Malays. Appl. Biol. (2022) 51(2): 9-21
https://doi.org/10.55230/mabjournal.v51i2.2184

GROWTH RESPONSE OF *Heritiera simplicifolia* (Mast.) Kosterm. AND *Scaphium macropodum* (Miq.) Beumée *ex* Heyne DUE TO ABIOTIC FACTORS IN THE NURSERY

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Accepted 29 March 2022, Published online 30 June 2022

ABSTRACT

In the earliest stage of development, non-dipterocarp wildlings require specific environmental conditions; they are only able to acclimate to harsher environmental conditions after this stage. As such, the environment acts as a limiting factor of early-stage development in non-dipterocarp shade-tolerant species. We examined the survival rates and growth rates of *Heritiera simplicifolia* and *Scaphium macropodum* from the family Malvaceae in the different sets of abiotic conditions. Three abiotic environmental factors medium type, greenhouse technique, and light intensity were varied. The experiment was conducted for six months in an area near Hulu Terengganu Hydroelectric Dam, at the edge of the Tembat Forest Reserve. Height, diameter, leaves numbers, and leaf area was recorded. Our results indicate that the wildlings preferred higher daytime relative humidity and natural air ventilation at night, and they grew more quickly under SN50 (358.74 Photosynthetically Active Radiation; PAR) than under SN70 (101.41 PAR). Subsoil supplemented with vermicompost improved wildling growth more consistently than subsoil supplemented with compost or burned mesocarp. The wildling's height relative growth rate (H_{RGR}) and survival were affected by all treatments. These results indicate that restoration efforts using young indigenous tree species at degraded sites, supply better growth environments and organic nutrients to the rhizosphere.

Key words: Non-dipterocarp, shade-tolerant/dependant, tropical forest restoration, vermicompost

INTRODUCTION

In tropical rainforests in Malaysia, climax tree species are predominantly dipterocarps and non-dipterocarps (Soerianegara & Lemmens, 1993). Most of these tree species are shade tolerant; they require shade at very early stages of development. However, their need for shade gradually decreases as seedlings grow older (Kuchelmeister & Huy, 2004). Shade-tolerant species are plant species that can survive under a specific minimum light intensity (Yamada & Suzuki, 1997). The slow growth rates of shade-tolerant wildlings prolong natural restoration processes in tropical rainforest ecosystems. The structure and diversity of tropical vegetation are also influenced by the discontinuous distribution of several biotic and abiotic factors, which act at different spatial and temporal scales (Arruda *et al*., 2015). Limiting factors, such as degraded soil and limited light availability, affect the distribution of shade-tolerant species (Stahl *et al*., 2013).

Nursing forest wilding can help to conserve tree species. However, only a few studies have compared the growth rates of shade-tolerant, non-dipterocarp wildlings to those of dipterocarp species during the early stages of development. Many studies have not addressed key environmental factors that can compromise wildling survival and growth (Grubb, 1998). Greenhouse techniques that mimic the conditions on the forest floor usually operate at a relative humidity of 80% (Rachel, 2014). Current practices in nursing wildlings involve gradually transferring wildlings from areas of low-light intensity to areas of high-light intensity; this method increases the amount of time each seedling must spend in the nursery.

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Huy (2012) found that three-month-old seedlings of *Scaphium macropodum* can grow under 50% shade. For this study, we assumed that the adaptions of other shade-tolerant species would be similar and could be used to reduce the duration of time spent in the nursery. Shade-tolerant plants are also acid-tolerant; they usually grow at the thin top layer of the forest floor, which is composed of organically rich soil containing microbes that aid in wildling growth and development (Lynch, 2011).

Deforestation creates many open areas, exposing plants to high-light intensities and making it difficult for shade-tolerant species to grow. With little being done to prevent this, shade-tolerant species have become vulnerable to genetic erosion and possible extinction (Soerianegara & Lemmens, 1993). This study aimed to determine the impact of varying limiting factors (humidity, light intensity, & available nutrients) on shade-tolerant, non-dipterocarp wildlings kept in a nursery for six months. To achieve this, wilding survival rates and growth parameters under different environmental conditions were determined. The growth parameters examined were height, diameter, number of leaves, leaf area, above-ground biomass, and below-ground biomass.

MATERIALS AND METHODS

Study site

The study was conducted at Hulu Terengganu Hydroelectric Power Plant (HTHEP), located in Tembat Forest Reserve (Figure 1), for six months in 2018. The average temperature was 24–31 ºC and the mean rainfall was 107.57 mm. The original vegetation of the study area was characterized as a lowland dipterocarp forest. Vegetation and the superficial soil layer were removed from 17.65 ha of land due to power plant construction.

