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GEOMETRIC MORPHOLOGIC VARIATION OF *DALBERGIA HUPEANA* HANCE LEAVES AND ITS RESPONSE TO DIFFERENT SPATIAL STRUCTURES

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Abstract

This study was envisaged to reveal the variations in leaf shape of *Dalbergia hupeana* and its adaptation to the forest competition. Four different pure Masson pine sample plots were set up, and the spatial structure of each plot was calculated; the leaves of *D. hupeana* from different positions were collected, and the outline reconstruction of leaves was performed using the Fourier/wavelet method. The results indicated that *D. hupeana* leaves in different plots showed wide variation. The leaf area, length, width, perimeter, roundness, circularity, form factor, and rectangularity exhibited significant differences among the plots. Discriminant analysis showed that both the Wavelet and Fourier analyses could effectively separate different plots with good accuracy. The forest matrix crowding index, diameter correlation index, DBH dominance, and Hegyi index were the key spatial indices that affected the leaf morphological variation. The study preliminarily investigated the effects of tree competition on functional traits of leaves, which can provide valuable information for forest management.

Introduction

Functional traits are described as an integration of the ecological and evolutionary history of a species, and can potentially be used to predict its response and influence on the ecosystem functioning (Chaturvedi *et al.* 2011). The study of interspecific variation in plant functional traits can provide insights into the fundamental patterns and trade-offs in the plant form and function, and the ecological and evolutionary importance (Furey and Tilman 2023). The coexistence of plants can be explained by seed traits and dispersal abilities (Tilman 1994, Sullivan *et al.* 2018), light capture and competition between the plants can be reflected in height, along with the leaf physiology and morphology (Westoby 1998, Reich 2014). The morphological, physiological and climatic traits of leaves can interact with the environment, directly or indirectly influencing the plant adaptation. Among them, phenotypic plasticity is an important response of organisms to changes in the external environment, and plants adjust their leaf phenotypes in response to new environmental conditions (Rutherford *et al.* 2017). It has been demonstrated that in addition to the genetic factors, changes in the environmental conditions significantly affect the leaf morphology (Heredia *et al.* 2009; Picotte *et al.* 2009). Geometric morphometrics utilizes the relative positions of morphological points, boundary curves and surfaces rather than linear, areal or volumetric variables (Lawing and Polly 2009). Geometric morphometrics provide a more comprehensive quantification of the biomorphology than other methods, and widely used in ecological and evolutionary studies (Martínez-Abadías *et al.* 2012, Heteren and Germonpré 2023, Escobar-Suárez *et al.* 2023).

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The spatial structure of a forest stand, *i.e.*, the spatial distribution of trees and their attributes in a forest stand, is the theoretical basis and prerequisite for sustainable forest management and development (Hui *et al.* 2016). A series of spatial indicator parameters can quantify many important forest distribution patterns, such as the size differentiation and spatial segregation of trees and canopy density (Kang 2011). Spatial structure not only determines the ecological function of a stand, but also reflects the potential of a stand to compete among the spatial ecological niches (Yang *et al.* 2024). The competition between trees is a widespread phenomenon in forest ecosystems that influences the plant growth, morphology and survival, as well as an important driver of the direction of plant community evolution (Liu *et al*. 2020). Masson pine (*Pinus massoniana* Lamb.) is a major coniferous tree species and widely distributed in the subtropical forests of South China (Quan and Ding 2017). However, some of these Masson pine forest stands exhibit a homogeneous stand structure due to insufficient management measures, and the study area has undergone a long period of stand restructuring, such as replanting broadleaf species and adjusting the distribution of trees (Su *et al.* 2023). The genus *Dalbergia* belongs to the family Fabaceae and contains over 250 species, which are distributed in the pantropical regions of Asia, Africa, and America (Klitgaard and Lavin 2005). *Dalbergia hupeana* Hance is known as premium rosewood because of its decorative qualities and excellent wood quality (Bhagwat *et al.* 2015), and is artificially planted in pure forests as a valuable tree species. In this study, the morphological changes of *Dalbergia hupeana* leaves in response to spatial structure in pure Masson pine forest was investigated and examined the mechanisms of leaf morphology evolution on a small scale.

