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Morphoanatomy and physiology of *Swietenia macrophylla* in different light environments: Insights into its invasive ability in the Philippines

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Abstract. *Agoto Jr. RNA, Hernandez JO, Park BB. 2024. Morphoanatomy and physiology of Swietenia macrophylla in different light environments: Insights into its invasive ability in the Philippines. Biodiversitas 25: 257-263.* Evidence supporting *Swietenia macrophylla* G.King's invasive ability is primarily inferential to date. The present study analyzed the variation in morphoanatomical and physiological traits of the species between shaded and sun-exposed environments to provide insights into its invasive ability in the Philippines. The variations in leaf area, seedling height, leaf pH, biomass, parenchyma and collenchyma cell thickness, lumen area of xylem vessels, stomatal conductance, and leaf relative water content were analyzed between shaded and sun-exposed light conditions. While stem and leaf biomass did not differ between the two light conditions, root biomass was 27% higher in the shaded than in the sun-exposed seedlings. Leaf pH was substantially lower in the shaded than in the sun-exposed condition. The vessel lumen area in both leaf and root was significantly larger in shaded than in sun-exposed condition by 10-15%. The parenchyma of seedlings in the shady area of the forest was thicker (c.a., 1-2 layers) compared to those in the well-lit environment, particularly in the leaf and root. While stomatal conductance was similar between the two light environments, shaded ones had a much larger leaf relative water content, up by 9-12%. Overall, we found significant morphoanatomical and physiological variations between shaded and sun-exposed seedlings, indicating invasive species' light-capture strategy and providing insights into *S. macrophylla*'s invasive potential in the Philippines.

Keywords: Big leaf mahogany, biological invasion, freehand technique, parenchyma cell, xylem vessels

INTRODUCTION

Invasive plants are becoming a serious ecological issue because of their rapid growth and efficient reproduction, causing significant economic losses worldwide (Assad et al. 2021; Yang et al. 2022). Industrialization has also resulted in considerable increases in plant introductions to places outside their native range, with many of these introductions being harmless while others causing environmentally damaging invasions (Stricker et al. 2015; Pyšek et al. 2020). Although there has been a recent increase in interest in this topic over the last 10-15 years (Chiu et al. 2023), critical areas of invasive plant research, such as studies on how the morphoanatomical and physiological traits of invasive plants change with varying environmental factors, may be significantly underrepresented. Studying these plant traits is important to understand invasion mechanisms further and provide insights into developing effective control strategies amid a changing environment (Liu et al. 2022).

Successful plant invasion is determined by many biotic and abiotic factors (Funk 2013; Ren et al. 2020; Zhang et al. 2020). Light availability is a major abiotic factor influencing a plant's growth and invasiveness. Invasive plants often exhibit plant traits that allow them to capture and utilize light more efficiently because of their higher adaptability to light settings and, thus, have a more competitive advantage than native plant species (Liu et al. 2022). However, their responses to irradiance can vary by species (Youn et al. 2021). Some invasive species can establish populations easily regardless of light conditions by modifying their shade tolerance and changing structure and composition. Specifically, the morphoanatomical and physiological traits related to plant hydraulics, gas exchanges, and adaptive mechanisms can be used as determinants of a plant's invasive ability (Funk 2013). Plants exhibiting higher traits related to physiology, leaf-area/shoot allocation, growth rate, size, and fitness often become invasive when introduced to new habitats (Moravcová et al. 2015; Rindyastuti et al. 2021). Studies have long demonstrated a strong correlation between biological invasion, phenology, reproductive dispersion traits (e.g., longer fruiting period), and even allelopathy of invasive plants (Moodley et al. 2013; Daly et al. 2023). Higher xylem vessel traits of non-native species have also shown better competitive advantage and less susceptibility to stress than co-occurring native species (Yin et al. 2015). Generally, a positive association between the area and density of metaxylem vessels, growth rate, and hydraulic conductance was also reported in some studies (Hernandez and Park 2022). These anatomical characteristics provide physiological benefits that improve plant performance regarding tolerance, adaptability, and competitive behavior (Perez-Harguindeguy et al. 2013). While morphoanatomical and physiological features have long been recorded in many invasive and potentially invasive plants, field study results have been variable, and no general pattern in the relationship between these traits and invasiveness has been reported.

