-offs in resource use. These traits do not function independently; correlations among traits reveal underlying mechanisms of plant adaptation to environmental conditions.

Pearson correlation analysis indicated strong interrelationships among the 11 leaf phenotypic traits of *P. densata* from southeastern Xizang. As shown in Figure 3, LL exhibited highly significant positive correlations with LA and LDW ($p < 0.01$), as well as a significant positive correlation with LWC ($p < 0.05$). LD showed highly significant positive correlations with LT, LA, LV, LFW, and LDW ($p < 0.01$), and highly significant negative correlations with LTD and SPAD ($p < 0.01$), as well as significant negative correlations with LWC and SLA ($p < 0.05$).

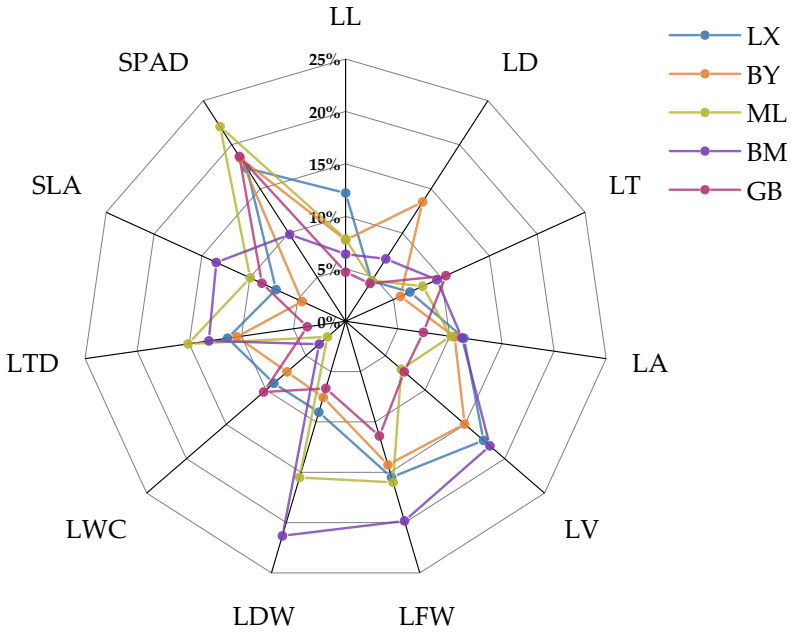


Figure 2. Radar plots of coefficient of variation (CV, %) of 11 leaf phenotypic traits of *Pinus densata* across five regions in southeastern Xizang. CV was calculated as (standard deviation/mean) × 100%. Higher values indicate greater trait variability. Abbreviations of leaf traits are as follows: leaf length (LL, mm), leaf width (LD, mm), leaf thickness (LT, mm), leaf area (LA, mm^2), leaf volume (LV, mm^3), leaf fresh weight (LFW, g), leaf dry weight (LDW, g), leaf tissue density (LTD, g/cm^3), specific leaf area (SLA, cm^2/g), leaf water content (LWC), and leaf greenness index (SPAD). Regional abbreviations: LX = Lang County, BY = Bayi District, ML = Milin City, BM = Bomi County, GB = Gongbujiangda County.