Materials and Methods

The study was conducted at the Hunan Cili Forest Ecosystem State Research Station located in Cili, Hunan Province, China. Four pure Masson pine sample plots (20 m ×50 m) were selected (M0-M3). The soil of the forest was mainly yellow-red and yellow, and belonged to the sub-tropical southeast monsoon humid climate zone. Terrestrial laser scanning radar (SLAM100, Feima Robotics, China) was employed to acquire the spatial data of the forest. Lida360 software (V6.0) was used to process the point cloud data (Fig. 1A), the point cloud pre-processing included: de-noising, Octree algorithm (Octree) thinning, ground point classification, improved progressive TIN densification (IPTD), ground point filtering, and normalization. The relative position, diameter at breast height (DBH) and other parameters of each tree were recorded-after processing.

Nine *Dalbergia hupeana* plants were selected from each sample plot, the leaf samples were collected from top and bottom of the tree's canopy, and a total of 312 leaves were collected. All sampled leaves were scanned (HP scanner, resolution 600 dpi). Image binarization analysis was carried out to obtain the contour information of the leaf (Fig. 1B), the shape R package was used for outline reconstruction based on Fourier/wavelet method, and then two data sets were obtained for the comparative analysis. Six morphological indices, including the roundness, circularity, rectangularity, elipticity, aspect ratio and form-factor was calculated (Table 1).

Preliminary analyses were initially carried out by comparing the morphological characteristics of leaves collected from 4 plots. They were analyzed using a univariate analysis of variance (ANOVA) test. A multiple comparison analysis (Tukey HSD) was used to assess the differences in the coefficients between samples. In addition, the reconstructed outline of leaf samples based on wavelet and Fourier method for different sample plots were plotted to analyze the leaf shape variation caused by multiple factors. The Fisher Linear Discriminant Model was used to evaluate the classification effect of leaf shape from 4 plots.

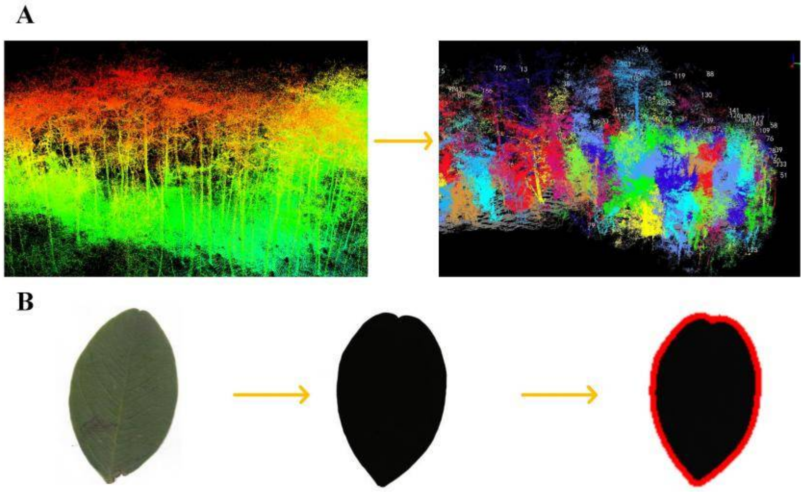

Fig. 1. Schematic representation of the extraction of spatial parameters (A) and contour outlines (B).

Table 1. Leaf morphological indices employed in the study.

Morphological index	Formula
Roundness	$4A/(\pi LL^2)$
Circularity	P/A^2
Rectangularity	$A/(LL*LW)$
Elipticity	$(LL-LW)/(LL+LW)$
Aspect ratio	LL/LW
Form-factor	$4\pi AP^2$

A: Leaf area, LL: Leaf length (mm), P: Leaf perimeter (mm), and LW: Leaf width (mm).

Nine spatial indicators were selected to quantify the spatial structure, including the Alemdag's tree competition index (Alemdag 1978), Clark-Evans index of neighborhood pattern (Clark and Evans 1954), Forest matrix crowding index (Seydack *et al*. 2011), Diameter correlation index (Davis and Pommerening 2008), DBH differentiation index (Pommerening 2002), DBH dominance index (Aguirre *et al.* 2003), Hegyi index (Hegyi 1974), Lorimer's Competition Zone Radius (Lorimer 1983), and Martin and Ek index (Martin and Ek 1984). In order to explore the relationship between the geometric morphologic matrix and spatial index, multiple regression tree (MRT) was used. The recursive partition method was used to measure the inter- and intra-group differences, the spatial index was used as the node of classification, and cross validation method was used to control the results. Mantel analysis was employed to detect the relationship between the geometric morphologic matrix and spatial indicator matrix.