Plantations of light-demanding *Swietenia macrophylla* G.King (Big-leaf mahogany) have been continuously established in the tropics and neotropics. One of the reasons is the growing demand for wood resources because of its fast growth trait (Pramono et al. 2019; Herrera-Feijoo et al. 2023) and various ecological and economic benefits (Moghadamtousi et al. 2013). Previous studies revealed the ability of the species to grow and survive vigorously in a wide range of environments, even following catastrophic disturbances (Grogan et al. 2014). However, the species can inhibit the growth of other plants under its canopy and negatively affect species diversity, indicating successful bio-invasion (Mukaromah et al. 2016). Results also showed that a thick layer of leaf litter of the species hinders the seedling growth of Philippines native trees (Galano and Rodriguez 2021). However, evidence supporting the invasive potential of *S. macrophylla*, if not lacking, is largely inferential to date. Studies investigating the morphoanatomical and physiological traits of the species in varying environmental conditions can help us understand its invasive potential.

Consequently, the present study analyzed the variation in morphoanatomical and physiological traits of *S. macrophylla* between shaded and sun-exposed environments to provide insights into its invasive ability in the Philippines. We expect that *S. macrophylla* seedlings have unique plant morphoanatomical and physiological traits related to capturing and utilizing light that can explain their invasive potential in the Philippines.

MATERIALS AND METHODS

Study area and experimental plant

Approximately 35-cm high seedlings of *S. macrophylla* were taken from two locations in Mount Makiling Forest Reserve (MMFR) at 490-675 meters above sea level: (i) under the forest canopy, hereafter referred to as shaded, and (ii) forest gap, hereafter referred to as sun-exposed (Baradi and Hernadez 2023; Figure 1). The shaded area has a lower light intensity (i.e., 338 to 815 lux) than the sun-exposed area (i.e., 2610 to 5932 lux). The light intensity (average of 5 readings) was measured using a digital lux meter (S/N: 202006984, 1-2 h before noon in three pre-identified points in each site. Large and mature tree species dominate the shaded area, such as Dipterocarps (e.g., *Shorea contorta* S.Vidal), *S. macrophylla*, *Vitex parviflora* A.Juss., and *Lagerstroemia speciosa* (L.) Pers. The sun-exposed had a canopy gap of about 15 to 20 m in width, with some seedlings of trees, shrubs, and even grasses/weeds growing within it. Moreover, the mean daily air temperature in the study area during the study period was 27.41°C, which was measured using a HOBO data logger.

Procedures

Measurement of morphological traits

In March 2023, young leaf, stem, and root samples were collected from ten healthy seedlings planted under the shaded and sun-exposed areas during dry season. Samples were first stored in a glass container with water to prevent desiccation. The conventional grid count method was used to measure leaf area (n=7) on a 1-cm grid paper by counting grids covered by leaf multiplied by the area of a grid. SLA was calculated by dividing the leaf by the oven-dry mass of the leaves, which were dried at 65°C for 48 hours. The leaf petiole was included in the SLA measurement because it is botanically a part of a leaf and shed at abscission along with the leaf midrib, veins, and blades. Seedling height measurement was done by measuring it from the seedling stem diameter to the highest terminal bud of an orthotropic branch using a meter stick.

Leaf, stem, and root biomass was obtained by oven-drying the samples at 65°C for 48 hours. The entire root system was carefully harvested, cleaned with tap water, and then manually measured the individual lengths of fine and coarse roots. The total root length was determined by adding the length of each seedling's fine and coarse roots. Fresh, healthy leaves were collected from *S. macrophylla* seedlings, washed, and cut into small pieces for pH determination. The leaf extract was obtained using a mortar and pestle. In addition, multiple pH readings were obtained and averaged using a pH meter to acquire a more accurate leaf pH range.

