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Original Article

Physiological characteristics of Indonesian medicinal plants under varying photosynthetically active radiation (PAR): Toward adaptive strategies under environmental change

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Abstract

Physiological traits such as photosynthetic rate (*A*), stomatal conductance (g_{sw}), and intrinsic water-use efficiency (*iWUE*) are influenced by photosynthetically active radiation (PAR); however, their specific effects on individual plant species remain insufficiently studied. The objective of this study was to evaluate *A*, g_{sw}, and *iWUE* in young and mature leaves under varying PAR levels (400, 1000, and 1600 µmol m^{-2} s^{-1}) across six Indonesian medicinal plants: *Dalbergia latifolia* (DL), *Murraya koenigii* (MK), *Murraya paniculata* (MP), *Syzygium cumini* (SC), *Syzygium polyanthum* (SP), and *Swietenia mahagoni* (SM), to better understand their light-intensity tolerance for cultivation purposes. Data analysis revealed that *A* was significantly affected by species, leaf age, and PAR, whereas g_{sw} and *iWUE* were influenced only by species and PAR ($\alpha = 0.01$). The results highlight the broad adaptability of *M. koenigii*, which may perform well across a wide range of light conditions. In contrast, *S. cumini*, *D. latifolia*, and *S. mahagoni* appear to be more shade-tolerant, while *M. paniculata* and *S. polyanthum* seem better adapted to high-light environments, potentially favoring drier habitats due to their elevated *iWUE* under intense light. Collectively, these findings provide valuable insights to guide sustainable cultivation and conservation strategies for Indonesia's medicinal plant resources.

Keywords: Intrinsic water use efficiency, Leaf age, PAR, Photosynthesis, Stomatal conductance

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Introduction

Indonesia is the world's center of plant diversity and is home to a wide range of medicinal plants that are highly valuable to society and the world. It is estimated to harbor at least 80% of medicinal plant species in Southeast Asia, including both native and introduced species (Cahyaningsih et al., 2021). The use of medicinal plants in maintaining health has been carried out for generations by the Indonesian people. Even before the vaccine became available, the Indonesian people relied on traditional medicines, whose essential ingredients were derived from various medicinal plants to prevent COVID-19 (Coronavirus Disease of 2019) (Nayaka et al., 2023). In response to the pandemic, around 79% of Indonesians have turned to medicinal plants to boost their immunity during the COVID-19 outbreak. The Indonesian government has also provided support by offering online resources, including books that provide recommendations on using various medicinal plants (Purwitasari et al., 2023). Outside of pandemic conditions, global demand for herbs and aromatic products has significantly increased, driven by the herbal, flavor, and fragrance industries. Over the past three decades, herbal medicines and supplements have surged, with more than 80% of the world's population relying on them for some aspect of primary healthcare.

The research focused on the physiological traits of six Indonesian medicinal plants, including *Dalbergia latifolia* Roxb. (Fabaceae; sonokeling) and *Murraya koenigii* (L.) Spreng. (Rutaceae, salam koja), *Murraya paniculata* (L.) Jack (Rutaceae, kemuning), *Swietenia mahagoni* (L.) Jacq (Meliaceae, mahoni), *Syzygium cumini* (L.) Skeels (Myrtaceae, jamblang), and *Syzygium polyanthum* (Wight) Walp. (Myrtaceae; salam). These species are distributed in Indonesia and are primarily used in traditional Indonesian medicine.

Dalbergia latifolia possesses the chemical structure of pterocarpan compounds in its stem bark, and the isolated compounds have the potential to serve as an anti-Human immunodeficiency virus (HIV) agent (Balqis, 2016). Tannin extracts from the bark are used in traditional medicine to treat diarrhea, worms, indigestion, and leprosy, as well as to stimulate appetite (Sukhadiya et al., 2020).

Murraya koenigii is recognized for its potential medicinal properties, featuring key phytochemicals such as lipids, essential oils, coumarins, carbazole carboxylic acid, carbazole alkaloids, and carotenoids. Various parts of the plant serve distinct purposes: the stem is used for cleaning, the bark as a hair tonic, the leaves as a stomachic, purgative, and febrifuge, the fruits as astringents, the roots as cooling agents, and the entire plant as a stimulant (Gahlawat et al., 2014). Moreover, the leaves are widely found in Aceh (Indonesia) and are commonly used in traditional Acehnese cuisine as a seasoning (Fachraniah and Novilasi, 2012).

Murraya paniculata has shown significant pharmacological potential in treating cancer, diabetes, hyperlipidemia, infections, oxidative stress, and other conditions (Joshi and Gohil, 2023). In tropical regions, such as Bengkulu (Indonesia), the Serawai ethnic community commonly uses kemuning leaves as a traditional remedy for asthma (Safitri et al., 2020). The Hindu community in Jagaraga, West Lombok (Indonesia), traditionally uses this cough plant (Eni et al., 2019).

Swietenia mahagoni has astringent properties derived from its bark and is used in decoctions to treat diarrhea, provide vitamins and iron, and manage hemorrhages. When infused into a red liquid, it purifies the blood, stimulates appetite, and restores strength, particularly for individuals recovering from tuberculosis (Orwa et al., 2009). *Syzigium cumini* is commonly used to treat hemorrhoids and postpartum conditions. (Henri et al., 2022). *S. polyanthum* has been identified as possessing anti-inflammatory properties, with molecular docking studies revealing interactions with molecules related to inflammation and antioxidants (Aditya et al., 2022).

Given the numerous uses of the six medicinal plants mentioned above, cultivation efforts are necessary to ensure the sustainable existence of these plants in terms of both quality and quantity. Currently, these plants grow wild and remain uncultivated, making their population might be more threatened by climate change, although the impact on species distribution varies from species to species (Cahyaningsih et al., 2021). Therefore, understanding physiological traits is crucial to developing optimal cultivation practices. Research on plant physiology plays a fundamental role in expanding knowledge about plant-environment interactions across different life cycle stages. Insights into these physiological characteristics help inform sustainable plant management practices and adaptation strategies.

