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Postprint: Relationship between Leaf Anatomical Structure and Drought Resistance of Oil Tea (*Camellia oleifera*) in High-Altitude Regions

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Abstract

To investigate the anatomical structural characteristics of oil tea (*Camellia oleifera*) leaves in high-altitude regions and their relationship with drought resistance, this study utilized 35 superior oil tea plants with excellent fruiting traits previously screened in the eastern high-altitude region of Guizhou Province as experimental materials. Paraffin sectioning was employed to observe leaf anatomical structures. Descriptive statistics and variance analysis, correlation analysis, and cluster analysis were conducted to screen typical leaf structural indicators reflecting plant drought resistance, and membership function was applied to comprehensively evaluate drought resistance and identify superior plants with stronger drought resistance. The results showed: (1) The number of palisade tissue cell layers in oil tea varied, with most consisting of 2 layers of neatly arranged and dense columnar cells, while very few exhibited 3 layers. The coefficient of variation for morphological indicators ranged from 11.15% to 26.73%, and among the 14 indicators, the palisade-spongy ratio showed the largest coefficient of variation. (2) Through cluster analysis and comprehensive ranking of correlation indices, the main indicators affecting oil tea drought resistance were identified as palisade-spongy ratio, leaf area, vein thickness, and palisade tissue thickness. TY05 exhibited the maximum vein thickness of 599.32 m, whereas TY16 showed the minimum vein thickness of 347.53 m. TY33 possessed the largest leaf area of 1,766.00 mm² with 2 layers of palisade tissue cells. TY08 demonstrated the maximum leaf thickness, palisade tissue thickness, and palisade-spongy ratio, being 673.33 m, 340.26 m, and 1.13, respectively. (3) Based on comprehensive membership function values, the superior oil tea plants with stronger drought resistance were TY26, TY08, TY03, TY27, and TY33, which can provide a material foundation for subsequent breeding of drought-resistant oil tea varieties. The findings of this study provide scientific basis

and theoretical reference for drought-resistant oil tea varieties in high-altitude regions.

Full Text

The Relationship Between Leaf Anatomical Structure and Drought Resistance in High-Altitude *Camellia oleifera*

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Abstract

To investigate the anatomical characteristics of *Camellia oleifera* leaves in high-altitude regions and their relationship with drought resistance, this study examined 35 superior *C. oleifera* individuals previously selected for excellent fruiting traits in the high-altitude area of eastern Guizhou Province. Leaf anatomical structures were observed using paraffin sectioning. Typical indicators reflecting plant drought resistance were identified through descriptive statistics, variance analysis, correlation analysis, and cluster analysis. Drought resistance was then comprehensively evaluated using membership functions to select superior drought-resistant individuals. The results showed: (1) The number of palisade tissue cell layers in *C. oleifera* varied, with most leaves composed of two neatly arranged, dense layers of long columnar cells and 极少数 exhibiting three layers. The coefficient of variation for morphological indicators ranged from 11.15% to 26.73%, with the palisade-to-spongy tissue ratio showing the highest variation among the 14 measured indicators. (2) Cluster analysis and comprehensive ranking of correlation indices identified the palisade-to-spongy tissue ratio, leaf area, vein thickness, and palisade tissue thickness as the primary indicators affecting drought resistance in *C. oleifera*. TY05 exhibited the maximum vein thickness of 599.32 m, while TY16 had the minimum at 347.53 m. TY33 showed the largest leaf area (1,766.00 mm²) and possessed two layers of palisade tissue cells. TY08 demonstrated maximum values for leaf thickness (673.33 m), palisade tissue thickness (340.26 m), and palisade-to-spongy tissue ratio (1.13). (3) Based on membership function values, the superior individuals with strong drought resistance were TY26, TY08, TY03, TY27, and TY33, providing a material foundation for future drought-resistant variety breeding. These findings offer scientific evidence and theoretical reference for selecting drought-resistant *C. oleifera* varieties in high-altitude regions.

Keywords: high altitude, *Camellia oleifera*, leaf, anatomical structure, drought resistance

Introduction

Camellia oleifera, belonging to the family Theaceae and genus *Camellia*, is an important woody oil crop widely distributed across 18 provinces in China. It thrives in regions with annual average temperatures of 14–22°C. *Camellia* oil contains various beneficial nutrients, including abundant unsaturated fatty acids, vitamins, and squalene, offering health benefits such as enhanced immunity, tumor suppression, and cholesterol reduction, earning it the reputation of “oriental olive oil”. The *C. oleifera* industry helps reduce China’s long-term dependence on imported edible oil, garnering national attention and public support. However, global climate change increasingly exposes plants to drought stress during growth and development. *C. oleifera* requires substantial water during its growth cycle, and drought during fruit expansion and oil conversion periods hinders nutrient accumulation, causing leaf yellowing and fruit drop, ultimately reducing yield and quality. Therefore, investigating drought resistance is essential for improving *C. oleifera* production.