Measurement of anatomical traits

Young leaf, stem, and root anatomical structures of shaded and sun-exposed *S. macrophylla* seedlings (n = 9) were examined through a freehand technique. A 1×1 mm leaf sample was taken from the midsection of the leaf, including the midrib and leaf blades. We took 1-2 mm long stem samples from the orthotropic branches of each shaded and sun-exposed seedling around the 5th node from the highest terminal bud. Only lateral coarse roots measuring 1-2 mm in diameter were evaluated in the present study.

Thin cross-sections of the leaf, stem, and roots (n=4) were then stained with a 5% safranin solution. Under a compound light microscope at 40 magnifications, the staining process was carried out to determine the anatomical tissues in the cross-section easily. The ImageJ processing program was used to measure the layer thickness (mm) of parenchyma and collenchyma cells and the area (μm) of xylem vessels in leaf, stem, and roots (Hernandez and Park 2022).

Measurement of stomatal conductance and relative water content

Healthy seedlings were randomly chosen to be measured for stomatal conductance (g_s, mol m^{-2}s^{-1}) using a hand-held leaf porometer (SC-1, Meter Group, Inc., United States). Daily measurements were obtained between 9:00 a.m. and 12:00 p.m. in the completely grown leaves at the 5-6 node orthotropic branch of *S. macrophylla* seedlings. Finally, 5-7 leaves were harvested to determine leaf Relative Water Content (RWC) using the procedures described in Jimenez et al. (2013). Petioles were soaked in water overnight, weighed again to acquire the Turgid Mass (TM), then oven-dried at 65°C for 48 hours. The RWC was then calculated as (FM - DM)/(TM - DM) × 100.