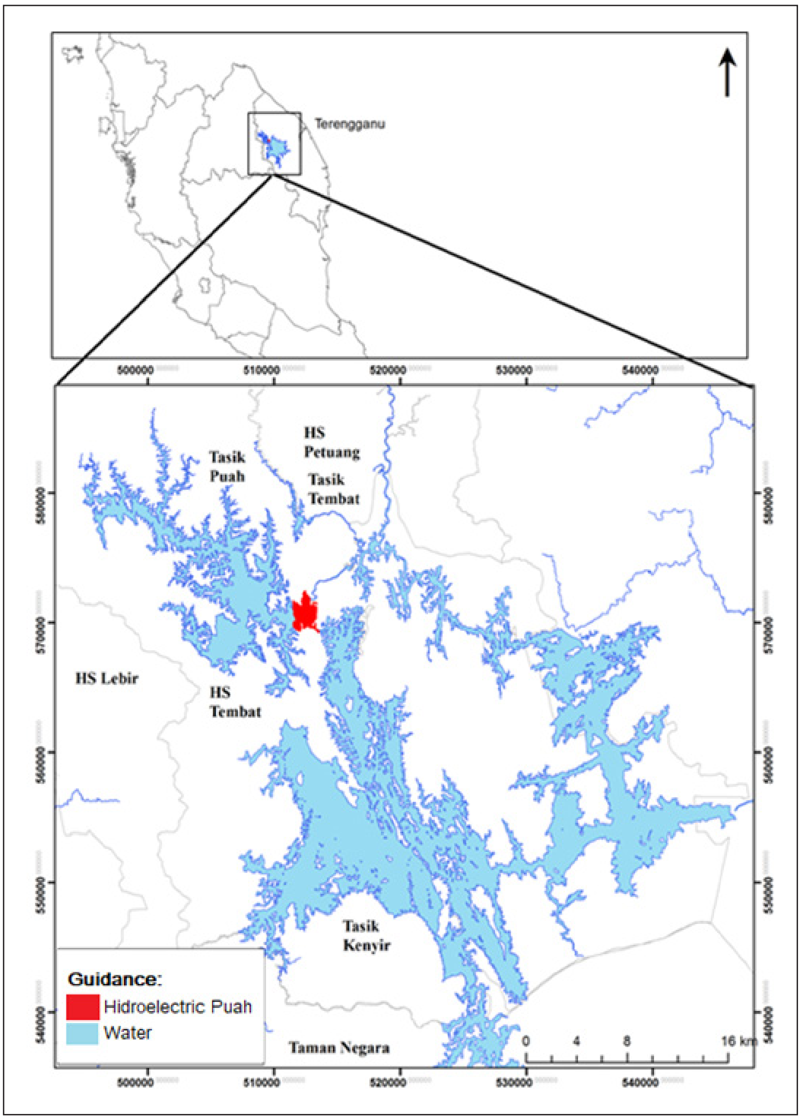


Fig. 1. Tembat Reserved Forest, Terengganu

Wildling selection and collection

The selected species were indigenous, shade-tolerant, and non-dipterocarp species of the Malvaceae family: *Heritiera simplicifolia* (Masters) Kosterm. and *Scaphium macropodum* (Miq.) Beumée ex K. Heyne (Soerianegara & Lemmens, 1993). Wildlings were selected using standard criteria: (1) a height between 15 cm and 30 cm, (2) a straight root, and (3) a straight stem (JPSM, 2014). The wildlings were collected from the Jerangau Forest Reserve, Terengganu, located 100 km from HTHEP.

Experimental design

The effects of three factors (medium type, greenhouse technique, & light intensity) were tested. Four media (C, M1, M2, & M3 – code refer Table 1), two greenhouse techniques (Relative Humidity 1 & Relative Humidity 2), and two levels of light intensity (50% & 70% shade netting) were used. A randomized complete block design (RCBD) was used to reposition the wildings' pots each month. The experiments were conducted for six months.

Media type

Jerangau is the place where the wildlings have been collected. Three experimental soil media (compost, M1; vermicompost, M2; and burnt mesocarp, M3) were applied using a subsoil-to-sand-to-nutrient ratio of 3:2:0.5; subsoil from the Tembat Forest Reserve was used as a control (Table 1). The ratio of 3:2:1 is a normal potting ratio. However, we decrease the ratio from 1 to 0.5 ratio for additional nutrients because it is enough for forest wildlings to grow in the early phase (recommended by Prof Jean Yong). Soil media were potted in a black polybag that was 9 inches tall and 6 inches in diameter. Each treatment had replicates for each species to determine the survival rates (*n*=40) and height growth rate (*n*=20). Soil nutrient content was obtained using a series of laboratory techniques (*n*=3).

Table 1. Media mixture types

Code	Media type	Total N (%)	P (μg/g)
J	Jerangau	0.04 ± 0.02a	11.42 ± 0.91c
C	Subsoil	0.04 ± 0.03a	12.33 ± 4.66c
M1	Subsoil: sand: compost	0.59 ± 0.57a	18.32 ± 0.65c
M2	Subsoil: sand: vermicompost	0.12 ± 0.09a	15.24 ± 4.72c
M3	Subsoil: sand: burnt mesocarp	0.19 ± 0.03a	81.63 ± 0.65b

Matching letters indicate no significant difference, with $p>0.05$ (n=3). Different letters indicate a significant difference, with $p<0.05$ (n=3).

