

Shade Tolerance, Biomass, and Individual Dynamics of Five Plant Species in the Understory of *Eucalyptus urophylla* Forest (Post-Print)

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Abstract

To understand the physio-ecological characteristics and growth adaptability of different plant species in *Eucalyptus urophylla* understories, five understory plant species with relatively wide distribution and high medicinal and economic value were selected as study subjects in the *Eucalyptus urophylla* forest at Heshan Station. Leaf traits, chlorophyll content, and photosynthetic light-response curves of each species were measured, while changes in biomass and fluctuations in individual numbers of the five understory plant species were analyzed based on quadrat survey data from the *Eucalyptus urophylla* forest in 2006 and 2011. The results showed: (1) Leaf width, thickness, single-leaf area, and other indices were largest in *Melastoma candidum* and smallest in *Ilex asprella*, with *Rhodomyrtus tomentosa*, *Gardenia jasminoides*, and *Litsea cubeba* being intermediate. The photosynthetic rates of *Rhodomyrtus tomentosa*, *Melastoma candidum*, and *Litsea cubeba* increased rapidly with increasing light intensity, with relatively high light saturation points. The photosynthetic rates of *Ilex asprella* and *Gardenia jasminoides* also increased with increasing light intensity, but their slopes were greater than those of *Melastoma candidum* and *Litsea cubeba*, reaching light saturation points quickly. Based on comprehensive cluster analysis of shade tolerance, the five species could be divided into two categories: Category 1 comprised shade-tolerant species *Ilex asprella* and *Gardenia jasminoides*, while Category 2 comprised less shade-tolerant species *Melastoma candidum*, *Litsea cubeba*, and *Rhodomyrtus tomentosa*. (2) With the growth of the *Eucalyptus urophylla* forest, the biomass of all five understory plant species increased to varying degrees. The most substantial increases were observed in *Melastoma candidum* and *Rhodomyrtus tomentosa*, which increased by 74-fold and 18-fold, respectively, while the smallest increase was in *Gardenia jasminoides* at only 1.3-fold. The biomass increase in the three species

Melastoma candidum, Rhodomyrtus tomentosa, and Litsea cubeba was primarily attributed to growth in individual height and ground diameter, whereas the biomass increase in Gardenia jasminoides and Ilex asprella resulted from contributions of individual number, plant height, and ground diameter. (3) During the growth process of the Eucalyptus urophylla forest, the shade-tolerant species Ilex asprella developed into a dominant shrub species within the forest as its individual density, plant height, and ground diameter increased. Although the density of Gardenia jasminoides increased to some extent, its small increments in plant height and ground diameter, along with low biomass, resulted in its development as a secondary shrub species. The individual densities of the three species Melastoma candidum, Rhodomyrtus tomentosa, and Litsea cubeba all declined. Although their ground diameter, plant height, and biomass showed some growth, their strong heliophilic nature could not adapt to the shaded environment within the forest, making them suitable only for growth in canopy gaps or forest edges with stronger light availability. Therefore, Ilex asprella and Gardenia jasminoides should be appropriately protected and planted during the management of Eucalyptus forests; under short-rotation management regimes, Melastoma candidum, Rhodomyrtus tomentosa, and Litsea cubeba could also be appropriately retained in canopy gaps and forest edges.

Full Text

Preamble

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Dynamics of Shade Tolerance, Biomass, and Individual Growth of Five Understory Plant Species in *Eucalyptus urophylla* Plantations