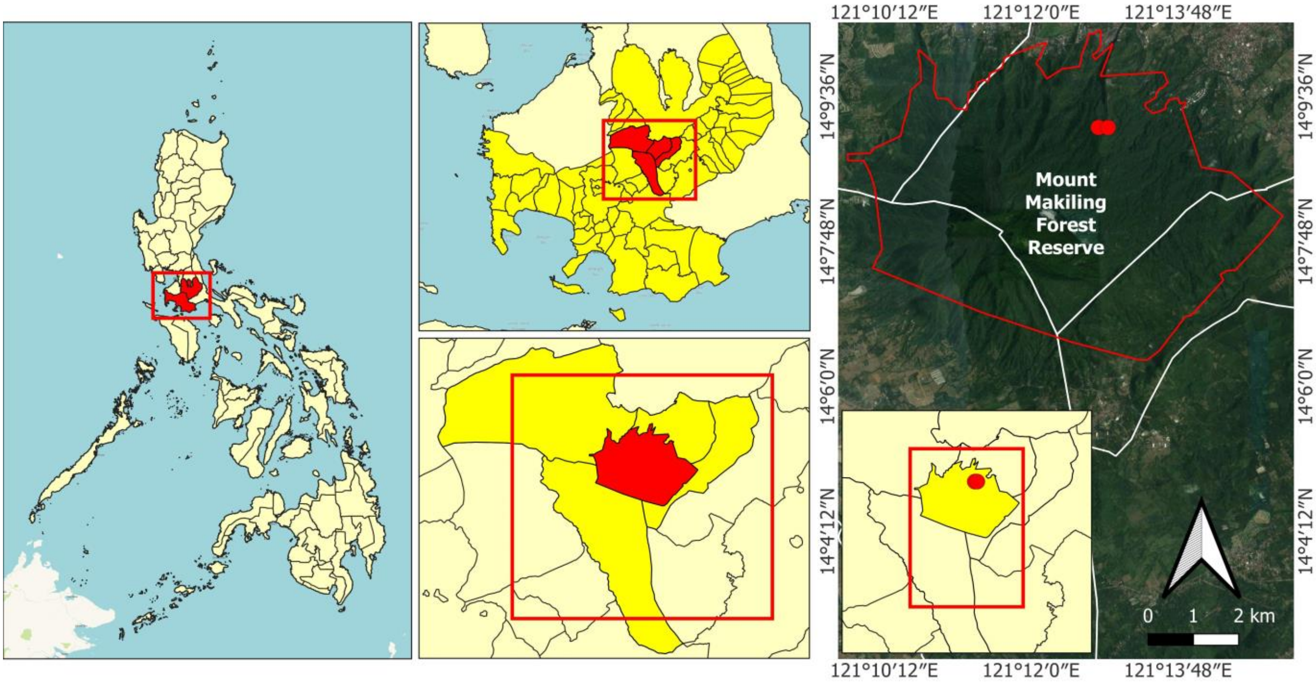

Figure 1. Location of the study site (red dot) where shaded (14° 9'13.16"N, 121°12'49.57"E) and sun-exposed (14° 9'13.07"N, 121°12'56.62"E) seedlings of *Swietenia macrophylla* were selected. Source: Makiling Center for Mountain Ecosystems (MCME), https://makiling.center/mt-makiling-maps/

Data analysis

The "Shapiro test" was used to analyze the normal distribution of the data. Significant differences in the thickness of parenchyma and collenchyma cells and the area of xylem vessels in leaf, stem, and root, as well as stomatal conductance and leaf relative water content between shaded and sun-exposed seedlings, were investigated using a one-way ANOVA. All statistical tests were carried out in R (version R-3.5.1), with a significance threshold of $\alpha = 0.05$.

RESULTS AND DISCUSSION

Morphoanatomical traits

The morphological traits of *Swietenia macrophylla* varied significantly between sun-exposed and shaded light conditions (Table 1). While stem and leaf biomass did not vary between light conditions, the root biomass was significantly higher by about 27% at shaded than in sun-exposed seedlings. A similar pattern was observed in total root length, i.e., shaded (47.09) > sun-exposed (29.51 cm). Our results contradict those of Youn et al. (2021), who observed that plants responded to shading by reducing allocation to root biomass while increasing allocation to leaf and stem. This suggests that roots of *S. macrophylla* are specialized to exploit deep shade. Such a characteristic exemplifies drought tolerance. This could also explain the ability of *S. macrophylla* to thrive in a wide range of environmental conditions, resulting in its invasiveness in certain regions (Coracero 2023). Root dynamics and behavior of many plants would change in response to shade or poor nutrient availability (Qi et al. 2019). *S. macrophylla* must balance the allocation to aboveground and belowground organs to meet the physiological demands, which generally depend on prevailing environmental conditions. Abiotic stress responses and water use efficiency of forest tree seedlings are improved in deep layers by an increased allocation to belowground biomass or leaf tissue production as a strategy to obtain limiting resources in different environments (Zhu et al. 2023).

While the leaf area did not vary between the two light conditions, the Specific Leaf Area (SLA) was significantly higher at shaded than sun-exposed seedlings (Table 1). This partly explains why the leaf biomass did not vary significantly between shaded and sun-exposed conditions. Such a pattern in SLA is expected in plants growing in areas characterized by low light availability as an adaptive response known as shade tolerance (Utari et al. 2023). Shaded seedlings of *S. macrophylla* may have invested in producing larger but thinner leaves to capture as much light as possible, resulting in higher SLA because of lower leaf mass per unit area. On the other hand, sun-exposed seedlings may have allocated more carbon to developing thicker leaves to strengthen structural stability in a well-lit environment. Moreover, the leaf pH was significantly more acidic in the shaded condition (i.e., 4.11) than in the sun-exposed condition (i.e., 6.12). The result is expected because of several factors, such as limited photosynthesis and changes in microenvironment and osmotic balance within and around leaves. Reduced light availability at shaded conditions may have decreased the rate of photosynthesis. Thus, the production of sugars and other organic compounds may have also decreased, which resulted in an accumulation of organic acids within the leaf.

