

Adaptability of Siamese Rosewood and Teak Seedlings to Varying Light Conditions

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ABSTRACT

Rosewood and Teak are valuable timber species, which have been heavily logged from both natural forests and plantations. Climate change has also contributed to a reduction in their numbers. We studied their light adaptability at the seedling stage to quantify the growth and physiological characteristics under 10% and 100% of full sunlight. Rosewood performed better, as indicated by the relative growth rate, chlorophyll content, and chlorophyll efficiency, under both shade and sunlight. We also simulated a sudden change in light intensity (gap opening up in the canopy) by exposing seedlings, previously under shade, to full sunlight. Rosewood seedlings responded faster (higher relative growth rate) to changing light conditions relative to Teak. We conclude that Rosewood seedlings can be planted either under shade, or in full sunlight, or in a location experiencing sudden change from shade to sunlight, while Teak seedlings should be planted under at least 10% sunlight, but not in full sunlight, as it can lead to chlorophyll and tissue damage.

1. INTRODUCTION

Siamese Rosewood (hereafter; Rosewood) (*Dalbergia cochinchinensis* Pierre ex Laness.), which is a dominant species in dry evergreen forests, and Teak (*Tectona grandis* L.f.), are commonly found in mixed deciduous forests of Thailand (Santisuk et al., 2018). Given the red and golden finishing of furniture derived from Rosewood and Teak, respectively, they are highly sought after hardwoods in the global market, resulting in excessive illegal logging (Aerts et al., 2009), especially of Rosewood. Appendix II of the Convention on International Trade of Endangered Species (CITES) states that Rosewood has been threatened with extinction and requires rigorous monitoring and regulation (Siriwat and Nijman, 2018).

Planting native species can help to diversify impoverished forests, attract seed-dispersing animals and assist natural regeneration (Elliott et al., 2003; Wydhayagarn et al., 2009). Using valuable timber species for restoration can serve both conservation and economic purposes. Being a leguminous tree, Rosewood is likely to form a symbiotic association with nitrogen fixing bacteria (Seemakram et al., 2021). It can also improve the soil chemical properties in

degraded sites, as its fast decomposing litter is rich in nitrogen, phosphorus, and organic carbon (Maikhuri et al., 2000; Mishra et al., 2003; Banerjee et al., 2004; Piotta et al., 2004). Teak is considered for the restoration of hydrological services (FAO, 2006) and to improve soil hydraulic properties (Mapa, 1995; Udayana et al., 2019). Moreover, Teak can be used as a shading tree in coffee plantations due to its large leaf area and high litter yield for soil humus (Khusnul et al., 2021).

Restoration of natural forests or plantations requires specific knowledge about the environmental factors affecting the growth, especially light conditions (Popma and Bongers, 1988). Leaf photosynthesis requires sufficient quantity and quality of light, with the under-story receiving less than optimal light (Rahman et al., 2021). Under natural propagation, seedlings grow under canopy until the older trees are cut down or die of natural causes (Snook et al., 2021), allowing light to penetrate through. A spurt in growth would guarantee that a tree dominates the gap and possibly ensure reproduction. Abrupt changes in light conditions can alter seedling performance in terms of successional status and wood

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traits, like wood density (Turnbull et al., 1993; Yamashita et al., 2000).

At low intensities, increase in light intensity causes an increase in the rate of photosynthesis, but the rate later reduces as an asymptotic maximum is reached (Singh and Singh, 2003; Fan et al., 2013). Most canopies are unable to reach the photosynthetic light saturation levels due to varying orientations and leaf shading (Zotz and Winter, 1993). It has been reported that Rosewood has the greatest growth under high light intensity (75-100%) (Phonguodume et al., 2012). While Teak requires a light intensity between 50-75% for optimum growth and development (Kadambi, 1972; Nwoboshi, 1972) and recently, Moonchun et al. (2017) reported an optimum growth of Teak seedlings between 40-80% of full sunlight. However, none of studies reported observations about a sudden light change from shade to full sunlight due to a gap opening or while transferring plants, growing in shade of a nursery, for transplantation to full sunlight conditions in the field.