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Abstract: To investigate the ecophysiological characteristics and growth adaptability of different understory plants in *Eucalyptus urophylla* plantations, five understory species with high economic and medicinal value—*Gardenia jasminoides*, *Melastoma candidum*, *Rhodomyrtus tomentosa*, *Litsea cubeba*, and *Ilex asprella*—were selected for study. Leaf characteristics, chlorophyll content, and photosynthetic light response curves were measured for each species. Additionally, the dynamics of biomass and individual number were analyzed based on

field sampling survey data from 2006 and 2011. Comparative analysis and cluster analysis revealed that: (1) Leaf width, thickness, and area of *M. candidum* were the largest, whereas those of *I. asprella* were the smallest. The net photosynthetic rate of the selected understory plants increased with increasing light intensity; however, *M. candidum* and *L. cubeba* reached their light saturation points more quickly. *G. jasminoides* and *I. asprella* had higher light saturation points than *M. candidum* and *R. tomentosa*. (2) Biomass of the five selected understory species increased with stand age, but the range of increment varied. The greatest increase was observed in *M. candidum* (74-fold), followed by *R. tomentosa* (1.3-fold). The least increase was observed in *L. cubeba*. The increase in biomass of *M. candidum*, *R. tomentosa*, and *L. cubeba* was mainly caused by the increase in individual height and basal diameter, whereas the increase in biomass of *I. asprella* and *G. jasminoides* was mainly attributed to the increase in individual number, height, and basal diameter. (3) *I. asprella*, a shade-tolerant understory species with high economic value, dominated the shrub community with increasing plantation age, mainly owing to the increase in density, individual height, and basal diameter. *G. jasminoides* showed lower dominance over the shrub community owing to lesser increase in individual height and basal diameter than those of *I. asprella*. The density of *R. tomentosa*, *M. candidum*, and *L. cubeba* showed an overall decline with stand age, with only minor increase in individual height, basal diameter, and biomass. *M. candidum* and *R. tomentosa* can only survive in forest gap and edge owing to light limitation. In conclusion, we suggested that *I. asprella* and *G. jasminoides* should be protected and re-introduced during plantation management for biodiversity conservation. Under the short-rotation management regime, *M. candidum*, *L. cubeba*, and *R. tomentosa* should be retained and re-introduced in forest gaps and edges.

Keywords: *Eucalyptus urophylla* plantations; understory plant; photosynthetic characteristics; leaf trait; biomass

Introduction

Plant functional traits such as leaf morphology, canopy height, and photosynthetic characteristics can reflect plant responses and adaptations to growth environments. These functional traits are closely related to plant resource acquisition and utilization efficiency and biomass. Leaves are important organs for seed plants to produce organic nutrients, and their morphology and function directly affect light interception and carbon acquisition, significantly influencing plant relative growth rate. Previous studies have shown that plants growing in well-lit habitats have significantly higher dark respiration rates, photosynthetic capacity, and leaf lifespan than those growing in shaded habitats. Compared with shade-tolerant plants, sun-loving plants have thinner leaves, lower leaf mass per area, and larger specific leaf area, while shade-tolerant plants have higher chlorophyll concentration. Plant shade tolerance is a composite trait for adapting to shaded environments and is considered a key characteristic for understanding

forest community succession and dynamics.

Research on shade tolerance has covered multiple levels from individual to ecosystem, including plant morphological characteristics, shade tolerance classification, and mechanistic theories such as the carbon gain hypothesis, stress tolerance hypothesis, and carbon reserve hypothesis. However, plant shade tolerance is influenced by multiple stresses including specific ecological environments and growth season duration, and there are significant differences in shade tolerance among plants. Current research on shade tolerance has primarily focused on crops, forage grasses, and other agricultural aspects, with few reports on understory plants in natural conditions.

Eucalyptus urophylla is one of the three fast-growing tree species recommended by the Food and Agriculture Organization of the United Nations and is an important strategic timber species in southern China. However, to improve timber growth and yield, eucalyptus plantations are typically established at high densities, reaching complete canopy closure within 3 years, which impedes understory vegetation regeneration and growth. Surveys of understory plant growth in *E. urophylla* plantations in South China have found that human disturbances such as planting density and tending have led to biodiversity loss. During the initial planting stage before canopy formation, plants such as *Dicranopteris dichotoma* and *Melastoma candidum* grow rapidly. However, as the *E. urophylla* canopy closes, species such as *Ilex asprella* and *Gardenia jasminoides* develop while other species decline. This population dynamics of understory individuals may be closely related to environmental filtering and selection in the understory.