The species' root, stem, and leaf anatomical traits also varied between sun-exposed and shaded light conditions (Figures 2-7). In both leaf and root, the vessel lumen area was significantly larger in shaded than in sun-exposed condition by about 10-15%, and a reverse pattern was found in the stem. The results suggest that the species adapt to shaded conditions, shedding light on its rapid seedling establishment even under a closed canopy. Seedlings in shaded conditions generally have poor photosynthetic activity, resulting in an excess water supply or a higher soil moisture level (Lee et al. 2023). Shaded *S. macrophylla* seedlings may have invested in producing larger vessels to cope with excessive soil water supply and enhance water transport efficiency (Hernandez and Park 2022). This further explains why shaded seedlings of *S. macrophylla* grew taller even in shaded areas. Increasing height necessitates mechanical support, which larger vessels can give to improve structural stability. Further, we may deduce that the species had higher root-specific hydraulic conductance because of larger vessels (Zadworny et al. 2018). Such a characteristic is particularly important for long-distance water movement (Boursiac et al. 2022).

The parenchyma of seedlings in shaded areas was thicker (c.a., 1-2 layers) than in sun-exposed conditions, particularly in leaf and root. Such a result can be attributed to the influence of different adaptive responses of *S. macrophylla* to low light conditions. Plants adapt in locations with low light by increasing leaf area with thicker parenchyma layers, which may house a greater number of chloroplasts, enhancing photosynthetic efficiency. Thicker parenchyma in leaves can make the most of the available light resources. In roots, it can also help maximize water absorption by expanding water storage spaces in the cortical layer, as shaded environments typically have more competition for resources among plants. Further, thicker parenchyma layers in the leaf and root suggest that *S. macrophylla* seedlings remained metabolically active even in shaded environments. Parenchyma cells perform various metabolic functions, including storage and synthesis of secondary metabolites and other compounds supporting plant growth and survival in shaded conditions (Ma et al. 2023). A different pattern was observed in the stem (i.e., sun-exposed > shaded condition). The result can be attributed to the unique functions of the leaf, stem, and root in response to varying light conditions. Stems, for example, serve an important function in water transport between roots and leaves; thus, they may require more structural support in thickened parenchyma cells to resist breaking in response to competition with nearby plants.

Further, the collenchyma in shaded seedlings was significantly thicker by 14-18% compared with sun-exposed ones in the leaf, stem, and root of *S. macrophylla*. This variation can be linked to the species' adaptation response to low-light environments, which increase the structural and mechanical strength of the leaf, stem, and roots (Cioć and Pawłowska 2020). Such a structural improvement can help shaded seedlings maintain an upright growth, as collenchyma cells are generally known for their flexibility across various environmental conditions. Because shaded seedlings must optimize light capture, such flexibility is crucial in the species' compensatory development strategies (Martinez-Garcia et al. 2023).

Table 1. Root, stem, and leaf morphological traits of sun-exposed and shaded seedlings of *Swietenia macrophylla* in Mount Makiling Forest Reserve. Different lowercase letters indicate significant differences between the two light conditions. Values in parenthesis indicate standard errors (n =9)

Morphological traits	Light conditions	
	Sun-exposed seedlings	Shaded seedlings
Root		
Dry biomass	135.57±1.44^{b}	186.03±2.12^{a}
Total root length (cm)	29.51±1.07^{b}	47.09±1.81^{a}
Stem		
Height	22.15±1.21^{b}	36.25±1.15^{a}
Dry biomass	165.72±2.14^{a}	170.23±1.19^{a}
Leaf		
Area	12.33±1.01^{a}	14.91±1.22^{a}
Specific leaf area	68.56±1.01^{b}	82.95±1.05^{a}
Dry biomass	115.12±1.21^{a}	116.09±1.12^{a}
pH	6.12±0.06^{a}	4.11±0.06^{b}