Kenzo et al. (2008) reported leaf ecophysiological response and height of trees affected by different canopy size openings in a degraded tropical secondary forest. It is important to determine species-specific light conditions to ensure a successful establishment of seedlings in degraded forests or plantations. We used various measurements including relative growth rate, stomatal conductance,

chlorophyll content, and chlorophyll efficiency to determine the adaptability of Rosewood and Teak seedlings to 10% (under-story) and 100% intensity relative to full sunlight. Additionally, we also simulated a canopy opening scenario under which the seedlings experienced a sudden change from shade to full sunlight.

2. METHODOLOGY

2.1 Seedling preparation

Rosewood and Teak seedlings were purchased in December 2014. Although their exact age was not documented by the nursery, the seedlings were all planted during the same year. The diameter at breast height (DBH) was measured between 0.40-0.55 cm, while their height was between 32-36 cm. Seedlings were transplanted into black plastic pots filled with garden soil and coconut fibre and fertilized with 200 g of slow releasing fertilizer (14-14-14 Osmocote Suffolk, UK). The pots were placed at the Faculty of Forestry, Kasetsart University, Bangkok, for a month before the experiment began, to acclimatize them to the conditions. The temperature during the year (February 2015 to January 2016) was between 27.5-32.5°C, while the relative humidity fluctuated between 52 and 68%. The vapor pressure deficit ranged between 1.8 and 3.2 kPa (Figure 1(a)) with the average daylight intensity measured between 20,000 to 120,000 Lux (Figure 1(b)).

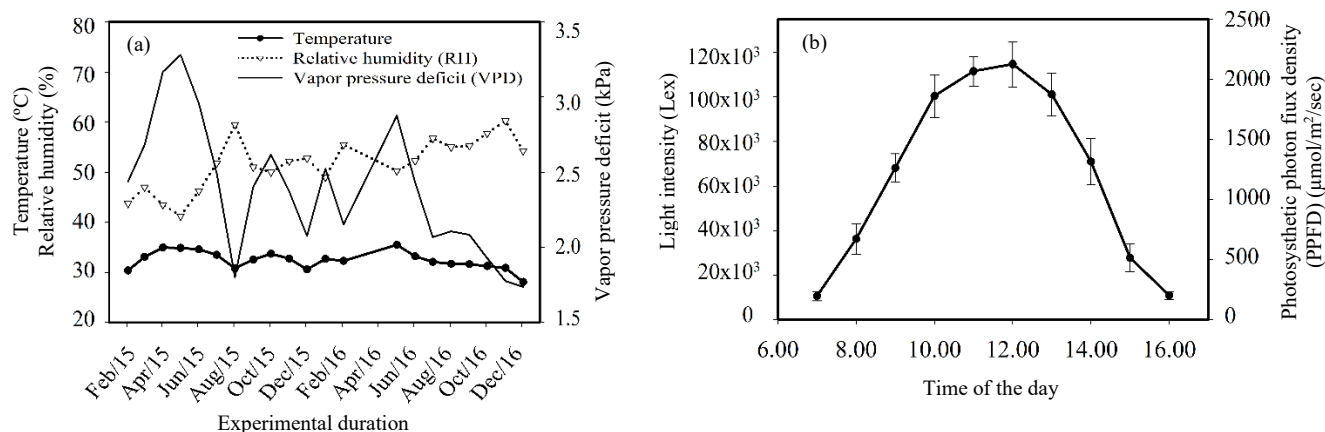


Figure 1. Weather data during the experiment; (a) temperature (solid line with closed circle), relative humidity (dotted line with triangle), and vapor pressure deficit (solid line) (b) average hourly light intensity at full sunlight (100%) over a day and photosynthetic photon flux density (PPFD).

2.2 Experimental treatments

2.2.1 Seedling response under full sunlight and shade conditions

The experiment was conducted for one year from February 2015 to February 2016, with the

seedlings divided into two treatment groups and seven random pots acting as replicates for each treatment. Full sunlight (100% sunlight; sun) and shade conditions (10% of full sunlight; shade) were the treatments. Seedlings were randomly placed in a

nursery of dimensions 1.5 m×2 m×3 m under each treatment, creating a split plot design (no replications of light intensity levels were done due to limited space).

The shaded area was covered with a black cloth preventing the penetration of ~90% sunlight. The ambient light conditions were measured through three light sensors (HOBO UA002-64, Onset Computer Corporation, Bourne, MA, USA) at a height of 1.50 m, every minute for three days prior to beginning the experiment. The light intensity in shade was $10.16 \pm 0.45\%$ relative to that under full sunlight. All the seedlings were irrigated with a sprinkler system programmed to water every other day between 6 am to 7 am, to ensure sufficient soil and air moisture.