Results and Discussion

The spatial index shows that P1, P4 and P5 index indicated stronger competition in M2 and M3, while P5 and P6 indicated that the M0 had higher average neighbour size. P8 indicated all the plots exhibited a clustered distribution. The P9 index indicated that M1 and M2 exhibited a bigger radius of the competitive zone (Table 2).

Table 2. Results of 9 spatial indexes of each sample plot.

Sample plot	P1	P2	P3	P4	P5	P6	P7	P8	P9
M0	36.96	1.16	0.49	3.70	10.06	0.44	1.90	0.48	5.43
M1	32.51	1.24	0.49	3.11	6.56	0.37	1.50	0.40	8.74
M2	40.73	1.13	0.50	3.53	8.34	0.37	1.58	0.36	8.70
M3	42.71	1.18	0.51	3.86	8.31	0.38	1.44	0.56	5.51

P1: Forest matrix crowding index, P2: Diameter correlation index, P3: DBH dominance, P4: Hegyi index, P5: Martin and Ek index, P6: DBH differentiation, P7: Alemdag's tree competition index, P8: Clark-Evans index of neighbourhood pattern, and P9: Lorimer's competition zone radius. M0-M3 represents four pure Masson pine sample plots.

Table 3. Leaf morphological indices of different leaf samples using ANOVA tests.

Morphological indices	Parameters	Sum of squares	Mean of square	*P*
Leaf area	Position	53	52.96	0.0604
	Sample plot	744	247.97	4.98E-10*
	Position×Sample plot	141	47.04	0.0252*
Leaf length	Position	0.28	0.2795	0.1998
	Sample plot	6.43	2.1441	8.08E-08*
	Position×Sample plot	1.74	0.5784	0.0178*
Leaf width	Position	4.74	4.736	0.0113*
	Sample plot	19.84	6.614	8.94E-06*
	Position×Sample plot	5.75	1.916	0.0502
Leaf perimeter	Position	18.6	18.59	0.0188*
	Sample plot	147.1	49.03	5.69E-09*
	Position×Sample plot	29.6	9.88	0.0324*
Roundness	Position	31717	31717	0.1995
	Sample plot	825789	275263	9.15E-09*
	Position×Sample plot	171927	57309	0.0314*
Circularity	Position	0.00194	0.001943	0.01701*
	Sample plot	0.01551	0.00517	2.62E-09*
	Position×Sample plot	0.00425	0.001418	0.00621*
Rectangularity	Position	0.00099	0.000991	0.189
	Sample plot	0.03378	0.011259	1.14E-11*
	Position×Sample plot	0.00133	0.000445	0.508
Elipticity	Position	0.0055	0.005497	0.136
	Sample plot	0.0076	0.002531	0.381
	Position×Sample plot	0.0098	0.003262	0.267
Aspectratio	Position	0.0074	0.007415	0.147
	Sample plot	0.0116	0.003863	0.349
	Position×Sample plot	0.0136	0.004539	0.276
Formfactor	Position	0.0062	0.006155	0.06594
	Sample plot	0.0246	0.008183	0.00401*
	Position×Sample plot	0.0068	0.002253	0.29295

* Indicates significant differences at the level of $p = 0.05$.

It was observed that the leaf area, length, width, perimeter, roundness, circularity, form factor and rectangularity exhibited significant differences among the 4 plots (Table 3). Leaf width, leaf perimeter and circularity of leaves showed significant differences among different positions (up and down). The results indicated a morphological differentiation among the different spatial structures and positions.

The boxplot of leaf morphological indices between the different plots and the multiple comparative analyses is shown in Fig. 2. The leaf area, length, and roundness of the M0 plot was significantly lower than those of the other plots. The leaf width and perimeter of M0 plot was significantly lower than those of M1 and M3. The circularity of M0 was significantly higher than that of the other plots. The rectangularity of M3 was significantly higher than that of other plots.