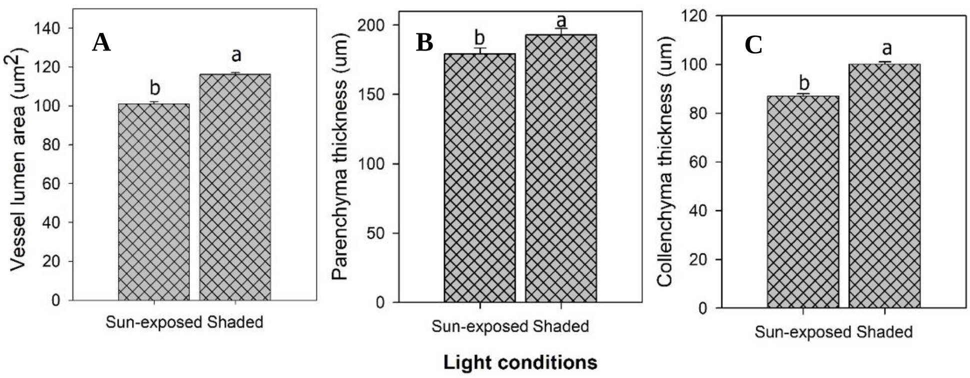

Figure 2. A. Vessel lumen area, B. Parenchyma thickness, and C. Collenchyma thickness of sun-exposed and shaded leaves of *Swietenia macrophylla* seedlings in Mount Makiling Forest Reserve. Different lowercase letters indicate significant differences between the two light conditions

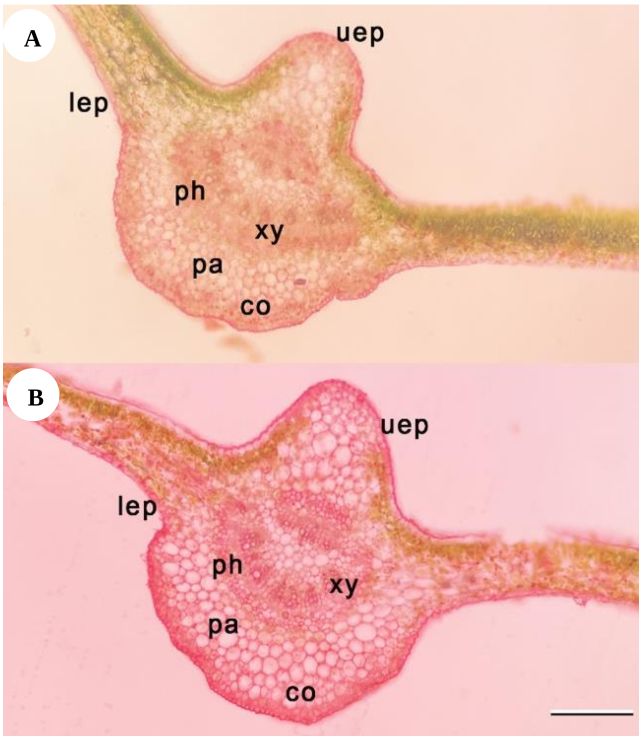

Figure 3. Leaf anatomy of: A. Sun-exposed and B. Shaded seedlings of *Swietenia macrophylla* in Mount Makiling Forest Reserve. Note: uep: Upper epidermis, lep: Lower epidermi, ph: Phloem, xy: Xylem, pa: Parenchyma, and co: Collenchyma

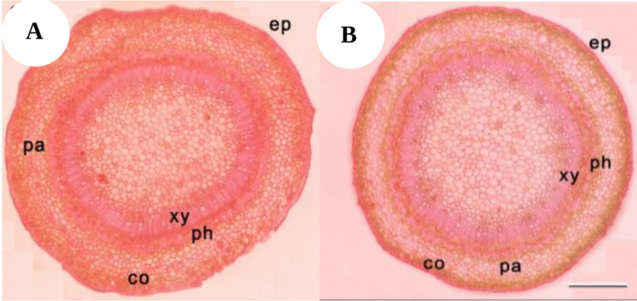

Figure 5. Stem anatomy of: A. Sun-exposed and B. Shaded seedlings of *Swietenia macrophylla* in Mount Makiling Forest Reserve. Note: ep: Epidermis, ph: Phloem, xy: Xylem, pa: Parenchyma, and co: Collenchyma