Greenhouse technique

The potted wildings by different media treatments were placed in a small greenhouse and two different techniques were applied. In the first greenhouse technique, the greenhouse was kept closed all day (RH1); in the second technique, the greenhouse was opened at night (RH2). The percentage of air relative humidity (RH%) and temperature (ºC) were recorded. Each treatment had replicates for each species to determine the survival rates (*n*=80) and height growth rate (*n*=80).

Light intensity

After two months of applying the greenhouse techniques, wildlings were transferred to areas with 70% shaded netting or 50% shaded netting. The wildlings were kept in these areas for the next two months. Each treatment had replicates for each species to determine the survival rates (*n*=40) and height growth rate (*n*=40).

Growth analysis

The wildlings' survival rate, relative growth rate (RGR), leaf proliferation, and leaf area were recorded. RGRs were calculated using the formula according to Feeley et al. (2007) as follows:

$$RGR = (\ln W2 - \ln W1) / (t2 - t1)$$

Where W1 was the plant height at t1 and W2 was the plant height at t2.

Statistical analysis

An ANOVA (SPSS 16.0) was performed to test for statistical significance among three or more factors and parameters, and an independent t-test was performed to test for statistical significance between factors or parameters. Different letters indicate statistically significant differences between treatments ($p<0.05$), while matching letters indicate no statistically significant difference between treatments ($p>0.05$).

RESULTS

Media treatment

Effects of medium type on wildling survival and growth rate

a. Effects of medium type on wildling survival rate

Heritiera simplicifolia wildlings grown in the control medium had the highest survival rate (92.5%), while those grown in M3 had the lowest survival rate (70.0%). Similar results were found for Scaphium macropodum wildlings; wildlings for *Scaphium macropodum* wildlings; wildlings grown in the control medium had the highest survival rate (93.8%) and wildlings grown in M3 had the lowest survival rate (83.8%) (Figure 2).

b. Effects of medium type on wildling height relative growth rate (HRGR)

The growth patterns of *H. simplicifolia* grown in the control medium fluctuated throughout the study. *Heritiera simplicifolia* grown in M2 and M3 exhibited growth patterns that were inverse to each other for months 1 to 4. The height relative growth rate (HRGR) of wildlings grown in M2 had a maximum HRGR in the first month of the greenhouse phase (height increment 2.84 cm) and then slightly decreased from that point. The HRGR of wildlings grown in M1 and M3 had a minimum in the first month but increased progressively, with the highest HRGR occurring during the shade net phase (height increment of 2.78 cm). Towards the end of the study, the HRGR for wildlings grown in M2 and M3 decreased to C and M1 levels, though both groups maintained positive growth patterns. The highest *H. simplicifolia* HRGR during the experiment was 0.028 cm cm^{-1} week^{-1} (M3, month 4) (Figure 3a). *Scaphium macropodum* grown in the control medium exhibited a gradual, incremental growth pattern throughout the study (Figure 3b). Wildlings grown in M2 and M3 had the highest HRGR for the majority of the study. The highest S. macropodum HRGR during the experiment was 0.0208 cm cm^{-1} week^{-1} (M2, month 5).

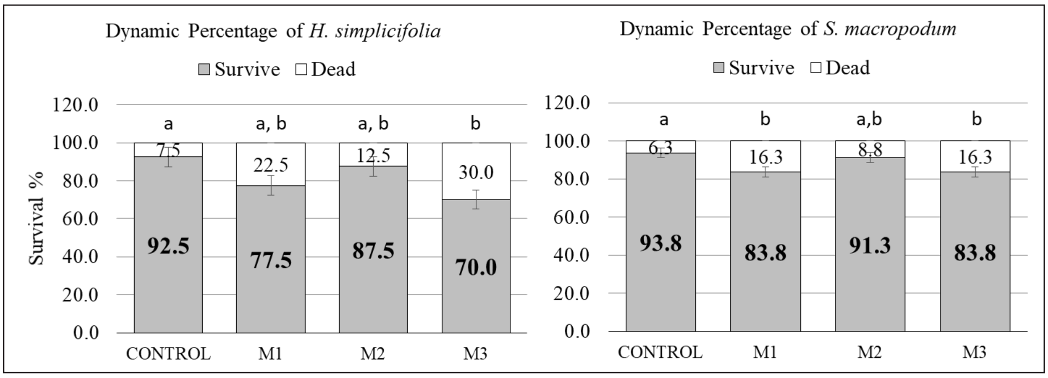


Fig. 2. Wilding survival rate of *H. simplicifolia* and *S. macropodum* grown in different media for six months. Matching letters indicate no significant difference, with $p>0.10$ ($n=40$). Different letters indicate a significant difference, with $p<0.10$ ($n=40$).