Observation of plant physiological characteristics related to photosynthetically active radiation (PAR) can be the basis for optimal cultivation efforts. PAR refers to the portion of the electromagnetic spectrum between 400 and 700 nanometers, which closely aligns with the visible light range. This specific range is vital for photosynthesis, as plants and most other photosynthetic organisms rely on it to drive the conversion of carbon dioxide and water into glucose and oxygen. Fluctuations in PAR can significantly influence plant growth and development (Mo et al., 2015). Light energy is a key component in photochemical processes within this waveband, as it generates ATP (adenosine triphosphate) and NADPH (nicotinamide adenine dinucleotide phosphate), which are essential for the Calvin cycle. These energy carriers are crucial in carbon fixation and contribute to other vital functions, such as nitrate reduction and the synthesis of amino acids and lipids (Malkin and Niyogi, 2015). Gaining insight into the link between PAR intensity and plant development is crucial for advancing agricultural practices and environmental planning, such as fine-tuning irrigation and fertilization or designing urban landscapes based on light availability.

In this study, the physiological characteristics of young and mature leaves were observed. Quantifying the leaf photosynthetic capacities of different ages remains challenging (Yang et al., 2025). Leaf lamina mass and area are closely correlated with a plant's photosynthetic capacity and competitive ability, whereas leaf age has been demonstrated to affect physiological processes, such as photosynthesis (Jiao et al., 2022). Plant physiological indices represent the level of physiological activity and offer insight into overall plant health. Investigating how these traits respond to varying levels of PAR is critical for advancing agronomic practices and breeding strategies. While leaves are not the sole site of photosynthesis, they are the primary organ responsible for this process, making their functional characteristics especially important in understanding plant function and ecosystem behavior. Leaf age and developmental stage have a significant influence on plant morphology and physiological functions (Jiao et al., 2022). Among environmental factors that affect plant growth, light plays a pivotal role in supplying the energy necessary to trigger numerous physiological processes (Abidi et al., 2013).

The objective of the study was to identify net photosynthesis (A), stomatal conductance (g_{sw}), and intrinsic water use efficiency ($iWUE$) on young and mature leaves under varying PAR levels to understand their light intensity tolerance for its cultivation efforts. The findings provide a scientific foundation for applying effective cultivation techniques to enhance growth and yield.

Material and Methods

Plant material

The study was conducted at the nursery area of the medicinal plants collection in the Bogor Botanical Gardens, Indonesia (6° 35' 51.4644" S, 106° 47' 58.4448" E). Six plant species were selected based on their medicinal importance in Indonesia. Plants were grown in polybags (25 x 25 cm) with a 2:1:1:1 ratio of soil, manure, burned rice husks, and fresh rice husk as growing media, and were irrigated daily by hand with tap water or as needed. The observed plants were six tree species: 1). *Dalbergia latifolia* (DL), 2). *Murraya koenigii* (MK), 3). *Murraya paniculata* (MP), 4). *Syzygium cumini* (SC), 5). *Syzygium polyanthum* (SP), and 6). *Swietenia mahagoni* (SM) (Figure 1). Three individual plants were observed for each species, aged around four years. Three healthy, pest and disease-free young and mature leaves were selected for observation from each plant.

The plants selected were relatively uniform in size within each species (Table 1). Plant height (cm) was measured from the ground surface to the growing point, and stem diameter (cm) was measured approximately 5 cm above the ground surface using a caliper. The leaf character's observations included leaf area (cm^2), leaf thickness, and stomatal density. The largest leaf was sampled for area quantification, and a centrally located, healthy leaf was selected for measuring thickness and stomatal density.

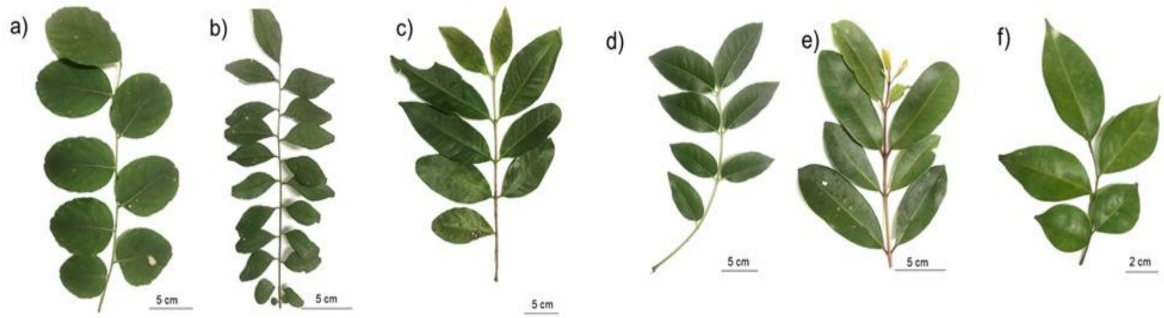

Figure-1. The leaves of six medicinal plants observed in Bogor Botanical Gardens, Indonesia. a) *Dalbergia latifolia*, b) *Murraya koenigii*, c) *Murraya paniculata*, d) *Swietenia mahagoni*, e) *Syzygium cumini*, and f) *Syzygium polyanthum.*

Table-1. Morphological characters of the six medicinal plant species observed in Bogor Botanical Gardens, Indonesia.