Studying the growth and shade tolerance of understory plants in *E. urophylla* plantations is important not only for understanding how understory plants respond and adapt to environmental changes during growth but also for elucidating community succession dynamics and biodiversity formation mechanisms. This study investigated leaf morphology, photosynthetic characteristics, biomass, and individual number dynamics of five understory plant species in *E. urophylla* plantations to clarify the ecophysiological characteristics and growth adaptability of major understory species, providing references for sustainable development and rational management of eucalyptus plantations.

1. Plot Survey and Biomass Calculation

1.1 Study Area Overview

This study was conducted at the Heshan Forest Ecosystem National Field Scientific Observation and Research Station (112°53 E, 22°40 N) in Guangdong Province. The climate is warm and rainy, with an average annual rainfall of 1,801 mm (ranging 1,700 mm), mean annual temperature of 21.70°C (maximum monthly mean 29.2°C, minimum 12.6°C), and mean annual relative humidity of 80%. The zonal soil is lateritic red soil with organic matter content of 0.56%–

1.64%.

The *E. urophylla* plantation was planted in spring 2002 and managed under normal forestry practices until 2004, after which it was left to natural succession. According to plot surveys, major understory plants in the plantation included *Litsea cubeba*, *Melastoma candidum*, *Rhodomyrtus tomentosa*, *Ilex asprella*, *Gardenia jasminoides*, *Baeckea frutescens*, *Eurya chinensis*, *Adiantum flabellulatum*, *Wikstroemia indica*, *Miscanthus sinensis*, *Dicranopteris dichotoma*, and *Clerodendron fortunatum*.

Permanent plots (30 m × 30 m) were established in the *E. urophylla* forest. Using the adjacent grid method, all shrub species in 5 m × 5 m subplots were surveyed in June 2006 and 2011, recording species, cluster number per unit area, height, basal diameter, and crown width. Crown width was measured with a steel tape, basal diameter with vernier calipers (precision 0.01 cm), and height with a measuring tape.

Biomass of shrub layer plants was calculated using allometric equations similar to those for trees. Based on 2006 field survey data, standard samples of each shrub species were selected, with three plants each larger and smaller than the standard harvested whole-plant to establish allometric relationships between organ biomass (branch, leaf, root) and basal diameter and height. The allometric equations were then used to calculate biomass for each species based on plot survey data. All biomass values reported refer to dry biomass.

2. Photosynthetic Parameter Measurement

Based on plot survey data, five naturally distributed understory species with high economic and medicinal value—*R. tomentosa*, *L. cubeba*, and *M. candidum*—were selected for further leaf morphological and photosynthetic measurements. Photosynthetic light response curves of mature leaves were measured using a LI-6400 portable photosynthesis system (LI-COR, Inc., USA).

The *E. urophylla* plantation was uniformly planted, and leaf area index in the fixed plots ranged 1.12–1.3 during the 2011 survey, indicating similar light environments within the forest. For photosynthetic measurements, five plants of each species with relatively uniform canopy cover were selected for in situ measurement between 9:00–12:00 on clear days. Measured leaves were healthy, vigorous branches on the upper canopy, appropriately distant from eucalyptus trees. Before measurement, all leaf materials were fully induced under natural light or 1000 mol m⁻² s⁻¹ light intensity.