2.2.2 Relative growth rate measurements

Relative growth rate (RGR) was determined using the measurements of diameter, height, and leaf number. Diameter at root collar (DRC) was measured at the edge height of a plastic pot with a Vernier calliper. Height was measured from the edge of a pot to the top of a seedling, while mature leaves were counted for each seedling. The RGR was then calculated per month using the equation;

$$\text{RGR (\%)} = \frac{\ln(G_2) - \ln(G_1)}{\text{time duration}} \times 100, \quad (1)$$

Where; G_2 is either the diameter, height, or leaf number measured at the end of experiment (February 2016); and G_1 is either the diameter, height, or leaf number measured at the beginning of experiment (February 2015).

2.2.3 Physiological measurements

All the physiological measurements were taken one time every month for 12 months from February 2015 to February 2016. Plant replications were accomplished by using seven plots for each treatment (shade and sunlight).

Stomatal conductance (G_s), chlorophyll content (CC), and chlorophyll efficiency (Fv/Fm) were also measured. G_s was measured around midday from 11 am to 2 pm (when the light intensity and air temperature was the highest during the day; Figure 1(b) with a Porometer (Decagon Device Inc., WA, USA). A mature expanded leaf from each plant was used to measure the listed parameters (7 replicates/month). CC and Fv/Fm was measured from predawn to early morning (5.30-7.00 am), to avoid excessive radiation stress during the day. Five different locations

were chosen on two mature expanded leaves, to measure CC with an SPAD meter (Model SPAD-502, Konica Minolta, Inc., Japan). Two mature expanded leaves were chosen to measure Fv/Fm using a chlorophyll fluorometer (Model OS-30p+, Opti-Sciences, Inc., Hudson, NH, USA). Two sliding clips were attached to each chosen leaf and left for 15 min for the leaf to adapt to the ambient dark lighting condition before the measurement.

2.2.4 Leaf-to-air vapor pressure deficit measurement

Leaf-to-air vapor pressure deficit (LAVPD) is the difference between vapor pressure of leaf and air and indicates the strength of driving force needed for transpiration. LAVPD is calculated using the equation;

$$\text{LAVPD} = e_{\text{leaf}} - e_{\text{air}} \text{ (kPa)}, \quad (2)$$

Where; e_{leaf} and e_{air} are the leaf and air vapor pressures, respectively.

$$\text{Vapor pressure (e)} = 0.61121 \exp \left[\frac{17.502T}{240.97+T} \right] \times \text{RH}, \quad (3)$$

Where; T is the temperature in Celsius and RH is relative humidity in %.

For e_{leaf} , T is the leaf temperature, which was measured at the same time when G_s was measured every month. RH of leaf is assumed to be close to 100%.

While e_{air} , T is air temperature which was measured at the weather station located 2 km away from study site on the same day when G_s was measured. RH was also measured from the same weather station.

2.2.5 Shade seedlings exposed to full sunlight

The response of Rosewood and Teak seedlings, growing in the understory for a year, was measured when they were suddenly exposed to full sunlight, simulating a gap opening up in the canopy. We used the seedlings (previously under shade for 1 year) for this experiment and exposed them for 9 months (March 2016 to December 2016) to 100% sunlight by removing the shade cloth. Seedlings were acclimatized for 3 months prior to the measurement during May 2016 to December 2016 (6 months). The same procedural steps used in the experiment sun vs. shade were followed to estimate the seedling growth.

2.3 Statistical analysis

The mean difference in relative growth and physiological parameters was analyzed through analysis of variance (ANOVA) with a pairwise test using least square difference (LSD). For the sun vs. shade experiment, a two-way split plot factorial design with two main factors was analyzed. The factors were the species (Rosewood and Teak) and light treatments (sun and shade conditions) with seven replicates (plants). Scatter plots with trend lines between LAVPD and G_s were created to determine the seedling behaviour over a range of driving force causing transpiration. For the shade to light experiment, a t-test was used to test the significance of the mean differences between the species.