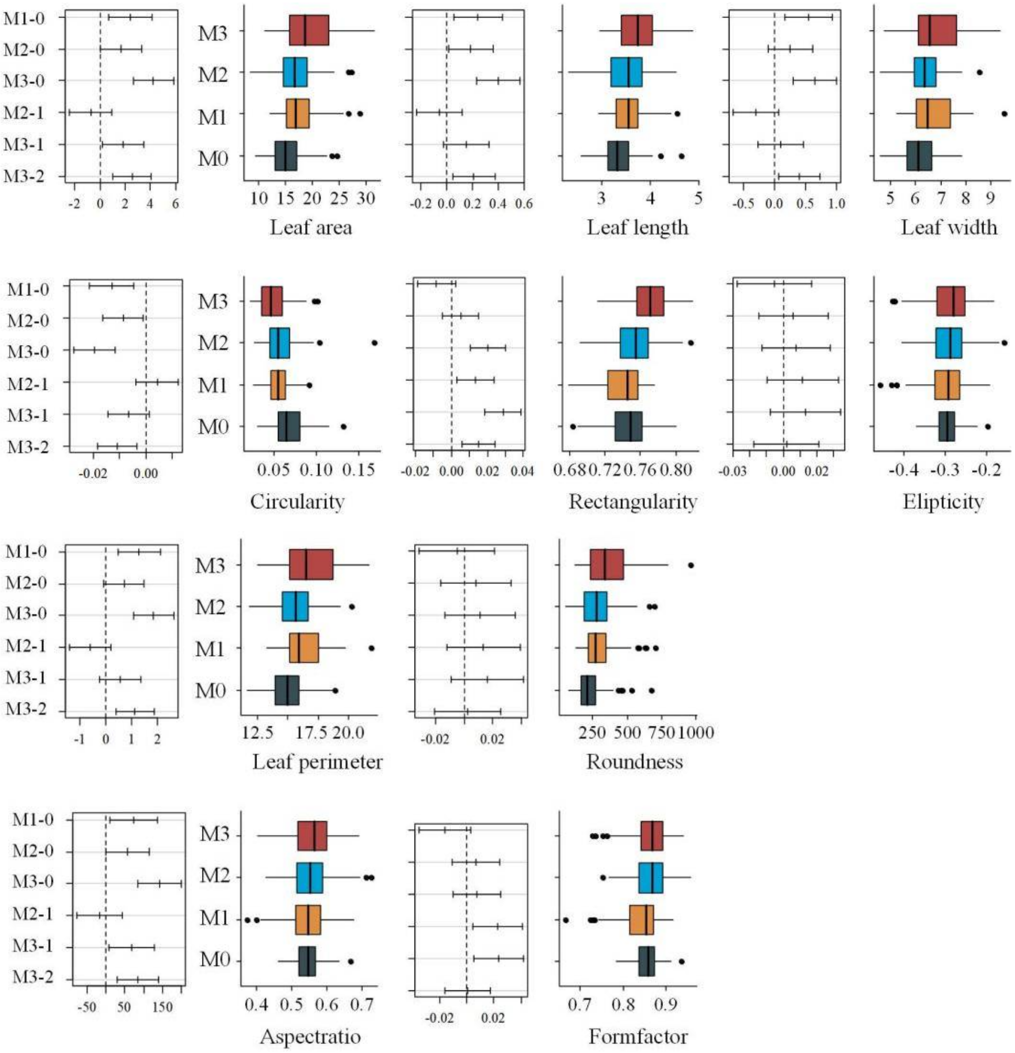

Fig. 2. Boxplot (right) and multiple comparison analysis (left) of 10 morphological indices. Tukey HSD analysis was performed at 95% family-wise confidence level.

To determine appropriate grouping, the Fisher linear discriminant model analysis was performed (Table 4). In the discriminant analysis based on Wavelet and Fourier analysis, LD1 and LD2 accounted for the largest proportion of variance. Among the four linear discriminant axis, the samples were best divided when LD1 and LD2 were used (Fig. 3A, C). Wavlet and Fourier analysis presented delineated plots, but overlaps were seen in the plots (Fig.3B,D).