No.	Species	Plant height (cm)	Trunk diameter (cm)	Leaf area (cm^2)		Leaf thickness (µm)	
				Young	Mature	Young	Mature
1	*Dalbergia latifolia*	127.33±13.05	1.45±0.27	21.01 ± 2.31	24.25 ± 2.31	171.97±17.07	227.46±30.66
2	*Murraya koenigii*	88.33±28.25	1.39±0.17	5.05 ± 2.52	8.15 ± 1.12	134.62±7.25	151.41±27.00
3	*Murraya paniculata*	179.00±14.18	1.57±0.05	9.78 ± 2.52	18.75 ± 0.33	152.23±10.06	154.05±24.99
4	*Swietenia mahagoni*	80.33± 8.39	0.99±0.02	22.19 ± 1.79	15.48 ± 4.60	221.37±29.54	204.95±26.92
5	*Syzygium cumini*	195.00±27.22	2.08±0.22	30.20 ± 4.50	43.28 ± 8.71	221.37±26.83	341.36±23.25
6	*Syzygium polyanthum*	177.67±67.69	1.82±0.07	26.36 ± 6.43	42.59 ± 7.80	232.38±13.71	183.14±22.11

Leaf area (cm^2) was measured using a KWF LAW-A Portable Leaf Area Meter. Leaf thickness and stomatal density were observed using an Olympus BX53 light microscope equipped with a Nikon SMZ1000 camera. Leaf thickness was determined from transverse sections of fresh leaf samples. Sections were cut directly in a drop of distilled water on a clean glass slide using a sharp razor blade to minimize tissue dehydration. The specimens were mounted with a coverslip to avoid air bubbles and examined under the same microscope at 10× magnification. Six replicate sections were analyzed per sample to ensure data reliability, and measurements were processed using ImageJ version 1.54j. Whereas, for stomatal density, leaf imprints were obtained by applying a thin layer of clear nail polish to the abaxial leaf surface. After drying, the film was peeled off, mounted on a glass slide, and examined at 20× magnification. Six fields of view were captured from each leaf impression, and stomata were counted using ImageJ version 1.54j.

Physiological observation

Physiological observations were measured using an Infrared Gas Analyzer (IRGA) (LI-6400XT photosynthesis System, LI-COR Inc., Lincoln, NE, USA). The chamber flow rate was set to 500 µmol s^{-1}, leaf temperature to 24° C, and reference [CO_2] to 370 µmol mol^{-1} (ppm). The relative humidity inside the chamber was maintained at 65–68% using a self-indicating desiccant. Under the same environmental setup, IRGA measurements were conducted at three different light intensities, i.e., 400 µmol m^{-2} s^{-1} PAR, 1000 µmol m^{-2} s^{-1} PAR, and 1600 µmol m^{-2} s^{-1} PAR, respectively. Measurements using a light intensity of 1000 µmol m^{-2} s^{-1} PAR were taken from 09:00 AM to 11:00 PM. Measurements using a light intensity of 1600 µmol m^{-2} s^{-1} PAR were taken from 11:30 AM to 1:30 PM and measurements using a light intensity of 400 µmol m^{-2} s^{-1} PAR were taken 2:00 PM to 16:00 PM. Measurement time selection was based on the fluctuation of the microclimate conditions in the nursery, where on 08.00-10.00 AM the average light intensity measured was 20,227.33 Lux, temperature was 28,67 ℃, and humidity was 63.4%. At 12:00-2:00 PM, the average of light intensity was 62,161.93 Lux, the temperature was 30,47 ℃, and the humidity was in the range of 63.8%. At 15:00-16:00, the average of the light intensity was 21.622 Lux, the temperature was 29.13 ℃, and the humidity was 66.53%, respectively, illustrating the same environmental conditions in the nursery for each measurement. Photosynthesis rates (A: µmol m^{-2} s^{-1}) and stomatal conductance to water vapour (g_{sw}: mol m^{-2} s^{-1}) were taken in steady state measurement, and intrinsic water use efficiency (*iWUE*) was calculated as A/g_{sw} (Faralli et al., 2019). For each species, three individual plants were selected as biological replicates, and from each plant, three leaves were observed, resulting in a total of nine leaves per species, both young and mature leaves. The young leaves were at the third leaf from the tip of a twig (fully expanded young leaves), and the mature leaves were at the fifth leaf from the tip of the twig of each plant. So, the total number of observations was 108.

Experimental design and data analysis

The data obtained were analyzed using Microsoft Excel 2021 and statistical analysis was conducted using The Statistical Tools for Agricultural Research (STAR 2.0.1, International Rice Research Institute, Philippines). One-way analysis of variances (ANOVAs) were performed to determine if there were interactions between samples or treatments for a given parameter measured. If the results were significant, then the analysis was continued using Duncan's Multiple Range Test (DMRT) with an α level of 0.05. All figures and graphs were generated using Python 3.11.

Results

Physiological characters

Impact of PAR intensity on leaf photosynthetic rates by leaf stage

The photosynthetic rate (A) is strongly affected by both plant species and the intensity of PAR. In this study, A was found to be strongly impacted by interactions between (1) plant species and leaf age, (2) plant species and PAR, (3) leaf age and PAR, and (4) the combination of plant species, leaf age, and PAR (Table 2).

IRGA measurements on young leaves of various plant species indicated significant variation in photosynthetic rates (A) in response to differing levels of PAR exposure. The maximum photosynthesis rate was exhibited by SC (17.97 µmol m^{-2} s^{-1}) and MK (17.90 µmol m^{-2} s^{-1}) under 400 µmol m^{-2} s^{-1} PAR; MP (27.32 µmol m^{-2} s^{-1}) under 1000 µmol m^{-2} s^{-1} PAR; and MP (23.62 µmol m^{-2} s^{-1}) and MK (23.73 µmol m^{-2} s^{-1}) under 1600 µmol m^{-2} s^{-1}, respectively (Figure 2a-c). IRGA measurement under 400 µmol m^{-2} s^{-1} PAR showed the highest A rate from SC (19.59 µmol m^{-2} s^{-1}) in mature leaves and from MK (16.02 µmol m^{-2} s^{-1}) in young leaves, which was significantly higher than that of other species. On the other hand, under 1000 and 1600 µmol m^{-2} s^{-1} PAR, A rate from MP was the highest in both young (27.32 and 23.63 µmol m^{-2} s^{-1}, respectively) and mature (28.23 and 23.44 µmol m^{-2} s^{-1}, respectively) leaves (Figure 2d-f).