The LI-6400 temperature controller was set to maintain leaf temperature at 25°C, using an open gas path with CO₂ supplied from a small cylinder controlled at 400 mol/mol. Light intensity was set from strong to weak at photosynthetic photon flux densities of 1500, 1200, 1000, 800, 500, 300, 200, 100, 80, 60, 40,

and $20 \text{ mol m}^{-2} \text{ s}^{-1}$ using the 6400-02B LED light source. After values stabilized, net photosynthetic rate (Pn) was recorded at each light level. The Von Bertalanffy nonlinear model was used to fit Pn-PFD curves for each species:

$$Pn = P_{max} \times (1 - e^{-\phi \times PAR}) - R_d$$

where Pn is measured net photosynthetic rate ($\text{mol m}^{-2} \text{ s}^{-1}$), Pmax is maximum photosynthetic rate ($\text{mol m}^{-2} \text{ s}^{-1}$), ϕ is apparent quantum efficiency (mol/mol), PAR is photosynthetically active radiation ($\text{mol m}^{-2} \text{ s}^{-1}$), and Rd is dark respiration rate ($\text{mol m}^{-2} \text{ s}^{-1}$). Light saturation point (LSP, $\text{mol m}^{-2} \text{ s}^{-1}$) and light compensation point (LCP, $\text{mol m}^{-2} \text{ s}^{-1}$) were calculated from the fitted curves.

3. Leaf Characteristic Measurement

After photosynthetic measurement, a 0.5 cm^2 leaf disc was taken from the middle of each leaf (avoiding main veins) using a hole punch. Chlorophyll and carotenoid contents were determined using a UV spectrophotometer (Lambda 650, USA) by measuring absorbance at 663, 645, and 470 nm.

Following these measurements, leaf length and width were measured with a LI-3000C leaf area meter, and thickness at the leaf middle was measured with a digital caliper. Leaves were then weighed to calculate specific leaf area (SLA = leaf area/dry weight). All reported values are means.

4. Data Analysis

Statistical analysis was performed using SPSS 22.0, Excel 2010, and SigmaPlot 13.0. One-way ANOVA was used to test significant differences among shrub species for each indicator. Results are presented as means.

3. Results and Analysis

3.1 Leaf Characteristics of Five Understory Plants

Leaf characteristic indicators are important plant growth traits. In the five understory plants, *M. candidum* showed the maximum values for leaf width, area, and other metrics, while *I. asprella* showed the minimum values for leaf length, width, and area, with *G. jasminoides* and *L. cubeba* intermediate. Shade-tolerant plants adapt to low light through increased leaf area and reduced non-photosynthetic organs relative to weight, typically becoming thinner with larger specific leaf area.

Among the five species, *M. candidum* had the smallest values for leaf width, unit leaf area fresh weight, and other metrics, while *I. asprella* had relatively large specific leaf area and *R. tomentosa* and *M. candidum* had relatively small specific leaf area, with *G. jasminoides* and *L. cubeba* intermediate. Based on leaf size, specific leaf area, and other metrics, *I. asprella* appears more shade-tolerant than *R. tomentosa* and *M. candidum*.

shows the leaf characteristics of the five understory plants.

3.2 Chlorophyll Content

Chlorophyll content is also an important leaf adaptation trait. Chlorophyll content differed significantly among the five shrub species ($P \leq 0.01$). *L. cubeba* had significantly higher chlorophyll and carotenoid contents than the other species, while *M. candidum* had the lowest chlorophyll content. Chlorophyll a/b ratios ranged 2.11–3.85, with *M. candidum* showing the highest ratio (3.85) and *I. asprella* the lowest (2.11). Except for the non-significant difference between *R. tomentosa* and *I. asprella*, all other interspecific differences in chlorophyll a/b ratio were significant.

shows the chlorophyll content of the five understory plants.

3.3 Photosynthetic Parameters of Five Understory Plants

Photosynthesis is a key indicator of plant growth. Net photosynthetic rates of all five species increased with light intensity. *M. candidum* and *L. cubeba* showed rapid increases in net photosynthetic rate with increasing light, with relatively high light saturation points. *G. jasminoides* also increased photosynthetic rate with light, but with steeper slopes than *M. candidum* and *L. cubeba*, reaching light saturation quickly. *I. asprella* and *G. jasminoides* had smaller maximum net photosynthetic rates.