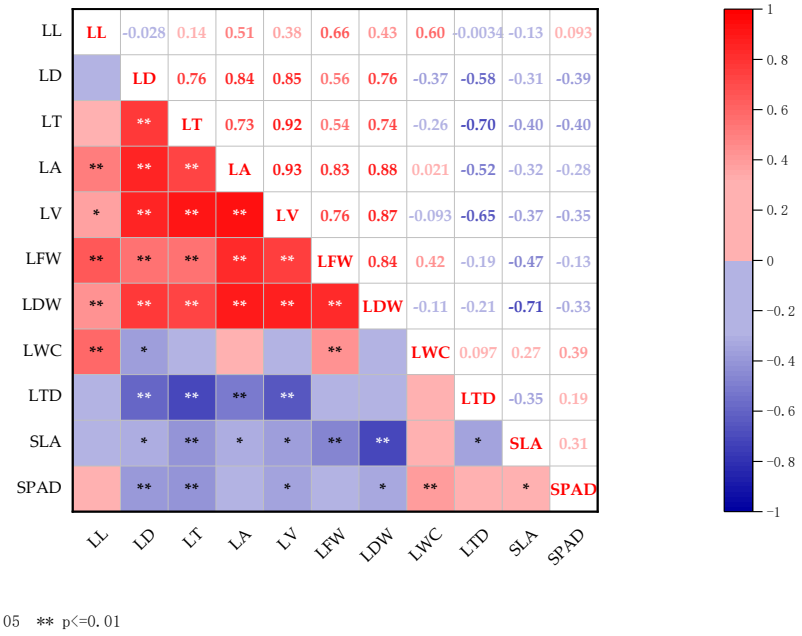


Figure 3. Pearson correlation matrix of 11 leaf phenotypic traits of *Pinus densata* in southeastern Xizang. Color intensity represent the strength of correlation; blue indicates positive correlation, red indicates negative correlation. Significance levels: * $p < 0.05$, ** $p < 0.01$. Abbreviations of leaf traits are as follows: leaf length (LL, mm), leaf width (LD, mm), leaf thickness (LT, mm), leaf area (LA, mm^2), leaf volume (LV, mm^3), leaf fresh weight (LFW, g), leaf dry weight (LDW, g), leaf tissue density (LTD, g/cm^3), specific leaf area (SLA, cm^2/g), leaf water content (LWC), and leaf greenness index (SPAD).

LT exhibited highly significant positive correlations with LA, LV, LFW, and LDW ($p < 0.01$), and highly significant negative correlations with LTD, SLA, and SPAD ($p < 0.01$). LA showed highly significant positive correlations with LV, LFW, and LDW ($p < 0.01$), a highly significant negative correlation with LTD ($p < 0.01$), and a significant negative correlation with SLA ($p < 0.05$). LV was highly significantly positively correlated with LFW and LDW ($p < 0.01$), highly significantly negatively correlated with LTD ($p < 0.01$), and significantly negatively correlated with SLA and SPAD ($p < 0.05$).

Both LFW and LDW showed highly significant negative correlations with SLA ($p < 0.01$). In addition, LFW exhibited a highly significant positive correlation with LWC ($p < 0.01$), whereas LDW showed a significant negative correlation with SPAD ($p < 0.05$). SPAD was highly significantly positively correlated with LWC ($p < 0.01$) and significantly positively correlated with SLA ($p < 0.05$). LTD showed a significant negative correlation with SLA ($p < 0.05$).

3.4. Principal Component and Cluster Analysis of Leaf Phenotypic Traits

Principal component analysis was performed on 11 leaf traits to investigate variation patterns among five regions (LX, BY, ML, BM, GB). The first two components (PC1 and PC2) had eigenvalues greater than 1, explaining 56.7% and 22.7% of the total variance, respectively, and cumulatively accounting for 79.4% of the variation. Subsequent analyses focused on these two components.

Loading analysis (Table 3) revealed that PC1 was strongly positively correlated with LD, LT, LA, LV, LFW, and LDW (loadings > 0.31), representing leaf biomass and size, and was interpreted as a leaf size axis. PC2 showed high positive loadings for LL and LWC (0.56 and 0.58, respectively), along with moderate loadings for LFW and SPAD, reflecting leaf length and water status, and was interpreted as a leaf length and water status axis.

Table 3. Loadings of leaf Phenotypic traits on the first two principal components.

Trait	PC1	PC2
LL	0.12	**0.56**
LD	**0.36**	−0.18
LT	**0.37**	−0.13
LA	0.38	0.12
LV	0.39	0.02
LFW	0.32	0.37
LDW	0.38	0.09
LWC	−0.07	0.58
LTD	−0.25	0.17
SLA	−0.24	0.00
SPAD	−0.22	0.34

Abbreviations of leaf traits are as follows: leaf length (LL, mm), leaf width (LD, mm), leaf thickness (LT, mm), leaf area (LA, mm^2), leaf volume (LV, mm^3), leaf fresh weight (LFW, g), leaf dry weight (LDW, g), leaf tissue density (LTD, g/cm^3), specific leaf area (SLA, cm^2/g), leaf water content (LWC), and leaf greenness index (SPAD). Regional abbreviations: LX = Lang County, BY = Bayi District, ML = Milin City, BM = Bomi County, GB = Gongbujiangda County.