Table-2. Summary of p-value from ANOVA of photosynthesis rate (A), stomatal conductance (g_{sw}), and intrinsic water use efficiency (*iWUE*) (α = 0.05).

Sources	A (µmol m^{-2} s^{-1})	g_{sw} (mol m^{-2}s^{-1})	*iWUE* (µmol mol^{-1})
Species	0.00**	0.00**	0.00**
Leaves age	0.42^{ns}	0.74^{ns}	0.66^{ns}
PAR	0.00**	0.00**	0.00**
Species:Leaf age	0.02*	0.83^{ns}	0.85^{ns}
Species:PAR	0.00**	0.00**	0.00**
Leaves age:PAR	0.00**	0.94^{ns}	0.65^{ns}
Species:Leaves age:PAR	0.00**	0.85^{ns}	0.97^{ns}

Note: ** = sources give a significant effect for observed variables at α = 0.01, * = sources give a significant effect for observed variables at α = 0.05, ^{ns} = sources do not give a significant effect for observed variables at α 1% and 0.05.

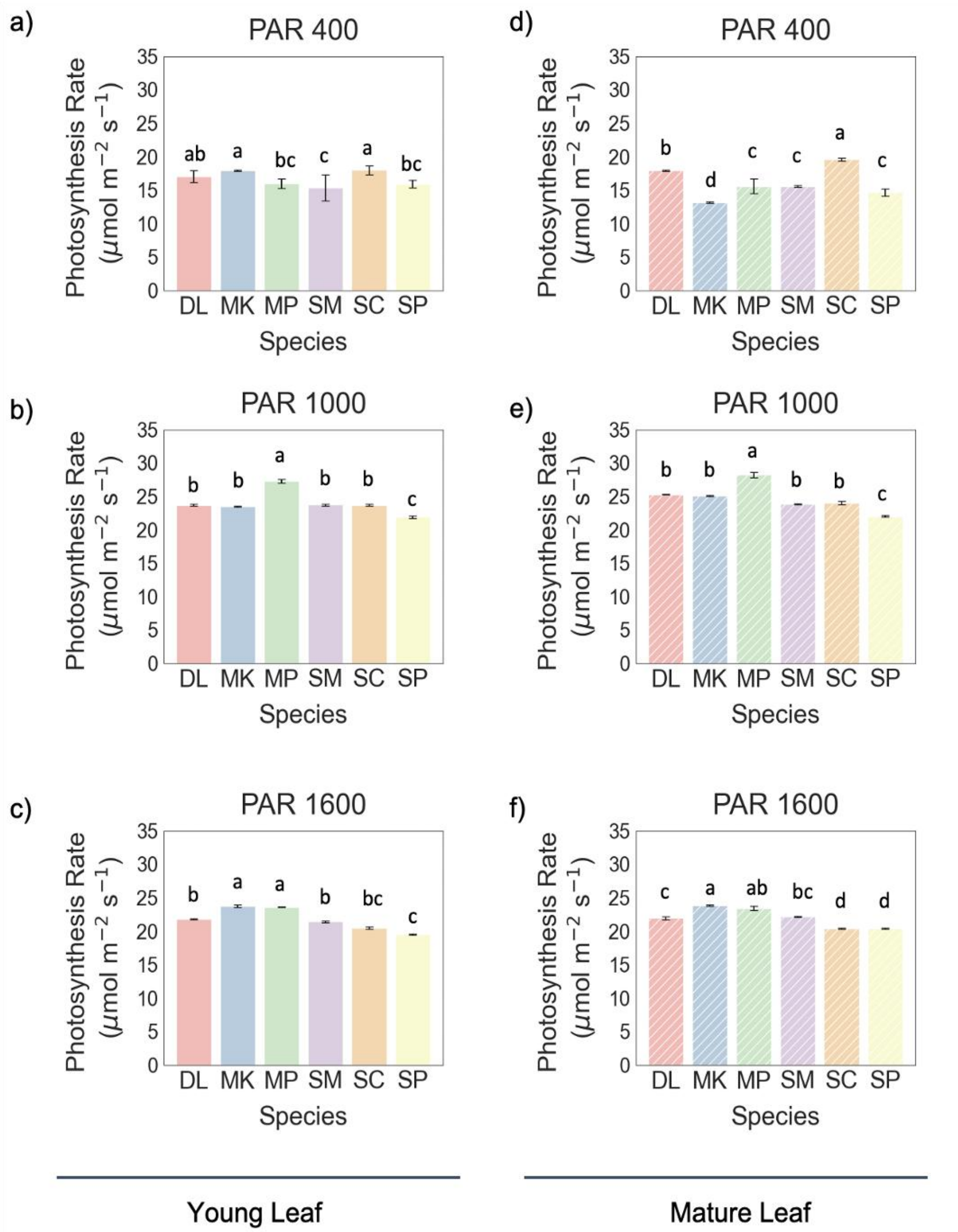

Figure-2. Photosynthetic rate (*A*: µmol m^{-2} s^{-1}) of young and mature leaves of six medicinal plants observed in Bogor Botanical Gardens Indonesia at each level of PAR (a,b,c=young leaves; d,e,f=mature leaves; DL= *Dalbergia latifolia*, MK= *Murraya koenigii*, MP= *Murraya paniculata*, SM= *Swietenia mahagoni*, SC= *Syzygium cumini*, and SP= *Syzygium polyanthum*. Note: Groups labeled with the same letter are not significantly different from each other at the specified significance level (α = 0.05).

These results showed that across both young and mature leaves, all species exhibited a similar trend: a higher A rate observed when plants were exposed to 1000 µmol m^{-2} s^{-1} PAR compared to 400 µmol m^{-2} s^{-1} PAR; however, a lower A rate was observed when plants were exposed to 1600 µmol m^{-2} s^{-1} PAR. Although *A* rate of the plants exposed to light under 1600 µmol m^{-2} s^{-1} PAR remained higher than when they were exposed to 400 µmol m^{-2} s^{-1} PAR. The decline from 1000 µmol m^{-2} s^{-1} PAR was statistically significant in all species except MK. This data suggested that while moderate increases in PAR enhance photosynthetic efficiency, excessive PAR may lead to photoinhibition in most species (Figure 2).