M. candidum had the largest dark respiration rate, while *I. asprella* had the smallest, with no significant differences among the other species. In light utilization, *I. asprella* and *G. jasminoides* had larger apparent quantum efficiency. *L. cubeba*, *R. tomentosa*, and *M. candidum* had larger light compensation points (26 ± 2 , 21 ± 2 , and $19 \pm 2 \mu\text{mol m}^{-2} \text{ s}^{-1}$ respectively), while *G. jasminoides* and *I. asprella* had smaller values (15 ± 1 and $16 \pm 1 \mu\text{mol m}^{-2} \text{ s}^{-1}$).

[Figure 1: see original paper] shows the photosynthetic light response curves of the five understory plants.

shows the photosynthetic parameters of the five understory plants.

3.4 Cluster Analysis of Shade Tolerance

Shade tolerance is influenced by numerous factors, and results may differ when analyzed from different perspectives. Under similar growth environments and canopy closure conditions, cluster analysis was performed using three variable

sets: leaf morphological indicators (leaf length, width, single leaf area, single leaf dry weight, SLA), chlorophyll content indicators (chlorophyll a, b, a+b, a/b, carotenoids), and photosynthetic parameters (dark respiration rate, maximum net photosynthetic rate, light compensation point, apparent quantum efficiency), plus a comprehensive indicator set combining all parameters.

When using leaf morphological indicators, the clustering distance was 10, grouping *I. asprella*, *R. tomentosa*, and *G. jasminoides* together, with *M. candidum* separate. Chlorophyll content indicators produced similar results. Neither approach accurately reflected actual shade tolerance.

When using photosynthetic parameters, *I. asprella* grouped alone, *R. tomentosa* and *M. candidum* together, and *G. jasminoides* and *L. cubeba* together, differing from the morphological and chlorophyll clusters but still not perfectly matching reality.

When using comprehensive indicators, the five species divided into two groups: shade-tolerant (*I. asprella* and *G. jasminoides*) and less shade-tolerant (*M. candidum*, *L. cubeba*, and *R. tomentosa*). This result best matched actual conditions.

[Figure 2: see original paper] shows the dendrograms of shade tolerance cluster analysis.

3.5 Biomass Changes of Five Understory Plants

Allometric equations relating dry biomass of each organ to height and basal diameter were established for each species. Based on plot survey data and these equations, total dry biomass in 2006 was: *R. tomentosa* 103.45, *G. jasminoides* 160.08, *I. asprella* 80.29, *L. cubeba* 217.76, and *M. candidum* 0.87 kg/hm². By 2011, all species showed biomass increases, with the largest increase in *M. candidum* (from 0.87 to 64.4 kg/hm²), followed by *R. tomentosa* (103.45 to 1884.72 kg/hm²). The smallest increase was in *G. jasminoides* (160.08 to 211.18 kg/hm²). *L. cubeba* and *I. asprella* increased to 1329.05 and 1096.95 kg/hm² respectively.

Biomass increases in *M. candidum*, *R. tomentosa*, and *L. cubeba* were mainly caused by increased plant height and basal diameter, while increases in *G. jasminoides* and *I. asprella* resulted from increases in individual number, height, and basal diameter.

shows the biomass of the five understory plants.

3.6 Population Dynamics of Five Understory Plants

Analysis of understory vegetation plots in the Heshan plantation showed that from 2006 to 2011, the density (clusters per unit area) of *R. tomentosa* and *M. candidum* decreased by 73.4% and 46.2% respectively, while *G. jasminoides* and *I. asprella* increased by 31.6% and 58.3%. The number of stems per cluster

increased for *M. candidum* and *I. asprella* but decreased for *R. tomentosa* and *G. jasminoides*.

All species except *G. jasminoides* showed substantial height increases, particularly *L. cubeba*, which exhibited large height gains due to its small tree biological characteristics. All five species also showed varying degrees of basal diameter growth.

shows the population dynamics of the five understory plants.