The PCA biplot (Figure 4) simultaneously displays trait vectors and regional samples in the space defined by PC1 and PC2. Trait vectors for LD, LT, LA, LV, LFW, and LDW were relatively long and formed small angles with the PC1 axis, confirming their strong contribution to PC1. LL and LWC vectors were closely aligned with the PC2 axis. Additionally, LFW and LDW vectors pointed in similar directions, indicating a strong positive correlation, while specific leaf area (SLA) and leaf tissue density (LTD) vectors pointed in opposite directions, reflecting the trade-off along the leaf economic spectrum.

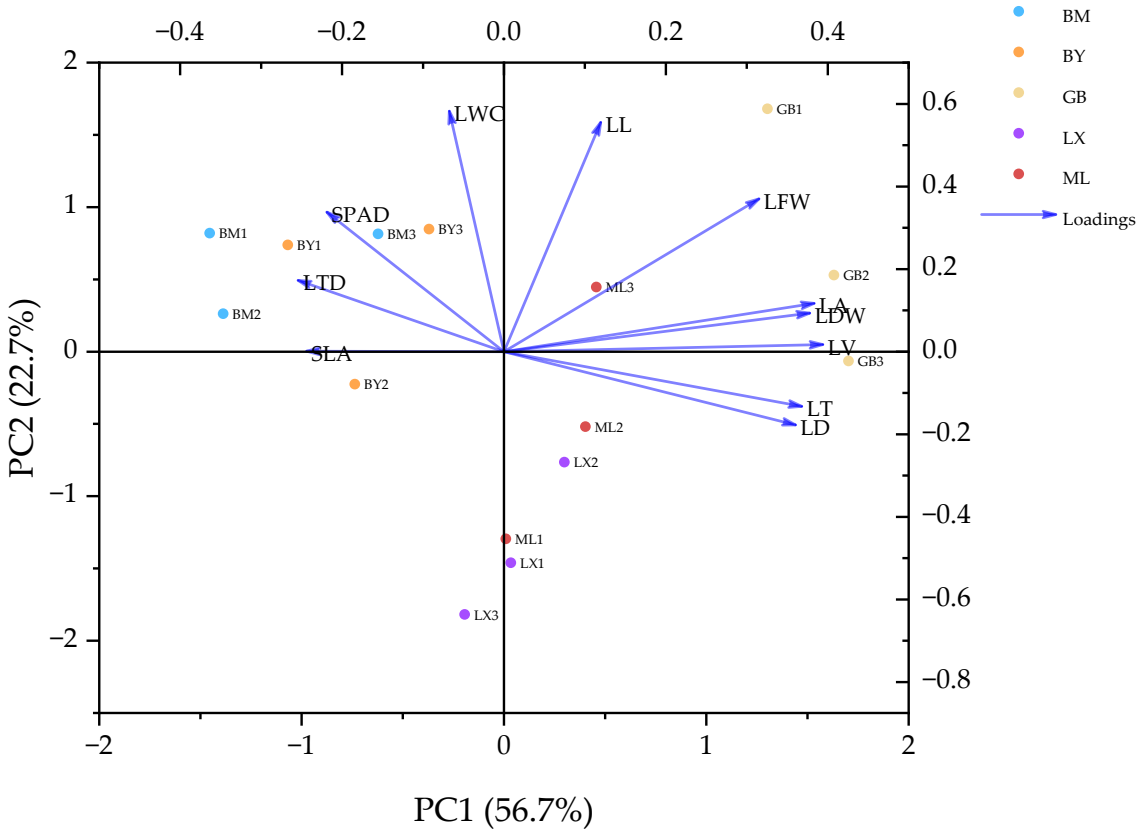


Figure 4. Principal component analysis (PCA) of leaf phenotypic traits of *P. densata* from five regions in southeastern Xizang. Arrows represent trait loadings based on the correlation matrix with symmetric scaling; longer vectors indicate stronger contributions to the principal components. Colored dots represent individual plots grouped by region. PC1 and PC2 explained 56.7% and 22.7% of the total variance, respectively. Abbreviations are the same as in Table 2. Abbreviations of leaf traits are as follows: leaf length (LL, mm), leaf width (LD, mm), leaf thickness (LT, mm), leaf area (LA, mm^2), leaf volume (LV, mm^3), leaf fresh weight (LFW, g), leaf dry weight (LDW, g), leaf tissue density (LTD, g/cm^3), specific leaf area (SLA, cm^2/g), leaf water content (LWC), and leaf greenness index (SPAD). Regional abbreviations: LX = Lang County, BY = Bayi District, ML = Milin City, BM = Bomi County, GB = Gongbujiangda County.

