Postprint: Anatomical Study of Photosynthetic Characteristics in Variegated Magnolia

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Abstract

Using fully green leaves, variegated leaves, and fully yellow leaves of variegated Magnolia as experimental materials, this study investigated the relationship between anatomical structure and photosynthetic characteristics of the three leaf types through analyses of leaf photosynthetic pigment content, leaf anatomical structure, and light response curves, thereby revealing the anatomical basis for photosynthetic characteristics in variegated Magnolia. The results showed that: (1) The yellow leaf spots in variegated Magnolia were chlorophyll-deficient type leaf spots resulting from reduced chlorophyll content caused by abnormal chloroplast structure. (2) The thylakoid structure in the yellow regions of variegated Magnolia was abnormal, which blocked ATP synthesis and impeded normal photosynthetic processes. (3) Anatomical observations revealed that fully green leaves possessed well-developed palisade tissue, with higher chloroplast integrity and pigment content than variegated and fully yellow leaves, resulting in higher net photosynthetic rates. (4) Significant differences existed in maximum net photosynthetic rate and light saturation point between fully green leaves and variegated leaves, with fully green leaves exhibiting greater tolerance to a wider range of high light intensities than variegated leaves. This study further elucidated that chloroplast structure influences photosynthetic characteristics in variegated Magnolia, providing a reference for the breeding of superior germplasm in variegated Magnolia.

Full Text

Preamble

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Photosynthetic Characteristics of Yulania denudata with Variegated Leaves Based on Anatomical Structure

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Abstract

This study investigated the relationship between leaf anatomical structure and photosynthetic characteristics in Yulania denudata with variegated leaves, using green leaves, variegated leaves, and yellow leaves as experimental materials. The research examined photosynthetic pigment content, leaf anatomical structure, and light response curves to elucidate the anatomical basis of photosynthetic traits. The results revealed: (1) Yellow leaf spots in variegated Y. denudata represent chlorophyll-type variegation caused by abnormal chloroplast structure leading to reduced chlorophyll content. (2) The yellow regions exhibited abnormal thylakoid structure, blocking ATP synthesis and impeding normal photosynthesis. (3) Anatomical analysis showed that green leaves possessed well-developed palisade tissue with higher chloroplast integrity and pigment content compared to variegated and yellow leaves, resulting in greater net photosynthetic rates. (4) Significant differences in maximum net photosynthetic rate and light saturation point were observed between green and variegated leaves, with green leaves tolerating a broader range of high light intensity. These findings clarify how chloroplast structure influences photosynthetic characteristics in variegated Y. denudata, providing valuable references for breeding superior germplasm.

Keywords: photosynthetic pigment, anatomical structure, chloroplast structure, photosynthetic characteristics, correlation analysis

Introduction

Color-leafed plants constitute an important element in landscape architecture and have become increasingly prominent in landscape design applications due to their enhanced aesthetic value (Chen et al., 2023). In China, provincial initiatives promoting combined quantitative and qualitative improvements in afforestation have emphasized "colorization" as a key practice, requiring increased application of colorful plants to enhance urban plant diversity (Zheng et al., 2019). *Yulania denudata* (Magnoliaceae) is a deciduous tree species. Variegated Y. denudata originated as a leaf variant discovered in seed-propagated populations in 2013 and has been subsequently propagated through successive generations of grafting, with stable and consistent ornamental performance observed over multiple years.

Yellow and albino mutations hold significant biological importance for studying photosynthetic systems in higher plants (Hortensteiner, 2009). Previous research on Y. denudata leaf anatomy (Yuan et al., 2023) and photosynthetic characteristics (Liu et al., 2014; Li et al., 2012) has focused exclusively on green leaves, with no reports on variant leaf types.

Plant leaf pigment composition and content not only influence coloration but also affect photosynthetic capacity (Huang et al., 2015; Pu et al., 2021). Pigment content variations reflect internal chloroplast structure and correlate with chloroplast distribution and density within leaf tissues (Kang et al., 2020). Current research on photosynthesis and leaf structure in variegated plants has primarily focused on species such as *Bambusa multiplex* f. *silverstripe* (Chen et al., 2017), *Pseudosasa japonica* f. *akebonosuji* (Cheng et al., 2018), and *Sinobambusa tootsik* f. *albostriata* (Chen et al., 2019). These studies demonstrate that green leaves exhibit higher chlorophyll content, intact chloroplast structure, and superior photosynthetic capacity. Research on *P. japonica* f. *akebonosuji* during its re-greening phase showed that increasing pigment content correlated with elevated net photosynthetic rates, while albino leaves lacked mature thylakoid structures. Studies on *S. tootsik* f. *albostriata* revealed that most white mesophyll cells lacked intact chloroplasts, resulting in consistently negative net photosynthetic rates. These findings establish a close relationship between leaf anatomical structure and photosynthetic characteristics, where structural features directly impact photosynthetic function (Kong et al., 2020).