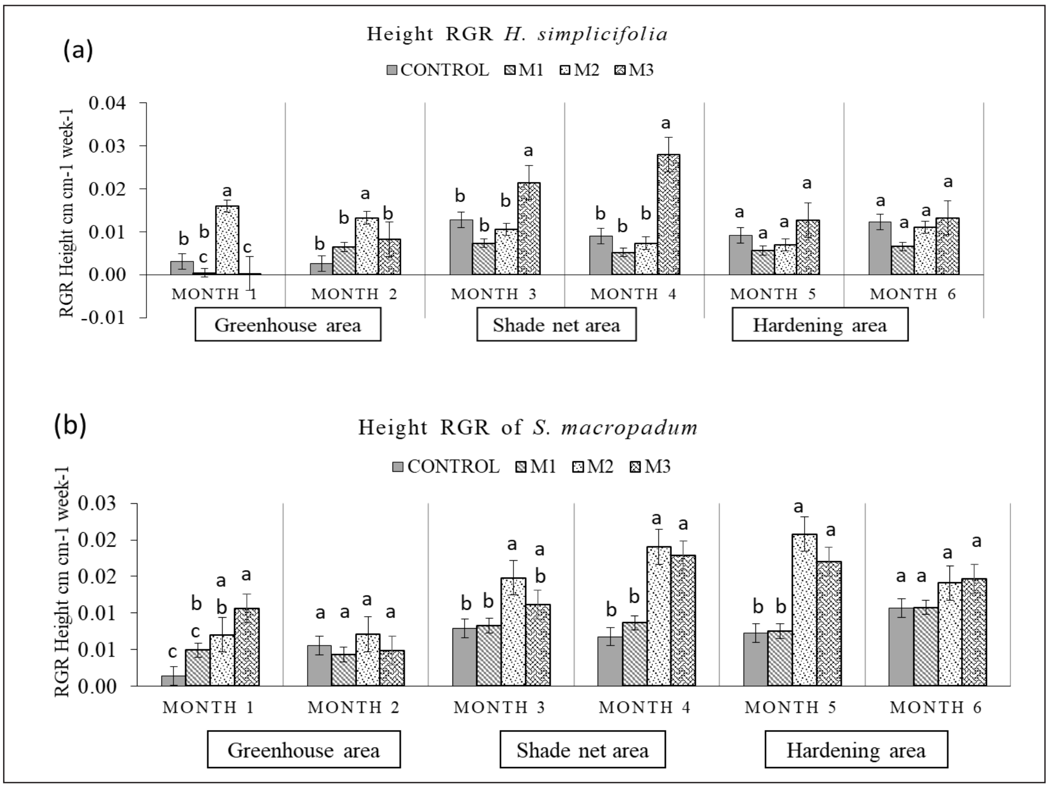


Fig. 3. Height relative growth rate of (a) *H. simplicifolia* and (b) *S. macropodum* grew in different treated media for six months. Matching letters indicate no significant difference, with $p>0.05$ ($n=20$). Different letters indicate a significant difference, with $p<0.05$ ($n=20$).

c. Wildling growth increments in different media after six months

Table 3 lists the mean height of the wildling growth increments for *H. simplicifolia* and *S. macropodum* in the different treated media after six months. The highest mean height increments for *H. simplicifolia* were 4.33 cm (M3) and 4.30 cm (M2). The lowest mean height increment was 1.98 cm (M1). The highest mean height increments for *S. macropodum* were 7.89 cm (M2) and 7.03 cm (M3). The lowest mean height increment was 3.87 cm (control treatment).

Relative humidity factors: greenhouse technique treatment

Figure 4 displays that two different air relative humidity (RH) levels, namely RH1 and RH2, have a constant relative humidity percentage in the range of 90%–100% for two months. Although there was no significant difference in relative humidity between RH1 and RH2 treatments, the mean temperature readings showed the opposite. RH1 has a higher temperature range of 27.2–29.1 ºC compared to RH2 with an almost normal ambient temperature range of 24.0–27.3 ºC between 7:00 p.m. and 12:00 a.m.

Effects of greenhouse technique on wildling survival rate and development

a. Effects of greenhouse technique on wildling survival rate

Figure 5 shows that the survival rate of *H. simplicifolia* wildings treated under RH2 (96.4%) was higher than the survival rate of wildings treated under RH1 (87.1%). There was a significant difference between the survival rates of RH1 and RH2 ($p<0.05$). Similar to *H. simplicifolia*, the survival rate of *S. macropodum* wildings treated under RH2 (97.9%) was higher than the survival rate of wildlings treated under RH1 (92.9%). There was a significant difference between the survival rates of RH1 and RH2 ($p<0.05$).