Stomatal conductance (g_{sw})

Stomatal conductance (g_{sw}) plays a critical role in regulating gas exchange and water loss, directly influencing photosynthesis and overall plant physiological performance. The statistical analysis revealed significant differences in g_{sw} across plant species and PAR intensity. Highlighting their species-specific adaptation to light intensity. A significant interaction between species and PAR further underscores the differential regulatory mechanisms among species under varying light conditions. In contrast, leaf ages, whether young or mature, did not significantly affect g_{sw} (Figure 3). Additionally, no significant interactions were detected between species and leaf age, between leaf age and PAR, or among the three-way interaction among species, leaf age, and PAR (Table 2), indicating that stomatal behavior was primarily driven by species traits and PAR intensity rather than by the developmental leaf stage.

IRGA measurement indicated no significant difference in g_{sw} was observed among all plant species, both at young and mature leaves, under 400 µmol m^{-2} s^{-1} PAR and 1000 µmol m^{-2} s^{-1} PAR. However, when plant species were exposed to 1600 µmol m^{-2} s^{-1} PAR, the significantly highest g_{sw} was recorded for SP (young leaf = 0.53 mol m^{-2} s^{-1} and mature leaf = 0.51 mol m^{-2} s^{-1}). The analysis also indicated a trend showing the lowest g_{sw} observed on MP (0.19 mol m^{-2} s^{-1}), although there was no statistical difference when compared to MK (0.21 mol m^{-2} s^{-1}), SM (0.27 mol m^{-2} s^{-1}), and SC (0.20 mol m^{-2} s^{-1}).

From this result, all plant species demonstrated a comparable g_{sw} response to PAR intensity, with g_{sw} values generally exhibiting an upward trend as PAR intensity increased (Figure 3). The highest g_{sw} values were typically observed at 1600 µmol m^{-2} s^{-1} PAR, except for the MP species (Figure 3). In MP, g_{sw} observed at young leaves increased from 0.12 mol m^{-2} s^{-1} under 400 µmol m^{-2} s^{-1} PAR to 0.22 mol m^{-2} s^{-1} under 1000 µmol m^{-2} s^{-1} PAR, followed by a decline to 0.19 mol m^{-2} s^{-1} under 1600 µmol m^{-2} s^{-1} PAR. Meanwhile, at mature leaves g_{sw} increased from 0.12 mol m^{-2} s^{-1} under 400 µmol m^{-2} s^{-1} PAR to 0.22 mol m^{-2} s^{-1} under 1000 µmol m^{-2} s^{-1} PAR, followed by a decline to 0.19 mol m^{-2} s^{-1} under 1600 µmol m^{-2} s^{-1} PAR. Notably, in the SC species, there is a trend that showed increasing g_{sw} measured under 400 µmol m^{-2} s^{-1} PAR to 1600 µmol m^{-2} s^{-1} PAR. However, these increases were not statistically significant.

In the DL, SM, and SP species, g_{sw} exhibited a consistent upward trend with increasing levels of PAR. However, the increase from 400 µmol m^{-2} s^{-1} PAR to 1000 µmol m^{-2} s^{-1} PAR was not significant, while the difference became significant when measured under 1600 µmol m^{-2} s^{-1} PAR. Similarly, in the MK species, g_{sw} increased with higher PAR; however, the difference between g_{sw} under 1000 µmol m^{-2} s^{-1} PAR and 1600 µmol m^{-2} s^{-1} PAR was not statistically significant. These results highlight that while stomatal conductance generally responds positively to increased PAR applied, the extent and sensitivity of this response vary across species.

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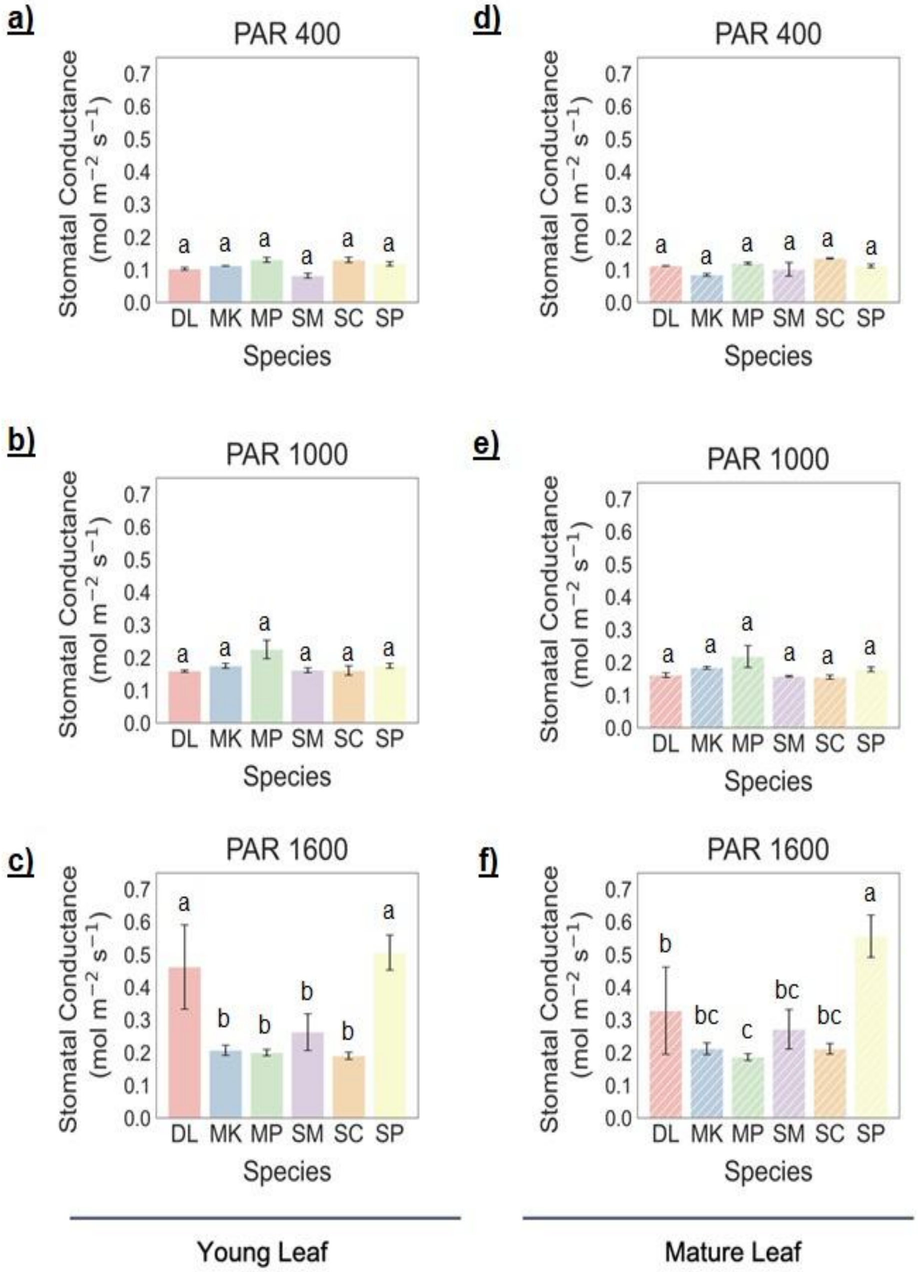