To investigate this relationship in variegated Y. denudata, we employed anatomical methods combining imaging analysis of palisade and spongy tissues with photosynthetic parameter measurements to address: (1) the anatomical classification of leaf variegation types in variegated Y. denudata, and (2) differences in photosynthetic characteristics among the three leaf types and their relationship with leaf structure.

Materials and Methods

1.1 Plant Materials

The experimental site was located at the open-air nursery of Shanghai Chenshan Botanical Garden. Three-year-old grafted seedlings of variegated Y. denudata were used, derived from a leaf variant discovered in 2013 seed-propagated populations. During the experimental period, plants exhibited flowering, with leaves displaying yellow-green variegation patterns; a minority showed entirely green or yellow leaves. This phenotypic expression remained consistent across both young grafted plants and mature individuals [Figure 1: see original paper]. Test leaves were selected from the upper-middle canopy of healthy plants, using mature leaves from each of the three phenotypes.

1.2 Experimental Methods

1.2.1 Photosynthetic Pigment Content Three fresh leaves from each phenotype were collected. After removing midribs, leaves were cut into pieces, mixed uniformly, and 0.1 g samples were extracted in 10 mL of 95% ethanol for 48 h in darkness until colorless. Extract absorbance was measured at 663 nm, 645 nm, and 470 nm using a microplate reader (Tecan Infinite M200 Pro) with three replicates. Chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Chl), and carotenoid (Car) contents were calculated.

1.2.2 Leaf Anatomical Structure Chloroplast Ultrastructure: Three leaves per phenotype were cut into 1 mm^2 sections and fixed in 2.5% glutaraldehyde at 4°C for 2–4 h. Samples were rinsed three times (15 min each) in 0.1 M H_3PO_4 buffer, post-fixed overnight in 1% osmium tetroxide at 4°C, then dehydrated through an ethanol series (30%, 50%, 70%, 80%, 95%, 100%, 100%) for 40 min each. After three 30-min treatments in 100% propylene oxide, samples were infiltrated with propylene oxide and embedding medium overnight, then pure embedding medium for 3–4 h. Polymerization occurred at 60°C. Ultrathin sections (70 nm) were stained with 3% uranyl acetate and 2.7% lead citrate, then observed via transmission electron microscopy (HITACHI).

Leaf Cross-Section Structure: Three leaves per phenotype were cut into 3 mm $\times$ 3 mm sections and fixed at room temperature for $>$24 h. Dehydration and embedding proceeded through an ethanol series (75% for 4 h, 85% for 2 h, 90% for 1.5 h, 95% for 1.5 h, 100% for 30–60 min twice), followed by ethanol-benzene mixture (10–20 min), xylene (10–20 min), and paraffin (1–2 h, three times). Sections (4–10 μm) were cut using a rotary microtome (Leica RM2016), dewaxed, and stained with toluidine blue. After clearing in xylene for 5 min and brief air-drying, sections were mounted with neutral balsam. Three slices per sample were examined, with three random fields per slice photographed using a microscope (Axio Scope A1).

1.2.3 Light Response Curves Measurements were conducted on two consecutive clear days (June 2–3, 2023) between 08:30–10:30 and 15:00–17:30 at 21–32°C. Three mature, healthy leaves per phenotype from the upper-middle canopy were analyzed using a LI-6400 photosynthesis system (LI-COR 6400) with red-blue light source. Photosynthetic photon flux density (PPFD) was set at 15 levels: 0, 10, 30, 50, 100, 200, 400, 600, 800, 1000, 1200, 1400, 1600, 1800, and 2000 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$. CO_2 flow rate was maintained at 500 $\mathrm{mol \cdot mol^{-1}}$.

1.3 Data Processing

Data were processed and analyzed using SPSS 20 and Origin 2022. Light response curves were fitted using a rectangular hyperbola correction model to calculate characteristic parameters. Figures and tables were prepared using Microsoft Excel 2021 and Origin 2022.

Results

2.1 Photosynthetic Pigment Content

Significant differences in photosynthetic pigment content existed among the three leaf types, decreasing in the order: green leaves > variegated leaves > yellow leaves. Total chlorophyll content in green leaves was 2.957 $mg \cdot g^{-1}$, while yellow and variegated leaves contained 65.61% and 5.51% of this value, respectively. The total chlorophyll-to-carotenoid ratio exceeded 1 in green and variegated leaves but was 0.489 in yellow leaves. Leaf coloration in variegated Y. denudata was associated with reduced total chlorophyll content and altered pigment ratios .