4. Discussion

4.1 Shade Tolerance Characteristics of Five Understory Plants

Shade tolerance is an important trait determined by genetic characteristics and adaptive responses to external light environments. As understory survivors in forest lower layers with generally weak light and relatively small space resources, plants have evolved various adaptations. Leaf characteristics such as leaf size and specific leaf area are commonly used as shade tolerance indicators. Shade-tolerant plants generally have large, thin leaves with high specific leaf area, which can serve as an index of leaf shade degree.

Among the five species, *M. candidum* had the smallest leaf width and unit leaf area dry weight but largest single leaf area and dry weight, while *I. asprella* had the smallest leaf dimensions. *R. tomentosa* and *M. candidum* had relatively small specific leaf area, while *L. cubeba* and *G. jasminoides* had relatively large values, all showing significant differences. However, cluster analysis using leaf morphological traits alone could only roughly assess shade tolerance, as some indicators like specific leaf area and leaf thickness did not completely align with shade tolerance characteristics, possibly due to plant community development stage.

Chlorophyll plays a crucial role in photosynthesis. Shade-tolerant plants generally have higher chlorophyll content to fully utilize blue-violet light in shaded environments, while sun plants have higher chlorophyll a/b ratios. In this study, *M. candidum* had the highest chlorophyll a/b ratio (3.85), suggesting it is not a shade plant. However, comprehensive consideration of photosynthetic parameters and cluster analysis indicated that *R. tomentosa* and *L. cubeba* are sun plants that cannot grow under canopies with transmittance below 10-20% and require full sunlight.

Photosynthetic parameters are important references for plant growth. Sun plants typically have higher maximum net photosynthetic rates, light saturation points, and compensation points than shade plants. In this study, *L. cubeba*, *R. tomentosa*, and *M. candidum* had larger maximum net photosynthetic rates and light compensation points, while *G. jasminoides* and *I. asprella* had smaller

values. However, cluster analysis using photosynthetic parameters alone also could not perfectly classify shade tolerance.

Cluster analysis using comprehensive indicators (leaf morphology, chlorophyll content, and photosynthetic parameters) successfully divided the five species into two groups: shade-tolerant (*I. asprella* and *G. jasminoides*) and less shade-tolerant (*M. candidum*, *L. cubeba*, and *R. tomentosa*). This conclusion best matched actual conditions, demonstrating that shade tolerance is a complex composite trait that cannot be accurately assessed with single indicators. Using comprehensive morphological and physiological indicators with cluster analysis provides a reliable, straightforward method for evaluating understory plant shade tolerance.

4.2 Population Dynamics of Five Understory Plants

The population dynamics revealed that as *E. urophylla* canopy closure increased, *R. tomentosa* and *M. candidum* densities continuously decreased and are expected to eventually exit the community. *I. asprella* and *G. jasminoides*, as shade-tolerant plants, can persist and develop into dominant understory species.

L. cubeba is a deciduous small tree that prefers warm, humid environments and is typically found at forest edges and in shrublands. In early plantation stages, its density was high, but it declined significantly with plantation age due to competition with faster-growing eucalyptus. It can be retained at forest gaps and edges.

M. candidum and *R. tomentosa* are small evergreen shrubs and positive pioneer species. *M. candidum* is light-demanding, while *R. tomentosa* is slightly shade-tolerant. Both species densities declined substantially with plantation development and are predicted to gradually 衰退. During early plantation stages, these species can be appropriately cleared to reduce nutrient competition with eucalyptus.

I. asprella commonly grows in mountain sparse forests and shrublands with some shade tolerance. *G. jasminoides* is an evergreen shrub that prefers shade as seedlings and subtropical humid climates. Both species can grow normally under eucalyptus canopy and show increasing trends in density, making them suitable for understory vegetation in eucalyptus plantations. This study suggests that *I. asprella* and *G. jasminoides* should be protected and planted during understory vegetation management to enhance biodiversity in eucalyptus plantations.

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[4] [Additional references continue in the same format...]

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