Figure-3. Stomatal conductance of young and mature leaves of six medicinal plants observed in Bogor Botanical Gardens Indonesia, at each level of PAR (a,b,c=young leaves; d,e,f=mature leaves; DL= *Dalbergia latifolia*, MK= *Murraya koenigii*, MP= *Murraya paniculata*, SM= *Swietenia mahagoni*, SC= *Syzygium cumini*, and *SP*= *Syzygium polyanthum*. Groups labeled with the same letter are not significantly different from each other at the specified significance level (α = 0.05).

Interestingly, when stomatal density (SD) was quantified from the young and mature leaf surfaces of all plant species, significant differences were observed among species, with the highest density on SM, followed by MP, DL, SP, SC, and MK, respectively (Figure 4). The observed variation in g_{sw} among species did not consistently correspond with differences in SD. While species such as SM exhibited both high SD and relatively high g_{sw}, others like SP demonstrated comparatively low SD but maintained elevated g_{sw}.

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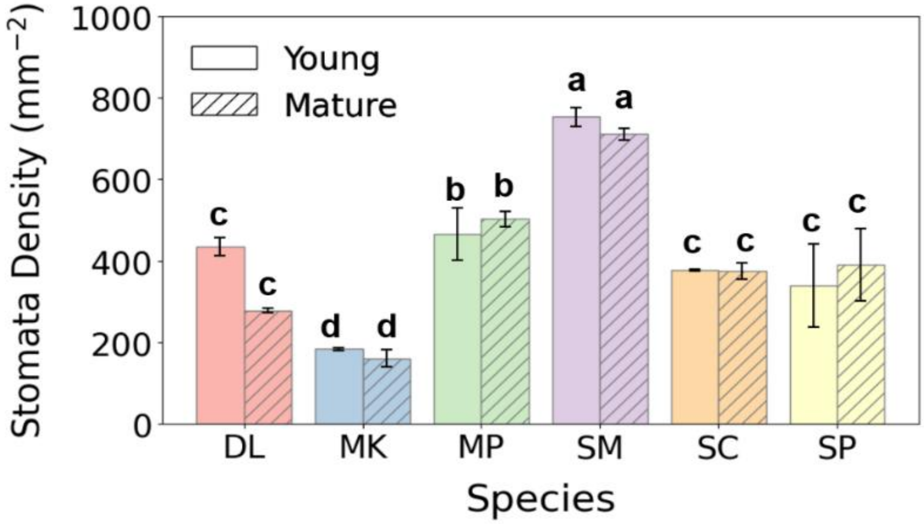

Figure-4. The stomatal density of young and mature leaves of six medicinal plants observed in Bogor Botanical Gardens, Indonesia (DL= *Dalbergia latifolia*, MK= *Murraya koenigii*, MP= *Murraya paniculata*, SM= *Swietenia mahagoni*, SC= *Syzygium cumini*, and SP= *Syzygium polyanthum*. Groups labeled with the same letter are not significantly different from each other at the specified significance level (α = 0.05).

Intrinsic water use efficiency (*iWUE*)

PAR stimulates photosynthetic activity by enhancing CO_2 assimilation, which can influence intrinsic water use efficiency (*iWUE*). Our findings revealed that significant variation in *iWUE* was impacted by species, PAR, and the interaction of species and PAR. The highest *iWUE* value was recorded in SM at 185.71 µmol mol^{-1} under 400 µmol m^{-2} s^{-1} PAR. Under 1600 µmol m^{-2} s^{-1} PAR, both DL (59.59 µmol mol^{-1}) and SP (39.48 µmol mol^{-1}) exhibited significantly lower *iWUE* than other species. However, no significant differences were observed among species under 1000 µmol m^{-2} s^{-1} PAR, both in young and mature leaves (Figure 5a-c). Meanwhile, in mature leaves, *iWUE* differences were not statistically significant under 400 and 1000 µmol m^{-2} s^{-1} PAR, but significantly different under 1600 µmol m^{-2} s^{-1} PAR, with the highest *iWUE* observed in MP (126.38 µmol mol^{-1}). These results suggested that *iWUE* is both species and light-dependent, with young leaves appearing to be more responsive to PAR variation (Figure 5e-f).