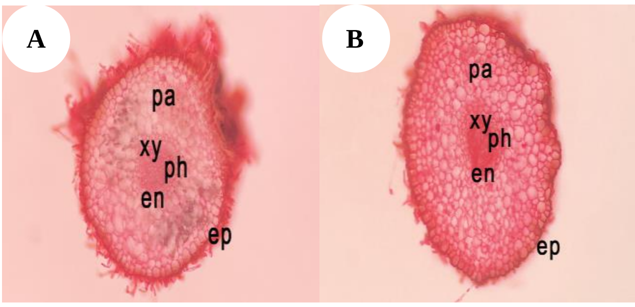

Figure 7. Root anatomy of: (A) Sun-exposed and (B) Shaded seedlings of *Swietenia macrophylla* in Mount Makiling Forest Reserve. Note: ep: Epidermis, ph: Phloem, xy: Xylem, pa: Parenchyma, and co: Collenchyma

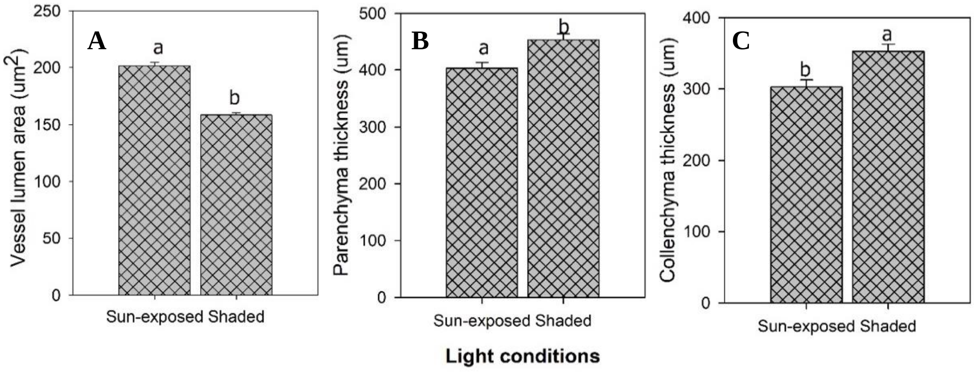

Figure 4. A. Vessel lumen area, B. Parenchyma thickness, and C. Collenchyma thickness of sun-exposed and shaded stems of *Swietenia macrophylla* seedlings in Mount Makiling Forest Reserve. Different lowercase letters indicate significant differences between the two light conditions

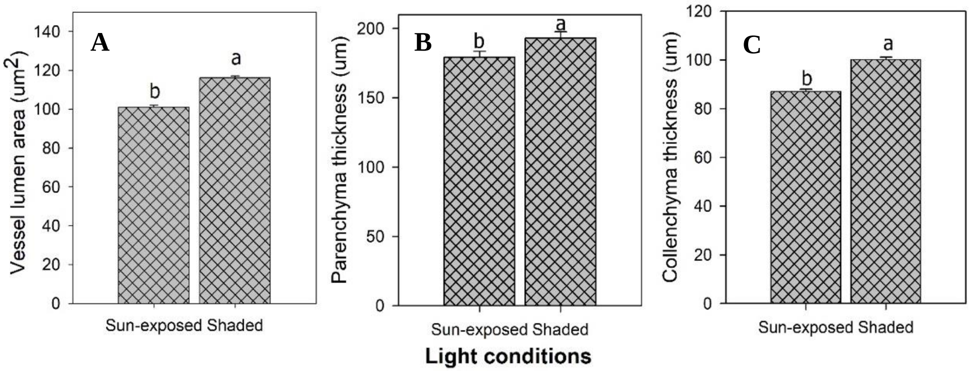

Figure 6. A. Vessel lumen area, B. Parenchyma thickness, and C. Collenchyma thickness of sun-exposed and shaded roots of *Swietenia macrophylla* seedlings in Mount Makiling Forest Reserve. Different lowercase letters indicate significant differences between the two light conditions