TABLE:1 Photosynthetic pigment content and proportion in leaves of three types

Phenotype	Chl a ($mg \cdot g^{-1}$)	Chl b ($mg \cdot g^{-1}$)	Total Chl ($mg \cdot g^{-1}$)	Car ($mg \cdot g^{-1}$)	Chl/Car
Green leaf	1.057$±0.232^a	1.900±0.724^a	2.957±0.113^a	0.693±0.184^b	1.099±0.006^a
Variegatedleaf	0.058±0.14				

Note: Different letters within the same column indicate significant differences ($P < 0.05$). The same below.

2.2 Leaf Anatomical Structure

2.2.1 Chloroplast Ultrastructure Green leaf mesophyll cells contained dense, intact chloroplasts with elongated or fusiform shapes, clear structure, and minimal starch granules. Thylakoids were tightly stacked into grana with compact lamellar organization. Yellow leaf chloroplasts were loosely arranged, irregular or nearly spherical, with damaged envelopes, light stroma, absent thylakoid structures, and numerous aggregated osmiophilic granules. Variegated leaves exhibited both chloroplast types: some maintained intact structure with differentiated thylakoid lamellae, while others showed degraded structure with osmiophilic granule accumulation [Figure 2: see original paper].

2.2.2 Leaf Cross-Section Structure Green leaf cross-sections showed the deepest staining, with flat upper epidermal cells (mostly rectangular) and elliptical or rounded lower epidermal cells. Palisade tissue cells were long and dense, clearly demarcated from spongy tissue. Chloroplasts were distributed throughout both tissues, particularly concentrated in palisade tissue. Variegated leaf upper epidermis was slightly flattened with rectangular to elliptical cells; chloroplasts were unevenly distributed in both tissues. Yellow leaf cross-sections showed the lightest staining with indistinct cellular morphology, likely due to cellular disintegration. Upper epidermal cells were elliptical or rounded with protrusions [Figure 3: see original paper].

All three leaf types shared similar tissue organization but differed significantly in palisade tissue thickness and the palisade-to-spongy tissue ratio. Palisade thickness in variegated and yellow leaves was 0.87× and 0.61× that of green leaves, respectively, while the thickness ratios were 0.71× and 0.43×. These findings suggest that coloration and photosynthetic characteristics in variegated Y. denudata may relate to palisade tissue thickness .

TABLE:2 Structural characteristics of transverse section of three types of blades

Phenotype	Upper epidermis thickness (m)	Lower epidermis thickness (m)	Palisade tissue thickness (m)	Spongy tissue thickness (m)	Palisade/Spongy tissue
Green leaf	18.574$±2.076^a	13.904±1.502^a	69.724±3.539^a	59.381±4.961^b	1.183±0.135^a
Variegated leaf	17.599±0.				

2.3 Light Response Curves

Light response curve fitting showed that at 0–200 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$ PPFD, net photosynthetic rates (Pn) in green and variegated leaves increased rapidly, with green leaves showing greater elevation. Between 200–800 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, green leaf Pn consistently exceeded variegated leaves. At 800–1000 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$, green leaf Pn plateaued after slow increase while variegated leaves plateaued then declined. Yellow leaves maintained respiration rates exceeding photosynthetic rates throughout.

Fitting results revealed determination coefficients of 0.999 and 0.998 for variegated and green leaves, respectively; yellow leaves could not be fitted. Maximum net photosynthetic rate (Pmax) and light saturation point (LSP) in green leaves (9.806 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$ and 1498.683 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) significantly exceeded variegated leaves, while light compensation point (LCP) was significantly lower (41.674 vs. 50.801 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) .

TABLE:3 Photosynthetic parameters of three types of leaves

Phenotype	Pmax ($\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$)	LSP ($\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$)	LCP ($\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$)	Dark respiration ($\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$)	R^2
Green leaf	9.806$±0.437^a	1498.683±59.913^a	41.674±0.480^b	2.384±0.135^a	0.998±0.000^a
Variegated leaf	6.452±				
Yellow leaf	-	-	-	-	-

2.4 Gas Exchange Parameters

Stomatal conductance (Gs) and transpiration rate (Tr) in green and variegated leaves increased with light intensity, both exceeding yellow leaves. Intercellular CO_2 concentration (Ci) followed similar trends across types: initial decline followed by gradual increase, with yellow leaves maintaining consistently higher levels. Water use efficiency (WUE) in green and variegated leaves rose rapidly at 0–200 $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, then declined slowly after 600 $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, while yellow leaves showed negative WUE throughout. Higher Gs and Tr in green leaves facilitated greater CO_2 consumption for photosynthesis [Figure 5: see original paper].