Table 2. Wildling mean height increments for different media after six months

	H. simplicifolia		*S. macropodum*	
Code	Absolute height (cm)	Mean height Month 6	Absolute height (cm)	Mean height
C	2.76bc	16.77b	3.86c	27.75a
M1	1.98c	18.44ab	4.63bc	29.57a
M2	4.30a	**20.08a**	**7.89a**	28.94a
M3	**4.33a**	16.51b	7.03a, b	28.33a

Matching letters indicate no significant difference, with $p>0.05$ ($n=20$). Different letters indicate a significant difference, with $p<0.05$ ($n=20$).

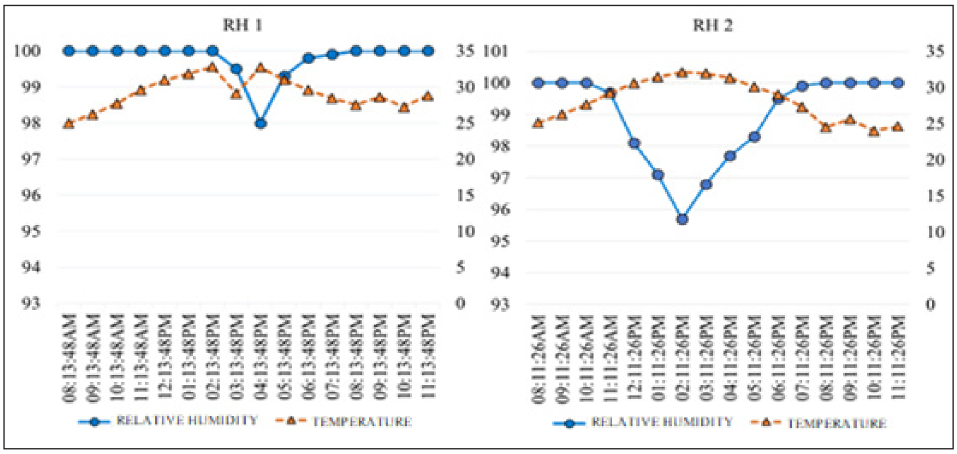


Fig. 4. Average of two months of relative air humidity and temperature in the nursery of *H. simplicifolia* and *S. macropodum* under greenhouse technique treatment of RH1 and RH2.

Figure 6 compares the survival rates of *H. simplicifolia* and *S. macropodum* for both greenhouse techniques. There was a significant difference between the species' survival rates under RH1 (p=0.001); *H. simplicifolia* wildlings had a survival rate of 87.1%, while *S. macropodum* had a survival rate of 92.9%. Meanwhile, there was no significant difference between the species' survival rates under RH2 (p>0.05); *H. simplicifolia* had a survival rate of 96.4%, and *S. macropodum* had a survival rate of 97.9%.

b. Effects of greenhouse technique on wildling development

Figure 7 displays *Heritiera simplicifolia* had better growth performance and a higher RGR in RH2 than in RH1. In RH2, the H_{RGR} increased by 0.013 cm cm^{-1} week^{-4} throughout the study (p=0.001). The wildlings consistently exhibited positive incremental growth under RH1 (p>0.05). Similarly, *S. macropodum* wildlings in RH2 had a higher H_{RGR} than wildlings in RH1. In both treatments, there was a slight increase in H_{RGR} from the beginning of the study to the end. There was a significant difference between species at the end of the study (p<0.05).

In Figure 8, *Heritiera simplicifolia* had a greater leaf proliferation rate in RH2 than in RH1 (p=0.01). However, the leaf proliferation rate in RH2 decreased to 1.0 towards the end of the study. Similarly, *S. macropodum* exhibited a greater leaf proliferation rate in RH2 than in RH1 (p<0.05). Initially, the leaf proliferation rate in RH2 was negative, but it increased slightly over time and became positive by the end of the study.

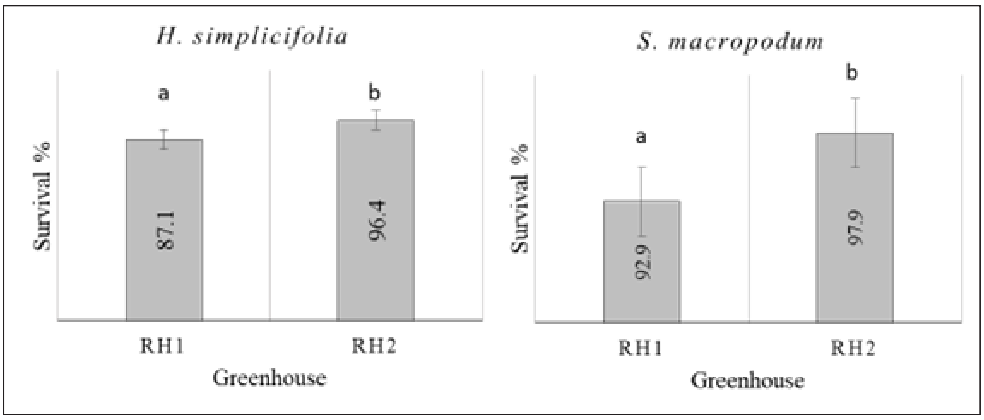


Fig. 5. The survival rate of *H. simplicifolia* and *S. macropodum* wildlings treated with different greenhouse techniques for two months. Different letters indicate a significant difference, with p<0.05 (n=80).