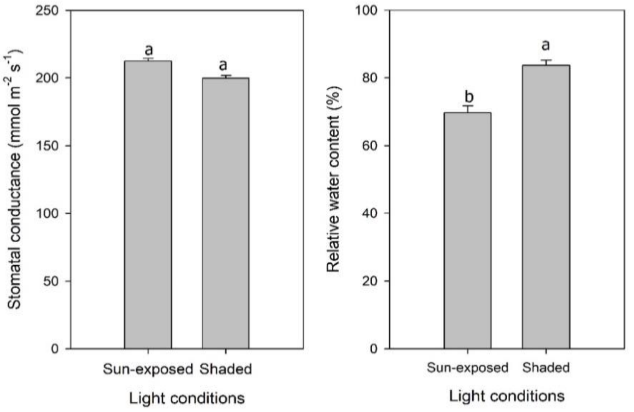

Figure 8. A. Stomatal conductance and B. Leaf relative water content of sun-exposed and shaded seedlings of *Swietenia macrophylla* in Mount Makiling Forest Reserve. Different lowercase letters indicate significant differences between the two light conditions

Physiological traits

In this study, the stomatal conductance of sun-exposed and shaded seedlings of *S. macrophylla* was similar, although it tended to be smaller in shaded conditions (Figure 8). Results can be attributed to adaptation to water availability and acclimation to shaded environments (Medina et al. 2014). Despite limited light availability, shady locations may have increased soil moisture due to lower evaporation. This shows that the species can optimize or ensure stomatal conductance across varied light conditions as an adaptation strategy. This implies that the species' seedlings may not require extensive modulation of stomatal conductance since they can maintain internal microclimate conditions for gas exchange even in the shade (Forero-Montaña et al. 2021). Further, a similar stomatal conductance between shaded and sun-exposed seedlings might also be attributed to the two light regimes having a similar leaf area. If the leaf area in both light conditions is similar, the seedlings may maintain a consistent stomatal conductance to ensure an adequate supply of CO_2 for photosynthesis regardless of light conditions. This trait could be interpreted as an adaptive response of *S. macrophylla* for ensuring resource efficiency by maintaining internal osmotic balance. This ensures that transpiration and photosynthesis rates are proportionate (Yang et al. 2021), preserving physiological homeostasis.

We found a significantly higher leaf relative water content in shaded seedlings than the sun-exposed ones by 9-12%, ascribed to varying microclimatic conditions caused by these different light regimes (Figure 8.B). Shaded habitats have lower light intensity, temperature, and evaporative demand than sun-exposed ones, reducing transpiration rates, atmospheric water vapor pressure deficit, and higher water retention in their leaves. A higher leaf relative water content also supports the larger xylem vessel area observed in the leaves and roots of shaded seedlings of *S. macrophylla.* Water transport from roots to leaves may have been more efficient in larger xylem vessels than in smaller ones, and such an efficiency may have contributed to higher leaf water content. Results suggest that shaded seedlings of *S. macrophylla* may exhibit efficient hydraulics or water movement from the soil to the leaves. This explains the species' ability to thrive under forest canopy and open degraded lands characterized by harsh environmental conditions. This makes *S. macrophylla* the most used reforestation tree species in the Philippines as early as 1911 (Coracero 2023).

In conclusion, the present study investigated for the first time the morphoanatomy and physiology of *S. macrophylla* in shaded and sun-exposed environments in Mount Makiling Forest Reserve, Philippines. Here, we discovered substantial differences in morphoanatomical and physiological traits between shaded and sun-exposed *S. macrophylla* seedlings. These plant characteristics were typical of invasive species' strategies for capturing and exploiting light. However, further comparison studies will be required to determine what distinguishes *S. Macrophylla* in its invasiveness in terms of morphoanatomy and physiology. The findings of this study shed light on the invasive potential of *S. macrophylla* and the invasion mechanisms of other invasive species in the Philippines. To have a better knowledge of *S. macrophylla's* invasiveness, further studies should be conducted into additional aspects contributing to its invasive ability, specifically its reproductive traits and allelopathic interactions.

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