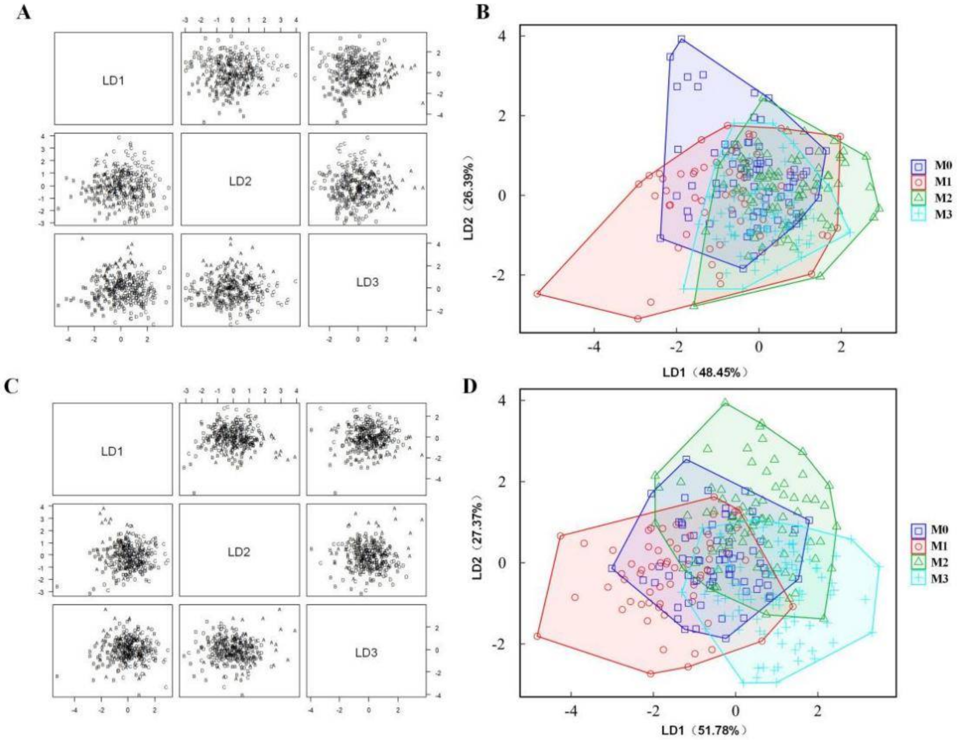

Fig. 3. Discriminant scatter plot of the Wavelet (A&B) and Fourier (C&D) coefficients for 4 sample plot using Fisher Linear Discriminant Model.

Discriminant analysis showed that the Wavelet analysis could effectively separate the different plots with a good accuracy (70.09%) than Fourier analysis (51.13%)(Table 4). In particular, the Wavelet analysis yielded the highest discrimination rate of M0 (72.22%), M1 (71.88%), M2 (68.60%) and M3 (68.54%). The discrimination rate obtained by the Fourier method was 45.83 (M0), 39.0 (M1), 55.8 (M2) and 59.55% (M1).The discriminant model employed in this study showed a good discriminant effect.

The reconstructed average leaf shapes based on the Fourier analysis are shown in Fig. 4. The reconstructed average leaf shapes were used to compare with each other. From the average leaf shapes between different plots, differences were mainly observed at the leaf width (Fig. 4A), the leaves in M0 were relatively wider, followed by M1, and the leaves in M2 exhibited a narrower shape. The differences between different positions were mainly at 180º190° and 180°-270° (Fig. 4B). The results were further confirmed by examining the variability of the mean wavelet coefficients and the proportion of variation between the two groups, summarized by the ICC (Fig.4C).

Table 4. Discriminant analysis and accuracy measures of different reconstruction methods.