Water is fundamental to plant growth and plays a decisive role in survival and reproduction. In arid or water-limited environments, plants must develop various adaptive mechanisms to cope with water deficit. Drought represents a common environmental stress factor that severely affects plant growth, development, and productivity. In high-altitude regions, thin atmospheric layers and intense solar radiation drive strong water evaporation. Combined with low temperatures, these conditions maintain low soil moisture, creating frequent drought conditions. Consequently, studying drought resistance and breeding drought-resistant varieties is particularly urgent for *C. oleifera* cultivation in the high-altitude regions of eastern Guizhou.

As a vital organ for metabolic activities, leaves are most sensitive to environmental changes, adjusting their anatomical structure to ensure normal physiological function. Plants growing in drought environments develop unique drought-resistant structural characteristics through long-term environmental sensing and morphological-anatomical adjustments. These features reflect adaptive capacity and remain stable despite transient environmental fluctuations, making leaf anatomical characteristics valuable indicators for drought resistance research. Numerous studies have demonstrated close relationships between plant drought resistance and leaf morphological-anatomical indices in species including *C. oleifera*, poplar, and others. Leaves exhibit strong plasticity, with long-term stress inducing changes in key indicators to mitigate damage.

Evaluating drought resistance through leaf anatomical structure is a classic method reported across many fields. Our research group previously applied this approach to study the relationship between anatomical structure and

drought/cold resistance in *C. oleifera* and tea plants. This study examined leaves from pre-selected superior *C. oleifera* individuals, measured anatomical parameters, and used descriptive statistics, variance analysis, correlation analysis, and cluster analysis to determine relationships between leaf anatomy and drought resistance. Typical indicators were identified from anatomical structures, and membership functions were employed to comprehensively evaluate drought resistance across 35 superior individuals, enabling selection of drought-resistant varieties and providing theoretical foundations for breeding.

Guizhou Province represents a major *C. oleifera* production area in China, with a planted area of 2,458.9 km². Common *C. oleifera* primarily occurs in low hilly regions below 800 m elevation, with limited natural distribution above 1,000 m. High-altitude *C. oleifera* may possess greater genetic diversity, facilitating adaptation to environmental stresses. Recent climate change-induced temperature increases and altered precipitation patterns have intensified drought impacts on the *C. oleifera* industry, particularly in high-altitude regions where drought-induced mortality occurs. Systematic research on high-altitude *C. oleifera* resources is lacking, and no drought-resistant varieties have been developed, making it crucial to screen for drought-resistant germplasm. Drought resistance research enhances understanding of growth characteristics and adaptability under different environmental conditions. Our group previously collected superior resources above 1,000 m elevation. Given the current drought conditions in these regions, drought resistance research is significant for developing *C. oleifera* cultivation and selecting drought-resistant individuals above 1,000 m elevation. Screening drought-resistant individuals can improve planting success rates in high-altitude regions and support sustainable industry development.

1.1 Experimental Site

The experiment was conducted in the high-altitude region of eastern Guizhou Province (107°44'55"–108°33'47" E, 27°17'5"–27°42'50" N). The terrain slopes from northwest to southeast, characterized by a mid-subtropical monsoon humid climate with typical vertical climate patterns. The region experiences hot summers with abundant sunshine, a long frost-free period, an annual average temperature of 17.1°C, annual precipitation of 1,100–1,400 mm, and 1,250 hours of sunshine.

1.2 Experimental Materials

The study utilized common *C. oleifera* from 35 superior individuals previously selected. In October 2023, leaves were collected from each of the 35 individuals, designated as TY01 through TY35. Three mature, healthy leaves from the fifth to seventh nodes of the sun-exposed canopy were sampled per individual, with nine replicates total. Leaf samples were cut into 5 mm × 5 mm sections centered on the main vein, avoiding the vein for mesophyll tissue sections. Samples were

immediately fixed in Carnoy's solution (3:1 ethanol:acetic acid) for 12 hours, then transferred to 70% ethanol and stored at 4°C.

1.3 Experimental Methods

Leaf Area Measurement: Three representative leaves per sample were selected for area measurement. Leaves were pressed flat on graph paper (1 mm per grid), their outlines traced, and area calculated. The average of three measurements was recorded as leaf area, along with leaf length and width.