2.5 Correlation Analysis

Pearson correlation analysis revealed significant positive correlations between palisade tissue thickness and photosynthetic pigments. Chlorophyll a, chlorophyll b, and total chlorophyll showed extremely significant positive correlations with each other and significant positive correlations with carotenoids. Net photosynthetic rate correlated significantly with upper epidermis thickness, palisade tissue thickness, and Gs, and extremely significantly with lower epidermis thickness. Gs correlated extremely significantly with upper epidermis thickness and significantly with lower epidermis thickness. Spongy tissue thickness correlated positively with Ci, while both correlated negatively with other parameters. WUE correlated significantly with leaf thickness. These results indicate strong relationships between palisade tissue, pigment content, and photosynthetic characteristics [Figure 6: see original paper].

Discussion

Photosynthetic pigments are primary determinants of leaf color, with chlorophyll and carotenoids influencing green and yellow expression, respectively (Zhang et al., 2014). In variegated Y. denudata, carotenoid dominance in yellow leaves caused yellow coloration. Thylakoid membranes harbor essential photosynthetic pigments for light reactions (Wang, 2011). Yellow regions in variegated and yellow leaves showed nearly absent chloroplast structure, with thylakoid degradation products forming lipid aggregates and increased osmiophilic granules, indicating chloroplast degradation at the monolayer stage and manifested as reduced pigment content. The greater reduction in chlorophyll content aligns with findings in flue-cured tobacco (Zheng et al., 2020). While cross-sectional structure showed no qualitative differences, tissue thickness and proportions likely caused color variation. Palisade tissue typically contains more chloroplasts than spongy tissue, linking higher pigment content to palisade thickness (Du et al., 2022). Our significant positive correlation between palisade thickness and pigment content supports this, as well-developed palisade tissue may enable dense chloroplast packing. Leaf variegation is anatomically classified into five types: chlorophyllous, air space, epidermal, pigmentary, and appendage (Zhang et al., 2020). Yellow variegation in Y.

denudata represents chlorophyllous-type variegation resulting from abnormal chloroplast structure rather than specialized anatomical features.

Light response parameters reflect photosynthetic capacity and photoinhibition levels (Wang et al., 2014). Both green and variegated leaves showed increasing Pn with light intensity, but green leaves exhibited stronger light reactions, generating more ATP for dark reactions. At high light intensity, both types experienced light saturation, though thicker green leaves reduced internal light transmission, preventing photosystem damage and maintaining higher Pn. Yellow leaves consistently showed negative Pn, suggesting they cannot meet their own metabolic demands and require plant-level resource allocation. In three *Geodorum* species, greater differences between LSP and LCP indicated broader ecological light adaptation (Xu et al., 2024). Similarly, green leaves of variegated Y. denudata showed higher LSP and lower LCP than variegated leaves, demonstrating wider light intensity adaptability.

Chlorophyll initiates photosynthesis, with chloroplasts as the primary site (Kirchhoff, 2019). Thylakoids provide the essential platform for Photosystems I and II and pigment-protein complexes. Light-driven electron transfer between protein complexes, initiated by chlorophyll excitation, generates ATP (Waters et al., 2009; Zhu, 2017). Studies on albino tea (*Camellia sinensis* 'Baiye 1') showed reduced ATP synthase with increasing albinism (Li et al., 2019). Analogously, abnormal thylakoid structure in yellow regions of variegated Y. denudata likely caused ATP synthase deficiency, blocking ATP synthesis and reducing net photosynthetic rates. Photosynthetic rate and Gs exhibit feedback regulation; Gs modulates water vapor and CO_2 exchange through stomatal aperture (Li et al., 2023). Increased stomatal opening in variegated Y. denudata enhanced photosynthesis and accelerated CO_2 consumption, reducing Ci and explaining the positive correlation between Gs and Pn and negative correlation with Ci. Leaf structure strongly correlates with photosynthetic capacity; well-developed palisade tissue increases net photosynthetic rates (Wang and Ren, 2010; Gao et al., 2021). Our significant positive correlation between palisade thickness and Pn supports this, as palisade tissue is the primary site of chloroplast synthesis, and increased thickness indicates higher chloroplast numbers and chlorophyll content, enhancing photosynthetic capacity—consistent with findings in *Duranta repens* 'Variegata' (Mao et al., 2021).

Photosynthesis varies with tree age (Zang et al., 2009; Han et al., 2020). Comparative studies on *Vatica guangxiensis*, *Kmeria septentrionalis*, and *Manglietia aromatica* have shown enhanced photosynthetic structures and increased photosynthetic rates from seedling to adult stages (Pan et al., 2023a, 2023b, 2024). Our grafted variegated Y. denudata exhibited adult characteristics, representing mature plant photosynthetic structure and function. Using leaves from the same plant eliminated individual variation.

In summary, yellow variegation in Y. denudata represents chlorophyllous-type variegation. Differences in chloroplast structure and palisade tissue thickness underlie color variation among green, variegated, and yellow leaves. Photosynthetic characteristic differences correlate with chloroplast developmental status, where abnormal chloroplast structure reduces chlorophyll content and photosynthetic performance.

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