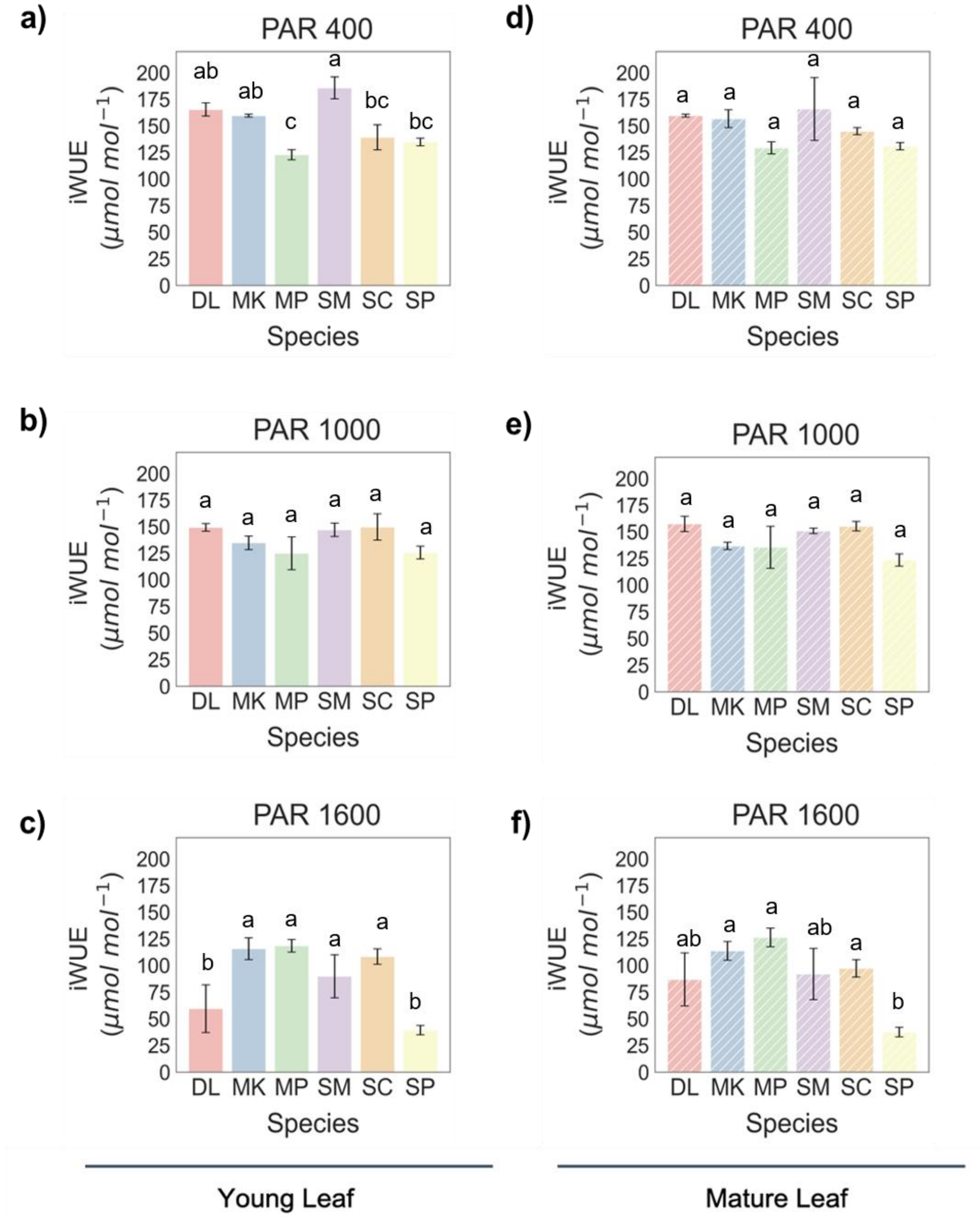

Figure-5. Intrinsic Water Use Efficiency of young and mature leaves of six medicinal plants observed in Bogor Botanical Gardens Indonesia at each level of PAR (a,b,c=young leaves; d,e,f=mature leaves; DL= *Dalbergia latifolia*, MK= *Murraya koenigii*, MP= *Murraya paniculata*, SM= *Swietenia mahagoni*, SC= *Syzygium cumini*, and SP= *Syzygium polyanthum.* Groups labeled with the same letter are not significantly different from each other at the specified significance level (α = 0.05).

Discussion

Our results revealed considerable variation in A, g_{sw}, and *iWUE* among the observed plant species. These findings aligned with those of Davis and Hidayati (2020), who reported significant interspecific differences in the plant's physiological characteristics. Similarly, Hidayati et al. (2013) documented variability in photosynthetic rates among several plant species, such as *Pometia pinnata*, *Garcinia xanthochymus*, *Syzygium polyanthum*, *Syzygium polycephaloides*, and *Palaquium obtusifolium*. The intensity of plant photosynthesis depends not only on

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the characteristics of the species but also on the amount of light entering the leaf surface (Chizhikova and Tishin, 2025).

Both young and mature leaves groups across all six medicinal plant species exhibited higher *A* as PAR increased from 400 to 1000 μmol m^{-2} s^{-1}, followed by a sharper decline at 1600 μmol m^{-2} s^{-1}, most likely due to the plants' limitation in photochemical efficiency (Sun and Wang, 2018). The sharper decline in *A* observed in the young leaves group suggested a lower light saturation point and a potential vulnerability to photoinhibition, in agreement with Zhang et al. (2019). However, *Murraya koenigii* (MK) showed only a minimal decline with no statistical difference at 1600 μmol m^{-2} s^{-1}, suggesting a greater tolerance to high irradiance and adaptability to diverse light environments. In contrast, *Syzygium cumini* (SC) maintained relatively higher *A* under low PAR (400 μmol m^{-2} s^{-1}), indicating a potential shade-adaptive strategy. Previous studies on *Chromolaena odorata* have shown that young leaves experience greater limitations to photosynthesis during induction, driven by both stomatal and biochemical constraints (Zhang et al., 2019). Zhang et al. (2019) also observed a lag between rising light intensity and net photosynthesis, particularly in young leaves, which may rely more heavily on photoprotective responses over carbon gain during photosynthetic induction. Interestingly, our findings revealed no significant difference in *A* between young and mature leaves, contrasting with the general understanding that photosynthetic activity tends to increase with leaf maturation (Nii et al., 1995; Wujeska-Klause et al., 2019). Budiarto et al. (2022) also reported that mature leaves of kaffir lime displayed higher photosynthetic rates than younger ones. This suggests that in the medicinal plants studied here, the leaf developmental stage may play a less pronounced role in photosynthetic performance compared to other species.