Regarding regional distribution, GB region samples were predominantly located in the positive direction of PC1, aligning with biomass-related vectors such as LA, LV, and LDW, indicating larger leaf area, volume, and dry weight in this region. BM region samples were situated in the negative direction of PC1, opposite to these trait vectors, corresponding to smaller leaf dimensions. Along PC2, LX region samples were distributed in the negative direction, opposite to LL and LWC vectors, reflecting shorter leaf length and lower water content. In contrast, GB, BM, and BY region samples were positioned in the positive direction of PC2, aligning with LL and LWC vectors, indicating longer leaves and higher water content. ML region samples showed intermediate positive scores on PC1 and slightly negative scores on PC2, representing moderate leaf size but relatively low water content.

Cluster analysis results showed that *P. densata* in southeastern Xizang was classified into three categories (Figure 5). LX and ML, which adopt a transitional strategy, were classified as the first category. The second category consisted of GB, representing a "slow investment-return" strategy. The third category included BY and BM, which represent a "fast investment-return" strategy. These results are generally consistent with the strategies of *P. densata* in the leaf economic spectrum.

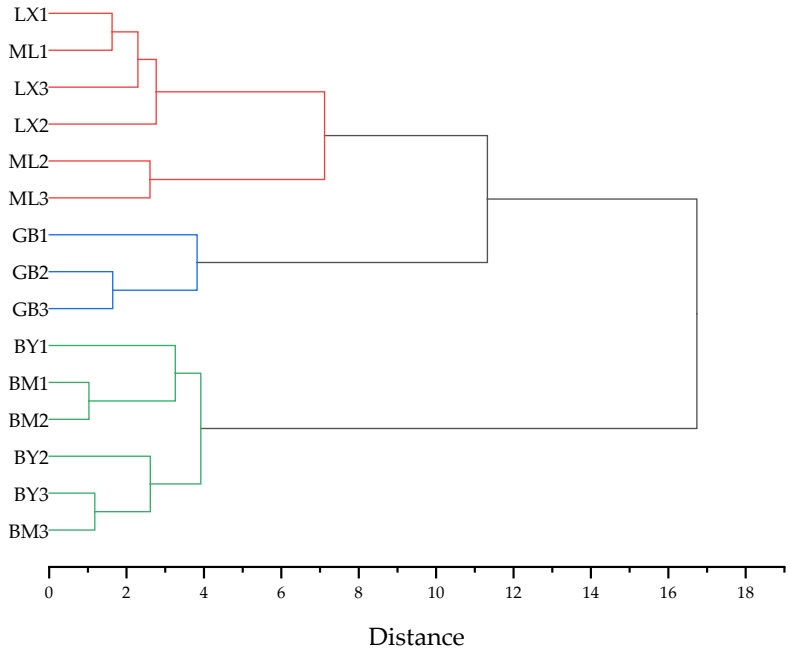


Figure 5. Dendrogram of hierarchical cluster analysis based on 11 leaf traits using Euclidean distance and Ward's linkage method. The 15 plots are classified into three strategies: the transitional strategy (LX = Lang County, ML = Milin County); the "slow investment-return" strategy (GB = Gongbujiangda County); and the "fast investment-return" strategy (BY = Bayi District, BM = Bomi County). Different colors represent different categories: red for the first category (transitional strategy), blue for the second category (slow investment-return strategy), and green for the third category (fast investment-return strategy).

4. Discussion

4.1. Regional Variation in Phenotypic Traits of P. densata

During plant evolution, environmental filtering exerts a significant influence on the combination of plant traits. Through continuous adaptation, trade-offs, and synergistic interactions, plants in different regions gradually develop optimal trait combinations that match their habitats [22,23]. Analysis of 11 leaf phenotypic traits of *P. densata* in southeastern Xizang revealed significant differences among counties (districts) for all traits except LL, with moderate levels of trait variation (CV: 2.27%–22.05%). This suggests that *P. densata* may exhibit complex environmental response patterns in the diverse habitats of southeastern Xizang, promoting the formation of distinct leaf trait combinations among populations in different regions.