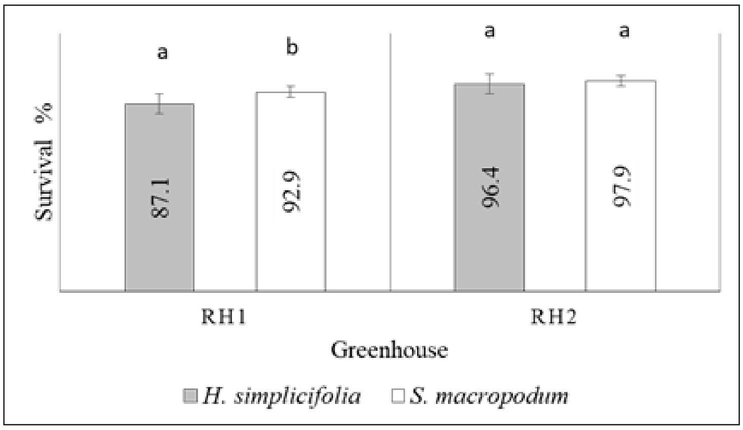


Fig. 6. The survival rate of *H. simplicifolia* and *S. macropodum* wildlings treated with different greenhouse techniques for two months. Different letters indicate a significant difference, with p<0.05 (n=80).

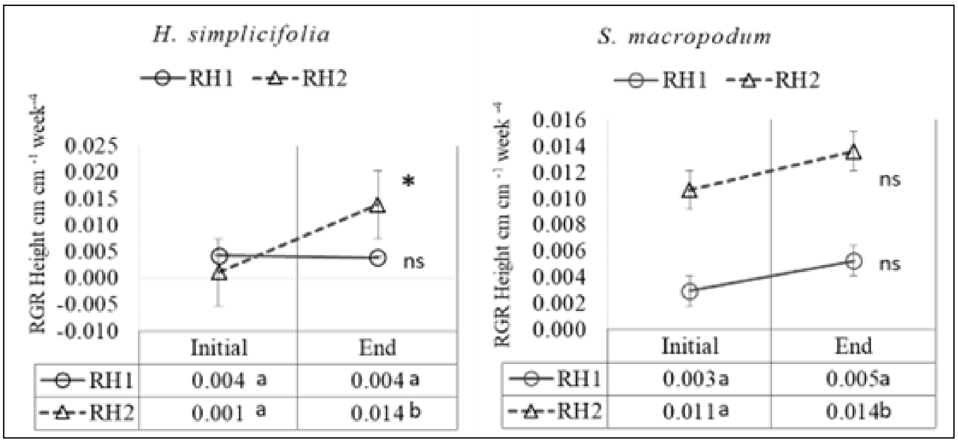


Fig. 7. Height relative growth rate of *H. simplicifolia* and *S. macropodum* treated with different greenhouse techniques for two months. Matching letters indicate no significant difference, with $p>0.05$ (n = 80). Different letters indicate a significant difference, with $p<0.05$ (n=80). For the month comparison, * indicates a significant difference, while 'ns' indicates no significant difference.

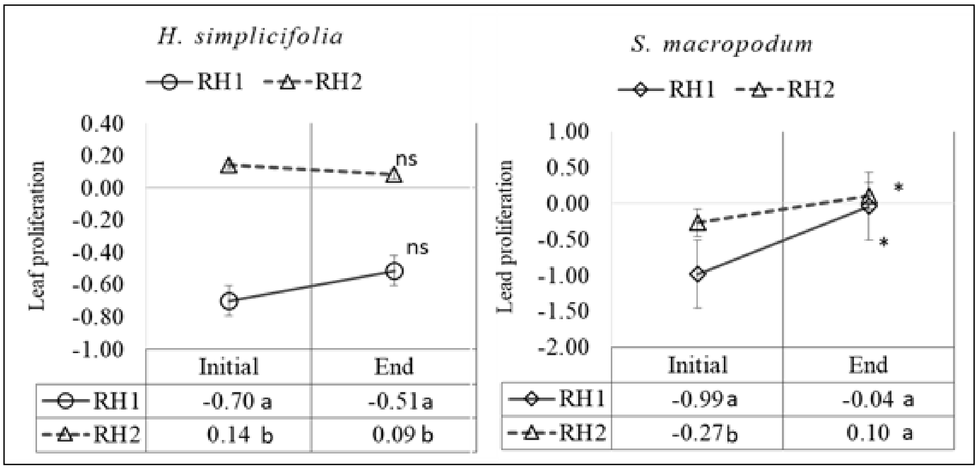


Fig. 8. Leaf proliferation of *H. simplicifolia* and *S. macropodum* wildlings treated with different greenhouse techniques for two months. Matching letters indicate no significant difference, with $p>0.05$ (n=80). Different letters indicate a significant difference, with $p<0.05$ (n=80). For the month comparison, * indicates a significant difference, while 'ns' indicates no significant difference.