3. RESULTS

3.1 Seedling response under full sun and shade

RGR was compared between sun and shade conditions for the two species. The relative diameter had no interaction difference between species and light conditions (Table 1). Only the light conditions had a statistically significant difference on the growth rate of diameter, with the plants under sun having a larger diameter compared to those under shade ($p < 0.001$) (Figure 2(a) and Table 1). Relative height had no significant interaction difference between the species and light conditions. Rosewood grew taller

than Teak ($p < 0.05$) and seedlings kept under shade tended to have a relatively shorter height ($p < 0.001$) (Figure 2(b) and Table 1). The relative leaf number followed a trend similar to relative height (Figure 2(c) and Table 1).

Physiological measurements, including G_s , CC, and Fv/Fm, are closely related to tree growth and development. Light is an important factor influencing the opening and closing of stomata. An open stomata increases the chances of CO₂ uptake, resulting in photoassimilation. Simultaneously, open stomata would help dissipate heat through transpiration. In this study, G_s was higher for Teak, both under sun and shade (Figure 2(d), Table 2). Both species are likely to be light-demanding, resulting in higher number of open stomata at higher light intensities. Chlorophyll is a key organelle for photosynthesis, with higher levels tending to increase food production. CC for both the species was higher for seedlings under shade compared to full sunlight (Figure 2(e), Table 2). For photosynthesis, both the quantity and quality of chlorophyll is important. Fv/Fm can also be used to indicate plant stress under different light conditions. Both species had no statistical difference in Fv/Fm, but this differed under each light treatment (Figure 2(f), Table 2). Seedlings under shade had a higher Fv/Fm than those in full sunlight.

Table 1. Analysis of variance (ANOVA) for RGR in rosewood and teak seedlings with the respective p-values.

Sources	DF	Sum square	Mean square	F-value	p-value
Diameter					
Species	1	0.0001613	0.0001613	2.256	0.146
Light	1	0.0030437	0.0030437	42.581	<0.0001***
Species × Light	1	0.0000004	0.0000004	0.006	0.939
Residuals	24	0.0017155	0.0000715	-	-
Height					
Species	1	0.000971	0.000971	5.573	0.027*
Light	1	0.001947	0.001947	11.176	0.003**
Species × Light	1	0.000441	0.000441	2.534	0.124
Residuals	24	0.004180	0.000174	-	-
Leaf number					
Species	1	0.001969	0.001969	4.366	0.047*
Light	1	0.006841	0.006841	15.171	0.0001***
Species × Light	1	0.000000	0.000000	0.0000	0.989
Residuals	24	0.010822	0.000451	-	-

* indicate significant differences at 95% while, ** indicate significant differences at 99%, and *** significant differences at 99.99% indicate confidence level.