The results indicate pronounced regional differentiation in leaf phenotypic traits of *P. densata* in southeastern Xizang, with distinct trade-offs observed among counties (districts). *P. densata* in Gongbujiangda County (GB) exhibited prominent values in leaf size- and biomass-related traits such as LD, LA, LV, and LFW, while its leaf tissue density (LTD) was significantly lower than that in Bayi District (BY). Larger leaves facilitate the absorption of diffuse radiation from the environment and exhibit superior transpiration efficiency, thereby enhancing material exchange and transport capacity, which helps plants maintain productivity under low-light conditions [24,25].

Lower LTD facilitates light transmission within leaves and CO_2 diffusion [26]. Compared to other regions, *P. densata* in Gongbujiangda County (GB) may develop larger, looser leaves to enhance photosynthetic capacity and biomass accumulation potential. Among physiology-related phenotypic traits, Bomi County exhibited significantly higher SLA and LWC than other regions. High SLA enables larger LA with relatively fewer leaves

for resource allocation. As water serves as the matrix for cellular physiological activities, elevated LWC ensures leaf physiological activity and photosynthetic capacity [27,28]. SLA and LWC are often correlated with environmental water factors [29], which may reflect that *P. densata* in Bomi County (BM) grows in a relatively humid habitat, although this requires further investigation. Lang County(LX), Bayi District(BY), and Milin City(ML) generally exhibited intermediate or transitional characteristics, indicating the continuous variation in phenotypic traits of *P. densata* across southeastern Xizang.

Plant responses to diverse environmental factors generate trait variation and synergistic interactions. Quantifying the degree of variation among traits is the first step in understanding how plants adapt to their environment [30,31]. Among the 11 phenotypic traits measured for *P. densata*, moderate variation was observed. Across the five regions, SPAD exhibited the highest coefficient of variation in all regions except Bomi County. SPAD shows significant plasticity in response to environmental changes, with variation occurring frequently across regions, elevations, and forest types [32,33]. This indicates high environmental sensitivity in *P. densata*'s SPAD, which adjusts in response to environmental shifts. LWC exhibited lower variability across regions and was the most stable trait, suggesting that maintaining leaf water balance is a common characteristic of *P. densata* in southeastern Xizang.

4.2. Correlations Among Leaf Phenotypic Traits of P. densata in Southeastern Xizang

Pearson correlation analysis of *P. densata* leaf phenotypic traits revealed widespread correlations among traits. Traits controlling leaf size (LL, LD, LA, LV) showed highly significant positive correlations with traits controlling leaf mass (LFW, LDW), while exhibiting negative correlations with LTD. This indicates that as *P. densata* leaves increase in size and mass, their density decreases—a synergistic pattern widely observed across the plant kingdom [34–36]. SLA and LTD serve as key indicators of plant drought tolerance. Plants with low SLA and high LTD typically possess thicker or denser cell walls, enhancing their resistance to physical damage caused by leaf dehydration during drought [36,37]. Analysis revealed a significant negative correlation between SLA and LTD in *P. densata* from southeastern Xizang. As a strongly heliophilous species, *P. densata* enhances drought tolerance by reducing investment in leaf structural traits while increasing investment in defensive traits, reflecting a trade-off in its leaf phenotypic characteristics. SPAD showed a significant positive correlation with LWC and a highly significant positive correlation with SLA, indicating that leaf photosynthetic capacity is closely linked to water status [38]. Adequate leaf water content facilitates chlorophyll synthesis and photosynthetic activity. SLA reflects a plant's ability to capture or intercept light per unit dry leaf weight [39]. The positive correlation between SPAD and SLA may indicate higher chlorophyll density in thin leaves (high SLA), compensating for reduced photosynthetic capacity due to structural weakness. Conversely, lower SLA suggests plants allocate more resources to non-photosynthetic systems [40], reducing investment in photosynthetic traits.