Reconstruction method		M0	M1	M2	M3	Accuracy (%)
Wavelet (70.09%)	M0	52	8	5	7	72.22%
	M1	6	46	9	3	71.88%
	M2	5	8	59	14	68.60%
	M3	13	2	13	61	68.54%
Fourier (51.13%)	M0	33	7	14	18	45.83%
	M1	11	25	12	16	39.06%
	M2	13	6	48	19	55.81%
	M3	11	7	18	53	59.55%

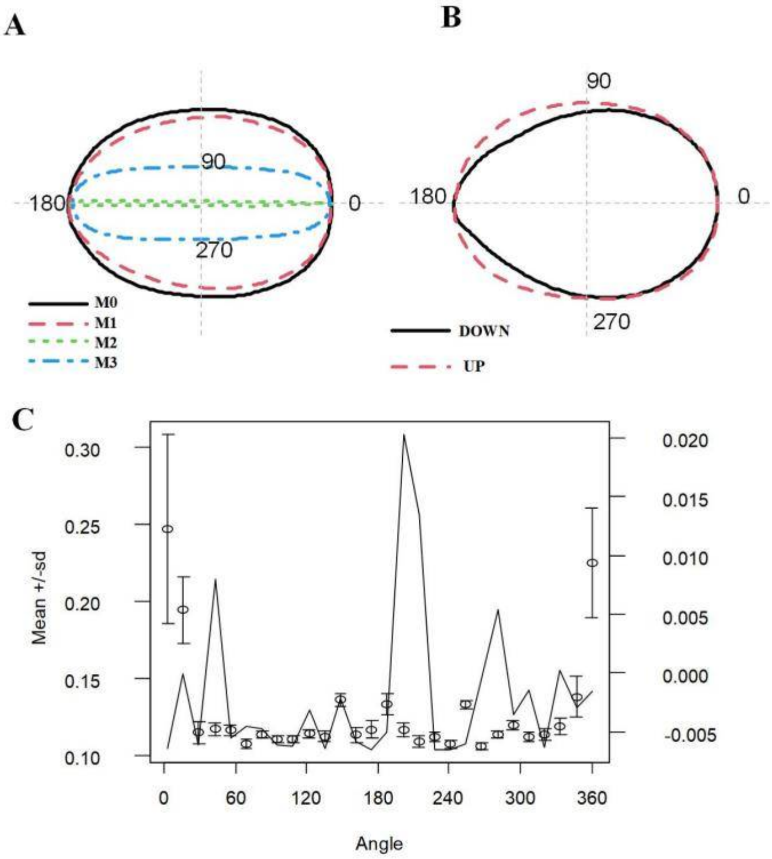

Fig. 4. Mean leaf shape based on Fourier reconstruction. A: Mean leaf shape between different sample plots, B: Mean leaf shape between different positions and C: Mean and standard deviation (dots and whiskers) of the Fourier coefficients for all combined leaf and the proportion of variance within groups for the intra-class correlation (ICC, black solid line).

From the results of MRT, all the samples were divided into 4 subgroups using three spatial indexes (Fig. 5A). The error, cross validation error and standard error of the model was found to be 0.979, 1.38, and 0.0237, respectively, and the samples were divided by P1 (matrix crowding index, 38.85), P5 (Martin and Ek index, 8.31) and P9 (Lorimer’s Competition Zone Radius, 7.109). The results indicated that the Matrix crowding index, Martin and Ek index and Lorimer’s Competition Zone Radius were the key spatial indices that characterized the leaf morphological variation. From the results of the Mantel test, the leaf morphological variation (Fourier coefficients) was significantly correlated with P1-P4 (Forest matrix crowding index, Diameter correlation index, DBH dominance and Hegyi index) (Fig. 5B). Additionally, P1 exhibited a significant positive correlation with P3 and P4, and a significant negative correlation with P2, while P3 was significantly positively correlated with P4. The divergence was further evident along both leaf sides of the generated leaf outlines, as shown in Fig. 4. These results were further supported by the proportion of variance within groups for the intra-class correlation.