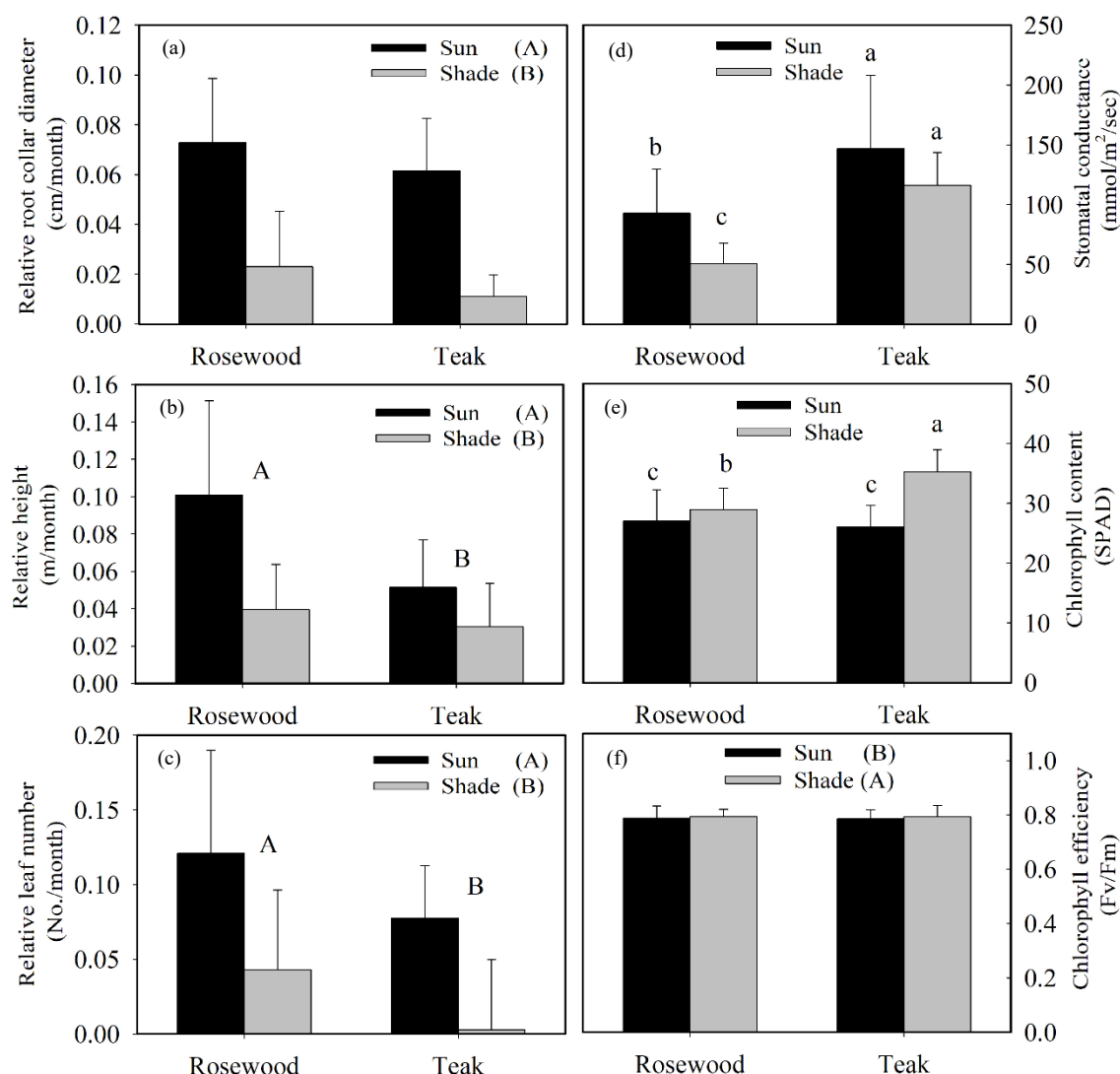


Figure 2. Relative growth (a-c) and physiological characteristics (d-f) of Rosewood and Teak seedlings. On the left panel; (a) relative diameter, (b) height, and (c) leaf number and on the right panel; (d) G_s , (e) CC, and (f) F_v/F_m for seedlings under sun (100%) and shade (10%) for 1 year (February 2015 to February 2016). The letters indicate a significant statistical difference (see Tables 1 and 2). The UPPERCASE letters indicate that only the main factor is statistically different while a lowercase lettering indicates that the interaction between the main factors is significantly different.

Table 2. Analysis of variance (ANOVA) for the relative physiological characteristics in rosewood and teak seedlings.

Sources	DF	Sum Square	Mean Square	F-value	p-value
G_s					
Species	1	3.0101	3.0101	129.150	<0.0001***
Light	1	0.5886	0.5886	25.252	<0.0001***
Species x Light	1	0.1924	0.1924	8.254	0.005**
Residuals	103	2.4006	0.0233	-	-
CC					
Species	1	616.9	616.9	39.78	<0.0001***
Light	1	1573.1	1573.1	101.44	<0.0001***
Species x Light	1	600.1	600.1	38.70	<0.0001***
Residuals	192	2977.6	15.5	-	-

* indicate significant differences at 95% while, ** indicate significant differences at 99%, and *** significant differences at 99.99% indicate confidence level.

Table 2. Analysis of variance (ANOVA) for the relative physiological characteristics in rosewood and teak seedlings (cont.).

Sources	DF	Sum Square	Mean Square	F-value	p-value
Chlorophyll efficiency (Fv/Fm)					
Species	1	0.00015	0.00015	0.299	0.584
Light	1	0.00222	0.00222	4.579	0.032*
Species x Light	1	0.00001	0.00001	0.014	0.905
Residuals	529	0.25691	0.00048	-	-

* indicate significant differences at 95% while, ** indicate significant differences at 99%, and *** significant differences at 99.99% indicate confidence level.