4.3. Environmental Adaptation Strategies of P. densata in Southeastern Xizang

Under the combined influence of external environmental factors and internal genetic factors, plants develop diverse combinations of traits, reflecting their distinct adaptation strategies [34]. The leaf economic spectrum is a one-dimensional, continuous trait combination continuum that reflects plants' tendencies in environmental adaptation strategies. At one end lies the rapid investment–return strategy, characterized by a larger specific leaf area (SLA), higher photosynthetic and respiratory rates, and shorter leaf lifespan. In suitable habitats, leaves grow rapidly, and plants tend to accumulate substantial biomass in a short time with minimal resource investment. The opposite end represents a slow

investment–return strategy, characterized by increased stress-related investments under environmental stress, with slow growth and gradual accumulation of biomass over extended periods [41–43].

Principal component analysis revealed an association between the variation patterns of leaf phenotypic traits and the environmental adaptation strategies of *P. densata* in southeastern Xizang. PC1 explained 56.69% of the total variance, serving as the core axis driving trait differentiation. Loading analysis indicated that PC1 was highly positively correlated with LV, LA, LDW, LT, and LW, but negatively correlated with SLA and leaf tissue density (LTD), suggesting that the positive direction of PC1 corresponds to the "slow investment–return" strategy of the leaf economics spectrum, while the negative direction corresponds to the "fast investment–return" strategy. Figure 4 shows that *P. densata* in GB adopts the "slow investment–return" strategy, constructing larger leaves over a longer period to enhance stress resistance and ensure efficiency in material synthesis and accumulation [44]. In contrast, *P. densata* in BY and BM follows the "fast investment–return" strategy, where a higher SLA indicates greater photosynthetic area per unit dry weight invested. Combined with a high leaf greenness index, this confers advantages in leaf growth and photosynthesis [45]. In ML, *P. densata* exhibits a moderately slow investment strategy, characterized by low SLA without the development of large leaves; in LX, it clusters near the origin of PC1, reflecting a more balanced strategy. These findings suggest that the populations in ML and LX may adopt a transitional strategy. The clustering results supported the classification of environmental adaptation strategies of *P. densata* based on the leaf economic spectrum.

4.4. Limitations and Future Perspectives

This study analyzed regional differences in the phenotypic traits of *P. densata* but lacks an in-depth explanation of the relationships between these traits and environmental factors. Furthermore, while SPAD was used as an indicator of leaf greenness, it does not fully capture actual chlorophyll content or photosynthetic efficiency. Future research will integrate plot-level environmental factors (e.g., temperature, precipitation, soil conditions) along with direct physiological measurements, such as gas exchange parameters (e.g., photosynthetic rate, stomatal conductance), to quantitatively assess their effects on leaf trait variation and elucidate the adaptive mechanisms of *P. densata* in response to heterogeneous habitats in southeastern Xizang. Such studies will provide a more comprehensive understanding of *P. densata*'s ecological strategies and its potential responses to climate change.

5. Conclusions

This study compared and analyzed 11 leaf phenotypic traits of *P. densata* in southeastern Xizang, yielding the following key conclusions:

Significant differences were detected among regions for all leaf traits except leaf length (LL), with moderate levels of variation (CV: 2.27%–22.05%). SPAD exhibited the highest environmental sensitivity, showing the largest coefficient of variation, while LWC was the most stable trait across regions.

Clear synergistic and trade-off relationships exist among traits: traits controlling leaf size and weight showed highly significant positive correlations with each other and both exhibited negative correlations with LTD; SLA showed a significant negative correlation with LTD and a significant positive correlation with SPAD.

Principal component analysis revealed that the phenotypic traits of *P. densata* across five counties (districts) in southeastern Xizang conform to the leaf economic spectrum, reflecting distinct environmental adaptation strategies: Gongbujiangda County (GB) adopts a slow investment–return strategy, characterized by larger and structurally less dense leaves;

Bayi District (BY) and Bomi County (BM) exhibit a fast investment–return strategy, with higher SLA and SPAD values. Milin City (ML) is positioned near the origin of the leaf economic spectrum, adopting a moderately slow strategy with low SLA and no significant expansion in leaf size. Lang County (LX) is also located near the origin, displaying a relatively balanced combination of traits, representing a transitional strategy along the leaf economic spectrum. The clustering analysis further classified P. densata into three groups, consistent with the PCA results.

In summary, *P. densata* forms diverse resource trade-offs and adaptation strategies through varying degrees of variation and combination of foliar phenotypic traits, reflecting its adaptation to the complex alpine environment of southeastern Xizang.

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