In our study, stomatal conductance (g_{sw}) was strongly influenced by both species and PAR intensity, with values generally increasing as PAR increased. In most species, peak g_{sw} occurred at a PAR of less than 1600 μmol m^{-2} s^{-1}; however, in *Murraya paniculata* (MP), g_{sw} declined at high PAR, indicating a slower stomatal response and possible hydraulic limitations. This result is consistent with previous findings in tropical canopy species where g_{sw} was higher in sun-exposed leaves compared to shaded ones (Kitahashi et al., 2008). These results highlight the species-specific stomatal regulatory mechanisms under varying light conditions. Moreover, the observed variation in g_{sw} is also linked to differences in *A*, as gas exchange capacity is closely related to photosynthetic activity (Niinemets et al., 2015). Stomata are the apertures that function as the gate for gas exchange between a plant and its environment. Meanwhile, stomatal density, together with Guard cell length (GCL), influences water-use efficiency and carbon isotope composition in temperate trees, with GCL showing consistent effects within species (Petrík et al., 2024). In this study, SP demonstrated comparatively low stomata density but maintained elevated g_{sw}. This result contrasts with previous findings, which show that an increasing stomatal density may significantly enhance the g_{sw} and leaf photosynthetic rate of *Arabidopsis* (Tanaka et al., 2013).

Although variation in g_{sw} among six medicinal plant species did not consistently align with differences in SD, *Switenia mahagoni* (SM) exhibited both high SD and relatively high g_{sw}, suggesting potential for enhanced *iWUE* under drought conditions. Similarly, studies on mutant rice have also found that high SD is associated with increased g_{sw}, while low SD improves *iWUE* and drought adaptation, underscoring the trade-off between gas exchange capacity and water conservation (Pitaloka et al., 2022). Previous research further supports that to reduce g_{sw}, stomatal responses can be adjusted in sensitivity and magnitude to suit local microclimates, especially in response to spatial and temporal changes in light, by optimizing stomatal size, density, and function across different parts of the canopy (Wang et al., 2022). SD was positively correlated with g_{sw}, *A*, and *iWUE*, while negatively correlated with specific leaf area, suggesting a key role in balancing gas exchange and *iWUE* (Xu and Zhou, 2008). SD was positively correlated with g_{sw}, *A*, and *iWUE*, while negatively correlated with specific leaf area, suggesting a key role in balancing gas exchange and *iWUE* (Xu and Zhou, 2008). It has been well known that higher *iWUE* can increase the establishment and survival of plants under water-deficit conditions and is related to trees' adaptability to drought (Hatfield and Dold, 2019). A relatively low water-use efficiency suggests that the plant has a relatively weak environmental adaptability (Wang et al., 2024). In this study, *iWUE* was observed to be species- and light-dependent; however, under low light, SM also exhibits relatively high *iWUE*, and MP maintains high *iWUE* under high light saturation.

Overall, this study shows how developmental stage and light exposure affect physiological traits. Three constant light PAR values, however, do not adequately capture the dynamic reactions of plants to changing light (Teixeira, 2020). It is important to consider additional environmental factors that impact photosynthesis in natural environments, such as light, temperature, humidity, and soil water status (Nouri et al., 2015). Considering that steady states are uncommon in nature, and irradiance in particular is subject to quick changes. Thus, it is crucial to understand the mechanisms that control the rapid responses of photosynthesis and how the environment influences this process. Future studies should consider long-term growth under a natural ecosystem setting, which will enhance predictive models and cultivation strategies for promoting resilience in the face of climate variability.

Conclusions

This study demonstrated clear interspecific variation in photosynthetic rate (*A*), stomatal conductance (g_{sw}), and intrinsic water-use efficiency (*iWUE*) among six Indonesian medicinal plants under different photosynthetically active radiation (PAR) levels. Species exhibited distinct light adaptations: *Murraya koenigii* showed broad adaptability, while *Syzygium cumini, Dalbergia latifolia,* and *Swietenia mahagoni* were more shade-tolerant. In contrast, *Murraya paniculata* and *Syzygium polyanthum* were better suited to high-light conditions, potentially favoring drier environments due to their higher intrinsic water-use efficiency *(iWUE)*. These results highlight the functional diversity and ecological niche differentiation among medicinal plants, providing a physiological basis for improved cultivation and conservation strategies under variable light environments.

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The authors have used Grammarly and QuillBot for linguistic polishing and proofreading. The AI was not used to generate any scientific content or ideas; the authors retain full responsibility for the integrity of the work.

Contribution of Authors

Astuti IP, Juhaeti T, Cahyaningsih R & Hidayat S: Conceptualization.
Juhaeti T, Husaini IPA, Pitaloka MK & Wardani FF: Data curation.
Wardani FF, Husaini IPA, Juhaeti T & Tyas KN: Formal analysis.
Juhaeti T, Aisyah SV, Hidayat S, Cahyaningsih R, Tyas KN & Hayati AN: Investigation.
Juhaeti T, Husaini IPA & Pitaloka MK: Methodology.
All authors: Roles/Writing – Original draft
Husaini IPA, Juhaeti T, Wardani FF, Pitaloka MK, Cahyaningsih R, Hidayat S, Tyas KN: Writing - review & editing.

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