The response of G_s to atmospheric demand, as indicated by LAVPD, is presented in Figure 3. G_s as a function of LAVPD was different between the species and light conditions with Rosewood having a linear and Teak having a curvilinear response. This indicates that G_s of Teak could be more sensitive to air dryness, with a higher reduction in G_s when elevated LAVPD. Under shade, LAVPD was low (1-3 kPa) while in sunlight, LAVPD was high, as indicated by values ranging between 1 to 12 kPa. G_s of Rosewood under sunlight had a weak linear relationship (negative slope) with LAVPD, while the response in shade increased linearly (positive slope). In other words,

seedlings under shade readily opened more stomata when air was slightly drier while the seedlings under full sunlight tended to close their stomata when the air was drier. However, the variation in G_s of Teak under both the light conditions followed a power law. For seedlings in shade, G_s responded weakly to LAVPD below 2 kPa and decreased rapidly thereafter (Figure 3(b)). Comparatively, after an initial rapid decrease in G_s for LAVPD values between 2-4 kPa, the relationship was weak thereafter. We conclude that Teak seedlings are relatively more sensitive to LAVPD, as evident by a rapid response to small changes in air vapor pressure.

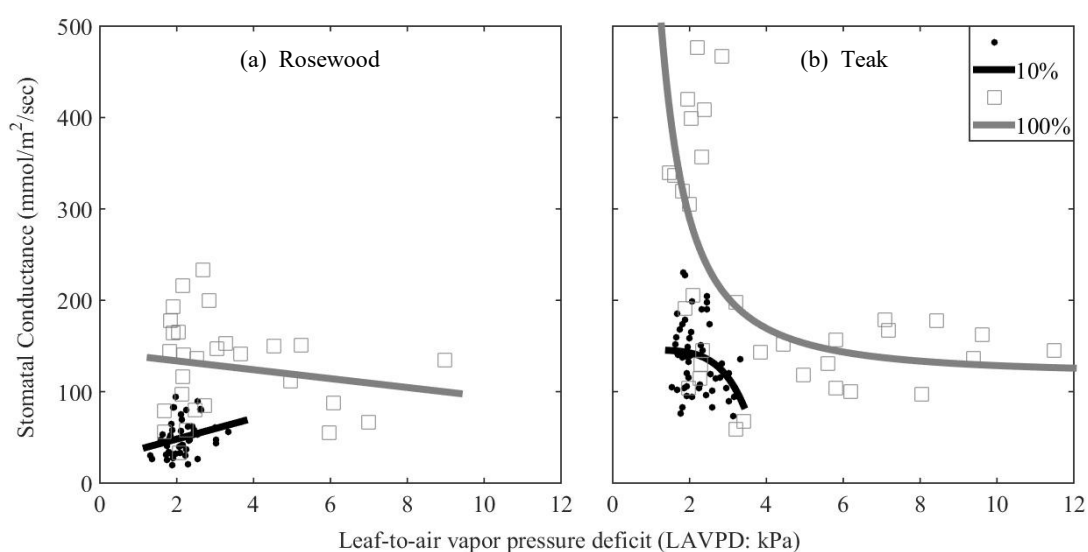


Figure 3. G_s response to LAVPD of seedlings exposed to full sunlight (open-squares with grey solid line) and those under shade (black dots with black solid line) of (a) Rosewood and (b) Teak. The trend lines indicate the differences in behaviour of both the species, with Rosewood having a linear response compared to a non-linear response in Teak.

3.2 Seedlings suddenly exposed to full sunlight after 1 year

With regards to seedling establishment (forest or plantation), a sudden change in light conditions from shade to full sunlight can affect the growth, depending on the seedling adaptability. We simulated such a scenario by exposing the seedlings, previously under shade (1 year), to full sunlight (9 months). The

interspecies relative growth and physiological characteristics were compared (Figure 4). Rosewood had a higher overall RGR compared to Teak (Figure 4(a)). Among the physiological characteristics, G_s was significantly higher for Teak. However, CC and Fv/Fm were significantly higher for Rosewood (Figure 4(b)).