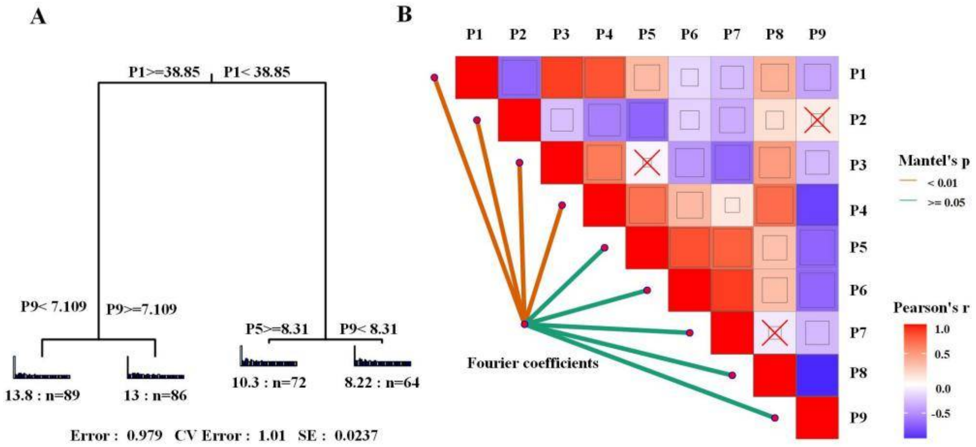

Fig. 5. Result of MRT and Mantel test. A: Bar represents the frequencies of sample distribution in each subgroup, B: Pairwise comparisons of spatial index, and ‘x’ indicates no significant correlation.

Leaf morphology is the result of a combination of genetic and environmental factors, and varies between and within species, reflecting plant survival strategies (Gong *et al.* 2020). At the interspecific level, leaf morphology varies among the species under similar environmental conditions in response to temperature, light, and other environmental conditions (Nicotra *et al.* 2008, Mocko *et al.* 2018). At the intraspecific level, different individuals of the same species show different leaf morphology in different environments, which is an adaptation to heterogeneous environments. Thus, intraspecific variation in leaf morphology contributes to the maintenance and renewal of populations (Jung *et al.* 2010). Statistical differences in the leaf shape analysis between four plots provided a clear indication of the differentiation in response to tree competition. The most significant variation was observed in the shape-related morphometric indices, such as leaf area, circularity, roundness, and rectangularity, which effectively differentiated the samples from different plots (Table 3, Fig. 2).

Analyzing a single spatial structural parameter of a forest stand in isolation can result in a one-sided conclusion (Zhu *et al.* 2016). Therefore, it is crucial to analyze the specific structural parameters, while concurrently considering other relevant structural attributes. In this research, multiple spatial parameters were employed to fully assess the degree of tree competition. There is a close and intricate relationship between the forest spatial structure and tree growth. Trees in the forest rely on resources such as light, water, nutrients, and space, and the spatial structure directly influences the distribution and availability of these resources. In densely packed forest stands, tree competition for limited resources gets intensified, restricting the growth of individual trees. Conversely, in more open forest stands, resources are more abundant, and the competition among trees is reduced, thereby promoting their growth (Kobe 2006). In hot and humid environments, a near-circular leaf shape promotes the water and air exchange with the outside environment (Hirokazu 2005). The leaves in M0 and M1 were observed to be more rounded than the others, which indicated a more humid and hotter environment. The spatial index-matrix crowding index of M0 and M1 was significantly correlated with the leaf morphological variation and was much lower than that in other plots. This index describes the DBH values of all competitor trees; wherein higher values mean that the surrounding competing trees have a larger diameter at breast height creating more competitive pressure on the target trees. In this study, the plants in M2 and M3 exhibited narrow leaves, thereby exhibiting a high intensity competition. Plants in M3 presented the largest leaf area, which reflects the poor light conditions. The Hegyi index takes into account DBH and the distance of competitor trees. The Hegyi index of M3 was highest, which indicated a closer distance to competitors, and a bigger leaf indicated the presence of limited light.

In the present study, the spatial structure of pure *P. massoniana* forest and assessed the response of leaf morphology to tree competition were studied. There were differences in the spatial structure between the different plots. The *D. hupeana* leaves in different plots showed a wide variation. The leaf area, length, width, perimeter, roundness, circularity, form factor, and rectangularity of *D. hupeana* leaves exhibited significant differences among the 4 plots. Discriminant analysis showed that both Wavelet and Fourier analysis could effectively separate the 4 plots with good accuracy. Forest matrix crowding index, Diameter correlation index, DBH dominance and Hegyi index were the key spatial indices that affected the leaf morphological variation. This study explored the morphological changes of *D. hupeana* leaves in response to different spatial structures in pure Masson pine forest and provides a theoretical basis for future management of pure forests.

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