Leaf Anatomical Structure: Conventional paraffin sectioning was employed. Fixed materials underwent ethanol gradient dehydration, clearing, paraffin infiltration, and embedding. Sections were cut using a Leica RM2235 microtome (Japan), then mounted, dried, dewaxed, stained with hematoxylin, coverslipped, and dried. Observations were made under an Olympus BX53 (LED) microscope (Japan). Image J software was used to measure leaf thickness (LT), vein thickness, cuticle thickness, upper epidermis thickness, lower epidermis thickness, palisade tissue thickness (TP), and spongy tissue thickness (TS). Derived parameters included palisade-to-spongy tissue ratio (P/S), tissue structure tightness, tissue structure looseness, vein protuberant degree, and coefficient of variation. Ten sections per plant were observed, with three fields per section, yielding 30 fields for data averaging.

1.4 Data Processing

Image J software measured anatomical thicknesses. Excel 2019 performed statistical calculations. IBM SPSS Statistics 26 conducted one-way ANOVA, significance testing ($P < 0.05$), and linear correlation analysis. Duncan's test performed multiple comparisons and hierarchical clustering. Photoshop 2022 created figures. Individual plant values were averaged, with 14 indicators selected for cluster analysis: X1–X14 representing leaf length, leaf width, leaf area, leaf thickness, vein thickness, palisade tissue thickness, spongy tissue thickness, palisade-to-spongy ratio, tissue tightness, tissue looseness, vein protuberant degree, upper epidermis thickness, lower epidermis thickness, and cuticle thickness.

The correlation index for each category was calculated as:

$$R^2 = 1 - \frac{\sum(1 - r^2)}{n}$$

where R^2 is the correlation index, n is the number of indicators in each category, and r^2 is the correlation coefficient between indicators.

Drought resistance was comprehensively evaluated using membership functions:

$$f(x_i) = \frac{X_i - X_{i \min}}{X_{i \max} - X_{i \min}}$$

for indicators positively correlated with drought resistance, and

$$f(x_i) = 1 - \frac{X_i - X_{i \min}}{X_{i \max} - X_{i \min}}$$

for negatively correlated indicators, where $f(x_i)$ is the membership value, X_i is the measured value, and $X_{i \min}$ and $X_{i \max}$ are the minimum and maximum values for each indicator.

Average membership values were calculated to evaluate drought resistance, with higher values indicating stronger resistance.

2.1 Leaf Morphological Observation

C. oleifera leaves are leathery with obtuse apices, cuneate bases, long hairs on the lower midrib, coarse hairs on petioles, and finely serrated margins. Leaves possess a prominent midrib with inconspicuous lateral veins [Figure 1: see original paper]. Leaf length ranged from 47.00–77.00 mm, width from 22.00–35.67 mm. TY15 showed the smallest leaf area (652.67 mm^2), while TY33 exhibited the largest ($1,766.00 \text{ mm}^2$).

2.2 Leaf Anatomical Structure Observation

Anatomical observation revealed that *C. oleifera* leaves consist of cuticle, upper epidermis, lower epidermis, palisade tissue, spongy tissue, veins, and stomata [Figure 2: see original paper]. The epidermis comprises a single layer of tightly arranged cells divided into upper and lower surfaces, with a cuticle layer and stomata restricted to the lower epidermis. Palisade tissue consists of 2–3 layers of densely packed, irregular columnar cells, with most leaves showing two layers [FIGURE:2:A] and 极少数 showing three layers [FIGURE:2:C]. Spongy tissue comprises loosely arranged elliptical cells. Veins contain collenchyma, xylem, phloem, and parenchyma tissues [FIGURE:2:B], distributed primarily between palisade and spongy tissues with well-developed vascular systems. Anatomical structures of leaves and veins for all 35 individuals are shown in [Figure 3: see original paper] and [Figure 4: see original paper].

2.3 Comparative Analysis of Leaf Anatomical Structure

Leaf thickness ranged from 403.33–673.33 m, averaging 522.95 m. TY08 showed maximum leaf thickness (673.33 m), palisade tissue thickness (340.26 m), and palisade-to-spongy ratio (1.13), with a vein protuberant degree of 0.68. TY17 exhibited the thinnest leaves. The palisade-to-spongy ratio displayed the highest coefficient of variation (26.73%) among all 14 indicators. The thinnest upper and lower epidermis were observed in TY14 (17.88 m) and TY21 (14.96 m), respectively, while TY20 showed the thickest upper epidermis (25.08 m).

TY08 also possessed the thickest spongy tissue (549.32 m), highest tissue looseness (1.14), and lowest palisade-to-spongy ratio (0.39). TY30 exhibited the thickest lower epidermis (32.84 m). Generally, upper epidermis thickness slightly exceeded lower epidermis thickness. Vein thickness ranged from 347.53–597.44 m, averaging 472.48 m, with TY05 showing maximum thickness (599.32 m) and TY16 minimum thickness (347.53 m). Average spongy tissue thickness was 364.06 m. TY01 had the thinnest palisade (126.88 m) and spongy (210.85 m) tissues. Cuticle thickness varied from 11.91–24.05 m, averaging 21.73 m.