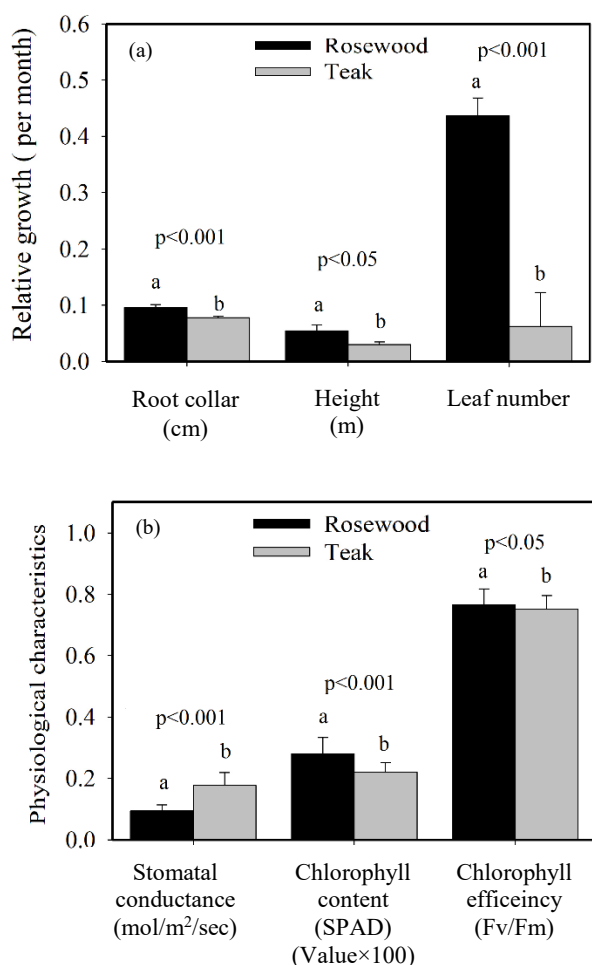


Figure 4. Relative growth (a) and physiological characteristics (b) of Rosewood and Teak seedlings, previously under 10% of full sunlight for 1 year (February 2015 to February 2016) exposed to full sunlight for 9 months (March 2016 to December 2016). The lowercase letters (a, b) indicate statistically significant differences between the species, as obtained from the t-test with the respective p-values indicated above the letters.

4. DISCUSSION

Rosewood and Teak are economically important timber species, and their natural populations have been indiscriminately logged for years. Future climate change is predicted to cause perceptible changes in the abundance of tropical species (Deutsch et al., 2008), leading to a reduction in the genetic diversity, especially in the peripheral population, as in Thailand, when compared to the centre of the population in Cambodia for Rosewood and India for Teak (Hartvig et al., 2018). A sustainable management will need a long-term conservation of genetic diversity to guarantee undiminished services over time. Light is a key factor affecting plant's growth and development and was the key parameter used to study the growth of Rosewood and Teak seedlings.

4.1 Seedling growth and physiological responses under full sunlight and shade

The growth rate of Rosewood (evergreen) was higher compared to Teak (deciduous), in both the light regimes and even more pronounced when the seedlings were moved from shade to full sunlight (Figures 2(a-c) and 4(a)). The most efficient growth (as indicated by RGR) in Rosewood has been previously reported under a wide range of light intensities (30-100% of full sunlight) (Moonchun et al., 2017) and (75-100%) (Phonguodume et al., 2012)). Sovu et al. (2010) stated that Rosewood is shade tolerant when young but can be light demanding as it matures. However, we confirmed that even as a seedling, Rosewood can both be shade tolerant and light demanding, as indicated by a similar growth rate under 10% and 100% light. For Teak, Moonchun et al. (2017) suggested that 40% of light resulted in optimum growth (with varying light intensity from 10, 20, 40, 60, 80, and 100% of full sunlight), while Nwoboshi (1972) reported that light intensity between 53-75% resulted in optimum growth. However, Teak shade intolerant at any stage of life, as reported by Kaosa-ard (1998) and we report that Teak grew better in full sunlight than in shade.

Light absorption is linked to the number of leaves and leaf area, with a higher leaf number and leaf area leading to more photosynthesis and net growth. In our study, Rosewood had a higher relative leaf number compared to Teak, as it has a compound leaf structure. Being an evergreen/semi-evergreen species, Rosewood does not shed its leaves throughout the year, while Teak, being deciduous with a simple leaf structure, sheds its leaves during the dry months (November to March), leading to a lower relative leaf number. Givnish (2002) reported that the deciduous species tended to have larger leaves so as to harvest maximum sunlight during the growing season, which is not the case with evergreen species. The thinner leaves of Rosewood (high specific leaf number; 180-240 in Rosewood vs. 120-180 g/cm² in Teak), led to more light absorption, or better growth (Figure 2(a-b)) and light adaptability (Figure 4(a)).