Light density factors: shade treatment

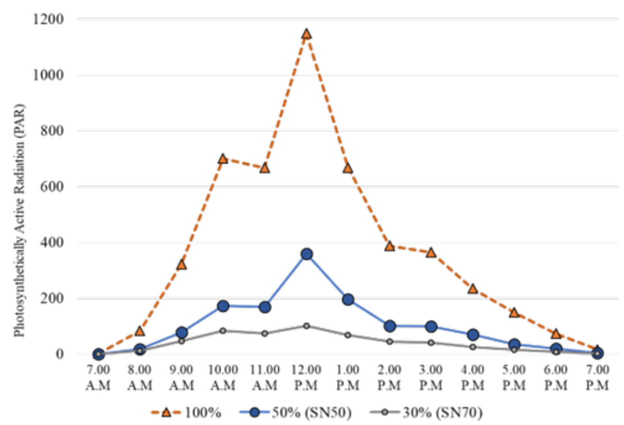
Figure 9 illustrates that 30% light intensity (SN70) had a low-light intensity with 101.41 PAR compared to 50% shading (SN50) with 358.74 PAR. There were no significant temperature range differences in the first month of shading treatment (26–31 ºC) for both treatment levels. However, at the end of the light intensity treatment study, there was a significant difference in temperature range, namely SN50 with a range of 30–34 ºC and SN70 with a range of 28–31 ºC from 7:00 a.m. to 6:00 p.m.

Effects of light intensity on wildling survival rate and development

a. Effects of light intensity on wildling survival rate

Figure 10 shows that the survival rates of *H. simplicifolia* wildlings exposed to 50% shade netting (SN50; 97.1%) were higher than wildlings exposed to 70% shade netting (SN70; 89.3%). The difference was statistically significant (p=0.001). Similarly, *S. macropodum* wildlings exposed to SN50 had a higher survival rate (92.9%) than wildlings exposed to SN70 (90.0%). However, there was no significant difference between treatments ($p>0.05$).

Figure 11 shows that the survival rate of *S. macropodum* wildlings under SN70 (90.1%) was higher than the survival rate of *H. simplicifolia* wildlings under SN70 (89.3%) ($p>0.05$). The *S. macropodum* wildlings under SN50 had a lower survival rate (92.9%) than *H. simplicifolia* wildlings under SN50 (97.1%) ($p<0.05$).



Keamatan Cahaya%	Teduhan	PAR
30%	SN70	101.41
50%	SN50	358.74

Fig. 9. Mean PAR on *H. simplicifolia* and *S. macropodum* under shading treatment SN50, SN70, and without shading in the nursery at Kenyir II Hydroelectric Power station.

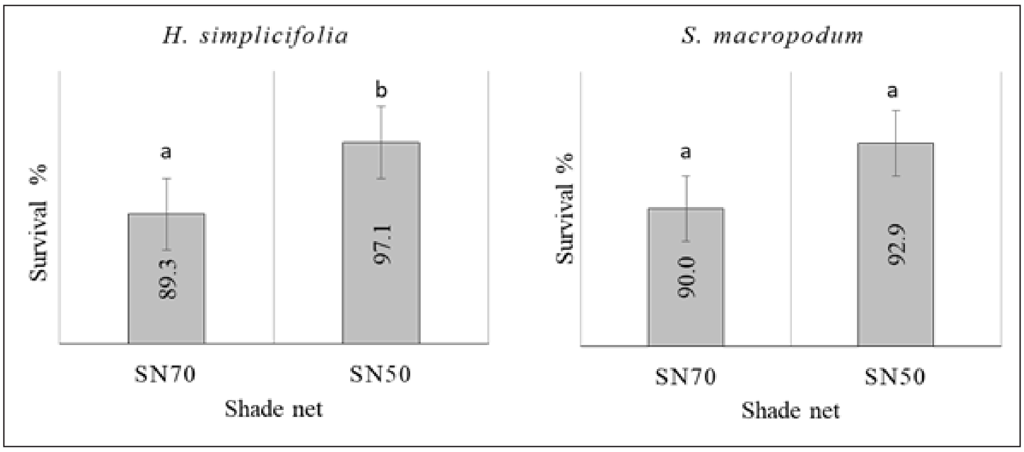


Fig. 10. Survival rates of *H. simplicifolia* and *S. macropodum* wildlings exposed to different light intensities for two months. Matching letters indicate no significant difference, with $p>0.05$ ($n=40$). Different letters indicate a significant difference, with $p<0.05$ ($n=40$).