2.4.1 Cluster Analysis

Standardized data for 14 leaf traits were analyzed using hierarchical clustering with between-group linkage and squared Euclidean distance. The dendrogram [Figure 5: see original paper] revealed four categories at a squared Euclidean distance of 4. Category 1 included leaf length, leaf width, palisade-to-spongy ratio, tissue tightness, tissue looseness, vein protuberant degree, upper epidermis thickness, lower epidermis thickness, and cuticle thickness. Category 2 contained only leaf area. Category 3 comprised leaf thickness and vein thickness. Category 4 included palisade tissue thickness and spongy tissue thickness.

Cluster analysis of 35 leaf samples using the same method produced another dendrogram [Figure 6: see original paper], classifying samples into three groups at a squared Euclidean distance of 5. Group characteristics are summarized in . Group 1 featured short, narrow leaves. Group 2 showed significantly thicker veins than other groups. Group 3 contained only TY33, characterized by large leaf area, thick leaves, inconspicuous veins, high palisade-to-spongy ratio, tight tissue structure, and thicker lower than upper epidermis.

2.4.2 Correlation Analysis

Correlation analysis of 14 anatomical indicators across 35 individuals revealed significant relationships . Leaf length and width showed extremely significant positive correlations with leaf area. Leaf thickness correlated significantly positive with vein thickness but significantly negative with tissue tightness, and extremely significant negative with tissue looseness and vein protuberant degree. Spongy tissue thickness showed extremely significant correlations with palisade-to-spongy ratio and tissue looseness. The palisade-to-spongy ratio exhibited extremely significant relationships with tissue tightness and looseness.

2.5 Comprehensive Evaluation of Drought Resistance in Superior Individuals

Based on the four typical indicators identified, membership function analysis comprehensively evaluated drought resistance across 35 superior individuals . Higher average membership values indicated stronger drought resistance. The top five drought-resistant individuals were TY26, TY08, TY03, TY27, and TY33.

Discussion and Conclusion

Environmental stresses, particularly drought, can arrest plant development by limiting water availability, altering biomass allocation, restricting cell mitosis, reducing leaf area, and promoting thicker veins and developed palisade tissues. As the primary organ interfacing with the environment, leaf structure most directly reflects environmental adaptability. Leaf anatomical structure critically influences water use efficiency and transpiration rate, thereby affecting drought resistance capacity. Consequently, leaf anatomy serves as an important reference indicator for drought resistance research, as demonstrated in studies on kiwifruit, Chinese toon, carambola, and other species.

Plant drought resistance represents a comprehensive adaptation involving morphology, physiology, and endogenous hormone levels, necessitating multi-indicator evaluation. For instance, evaluating drought resistance in camphor trees requires leaf thickness, midrib vessel diameter, palisade thickness, and stomatal density. This study identified palisade-to-spongy ratio, leaf area, vein thickness, and palisade tissue thickness as key indicators for *C. oleifera* through cluster analysis and membership functions. The palisade-to-spongy ratio showed the highest coefficient of variation (26.73%). Although leaf thickness and vein thickness shared identical correlation indices (0.347), vein thickness exhibited greater variation (15.20% vs. 12.13%), making it the more effective indicator. Previous research identified vein thickness as valuable for evaluating drought resistance in tea plants and *C. oleifera* varieties. Palisade thickness served as an indicator for ancient tea trees, while palisade-to-spongy ratio was primary for evaluating 'Cenruan' series *C. oleifera*. However, differences exist among studies, possibly due to varietal differences and diverse environmental adaptation strategies. Spongy tissue thickness was identified as an indicator for fragrant *C. oleifera*, but in this study, palisade thickness was selected for high-altitude Guizhou *C. oleifera* due to its higher variation coefficient (24.05% vs. 20.45%), likely reflecting geographic, climatic, or varietal differences. Stomatal density, though recognized as valuable in other studies, was not examined here and warrants future attention.

Clustering results, membership function analysis, and comprehensive ranking mutually validated the findings. Group 1 generally showed poor average performance and low drought resistance, except for TY08, which exhibited maximum palisade-to-spongy ratio, leaf thickness, and palisade thickness, making it suitable for drought-resistant breeding despite moderate other indicators. Group 2 performed best in TY26, followed by TY27 and TY03, representing drought-resistant varieties. Group 3 contained only TY33 with superior phenotypic indicators and good overall performance, suitable for breeding varieties with excellent leaf traits. The selected superior individuals (TY26, TY08, TY03, TY27, TY33) provide reference materials for drought-resistant breeding and biological data for studying drought tolerance mechanisms. As plant drought

resistance results from multiple interactive factors, future evaluations should integrate physiological-biochemical indicators and explore molecular mechanisms through drought-resistant genes.

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