A relatively lower G_s of the thin-leaved Rosewood (Figure 2(d)) resulted in better light penetration and any increase in leaf temperature was countered by a lower sensitivity to LAVPD (Figure 3), as indicated by the slope of the scatter plot between G_s and LAVPD. Any changes in the driving gradient of atmospheric vapor pressure would cause little to no change to the stomatal closure and photosynthesis rate.

Hence, Rosewood may be resilient to future climate change scenarios. Teak is relatively more sensitive to variable light intensity and atmospheric demand (Figures 3 and 4), which could be due to its deciduous nature and large leaf trait (10 times larger than Rosewood leaflets). Large leaves generally have a thicker boundary layer, causing inefficient heat dissipation under high light intensity (Whitmore, 1998). A higher measured G_s (Figures 2(d) and 4(b)) for Teak could be due to an urge to transpire and reduce its leaf temperature. This response in Teak can be used to indicate any changes in tropical atmospheric conditions, especially when the air is drier, with the response being a rapid closure of the stomata to hotter and drier air.

4.2 Seedlings suddenly exposed to full sunlight after 1 year

In mixed forests with multilayer stories, an over-story comprising of a fast growing species and bamboo would dominate the canopy, resulting in an uneven distribution of light for the seedlings (Ådjers et al., 1995). A sudden change in light conditions would mostly be a result of branch pruning or death of big trees. Any small or large gaps would allow more direct sunlight for the seedlings. In our study, a sudden change in the light conditions from 10% to 100% was investigated to measure the responses of both species simulating a gap opening. The RGR for Teak was low when kept under shade and when suddenly exposed to full sunlight, and was lower than Rosewood (Figure 4(a)). So, Rosewood seedlings had a relatively higher adaptability to variable light conditions and could dominate Teak in terms of growth, when planted at the same time and competing for similar light conditions, in a forest or plantation setting. Therefore, during the seedling stage, Rosewood grows well under shade and sunlight conditions which includes a sudden change from 10% to 100% sunlight when compared to Teak. We also observed that CC and Fv/Fm of both species decreased when exposed to full sunlight and was pronounced in Teak (Figure 4(b)) due to a higher radiation damage. This observation is supported by a previous study reporting that optimum light condition for Teak growth is not under shade or under 100% sunlight but between 40-75% of full sunlight (Moonchun et al., 2017), as intense sunlight resulted in chlorophyll damage. Similar to the findings of Galeano et al. (2019), who indicated that light saturation point, where the photosynthesis rate would reach its maximum in Teak was around 1,217

$\mu\text{mol}/\text{m}^2/\text{s}$, which is correlated with a light intensity of 60% in the present study (Figure 1(b)). If Teak receives a light intensity higher than 60%, it would lead to leaf injury in the form of leaf burning and necrosis due to chlorophyll damage.

Reforestation requires species diversity and floristic composition as well as management. Suryanto et al. (2021) suggested that an agroforestry system should incorporate a mixed cropping model, in order to guarantee a sustainable forest regeneration. Teak should be planted at the edge of the area because it requires a higher light intensity (Suryanto et al., 2021). While Rosewood after establishment can grow most efficiently in a gap larger than 64 m², due to sufficient direct sunlight for growth (Sovu et al., 2010). Rosewood is considered as an intermediate pioneer species with a high growth rate during early stage of development and can rapidly colonize with only a few seedlings (So, 2000). Also Rosewood behaves as an anisohydric species, maximizing its carbon assimilation at the risk of hydraulic failure. This behaviour is associated with its higher growth during the early stages of establishment (Hung et al., 2020). Thus, Rosewood can both be shade and light tolerant during its early establishment and can become light demanding when nearing maturity, assuring a successful establishment in both the forest and plantation settings.

5. CONCLUSION

Light is a major factor responsible for plant growth and development in every stage of its life. A sudden change from shade to full sunlight resulting from gap opening or transferring nursery seedling to the field can cause damage to Teak leaves relative to those of Rosewood. Also, at all the reported light intensities (100%, 10% or sudden change light conditions), the growth of Rosewood was relatively greater than Teak, as indicated by a higher growth and chlorophyll content, and lower water loss, due to lower stomatal opening. We conclude that Rosewood seedlings can grow better in both shade and under full sunlight conditions and can also adapted well under abrupt changes in light intensity. Teak should not be planted under a shade of 10% of full sunlight or full sunlight, as that would reduce its growth rate.

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