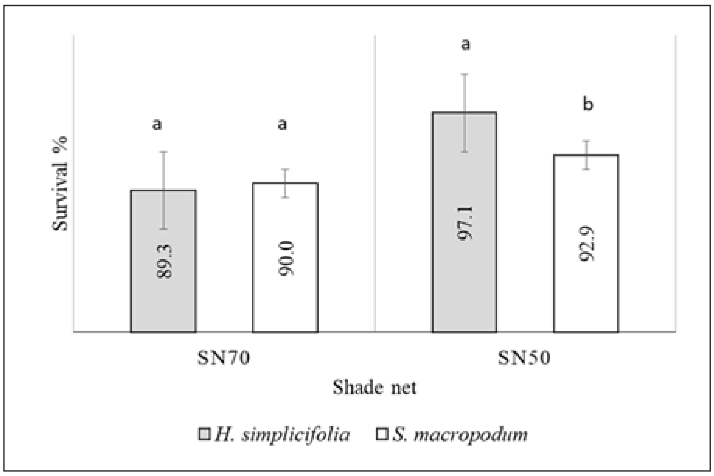


Fig. 11. Survival rates of *H. simplicifolia* and *S. macropodum* wildlings exposed to different light intensities for two months. Matching letters indicate no significant difference, with $p>0.05$ ($n=40$). Different letters indicate a significant difference, with $p<0.05$ ($n=40$).

b. Effects of light intensity on wildling development

Figure 12 displays that *H. simplicifolia* wildlings under SN50 had a higher H_{RGR} than wildlings under SN70; this difference was statistically significant (p=0.001). The H_{RGR} for wildlings under SN50 decreased over time (p=0.019), while the H_{RGR} for wildlings under SN70 exhibited constant growth throughout the study (p>0.05). *S. macropodum* wildlings under SN50 had the highest H_{RGR} at the beginning of the study, but the H_{RGR} decreased by the end of the study. There was a significant difference between treatments at the beginning (p=0.001) and the end of the two months (p=0.026).

c. Leaf area

Figure 13 illustrates that the mean leaf area of *S. macropodum* wildlings (70 cm^2) was larger than the mean leaf area of *H. simplicifolia* wildlings (30 cm^2). The mean leaf area of wildlings under SN50 was larger for both species than the mean leaf area for wildlings under SN70. The differences in leaf area between wildlings under SN70 and SN50 were statistically significant for both species at the beginning and the end of the study (*H. simplicifolia*, p=0.002 and p=0.001; *S. macropodum*, p=0.001 and p=0.002).

DISCUSSION

Shade-tolerant plant mechanisms and nutrient supplies

Adequate nutrients in the subsoil

Based on the results presented in Figure 2, the control medium had the highest wildling survival rate for both species over the six-month study compared to the other media. This is likely because the control medium was subsoil obtained from the Tembat Forest Reserve, which was previously a primary forest. As such, the control medium had sufficient nutrients for the wildlings to survive despite subsoil having fewer nutrients than topsoil (Gregory *et al*., 2016).

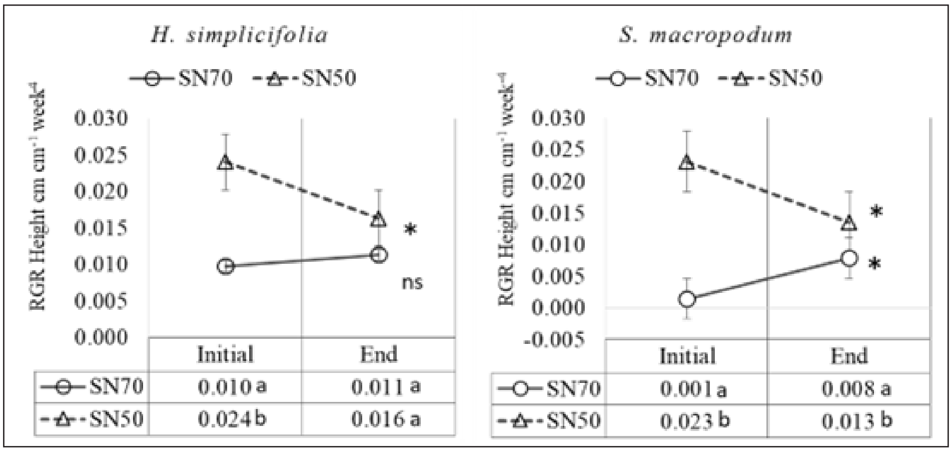


Fig. 12. Height relative growth rate of *H. simplicifolia* and *S. macropodum* exposed to different light intensities for two months. Matching letters indicate no significant difference, with p>0.05 (n=40). Different letters indicate a significant difference, with p<0.05 (n=40). For the month comparison, * indicates a significant difference, while 'ns' indicates no significant difference.

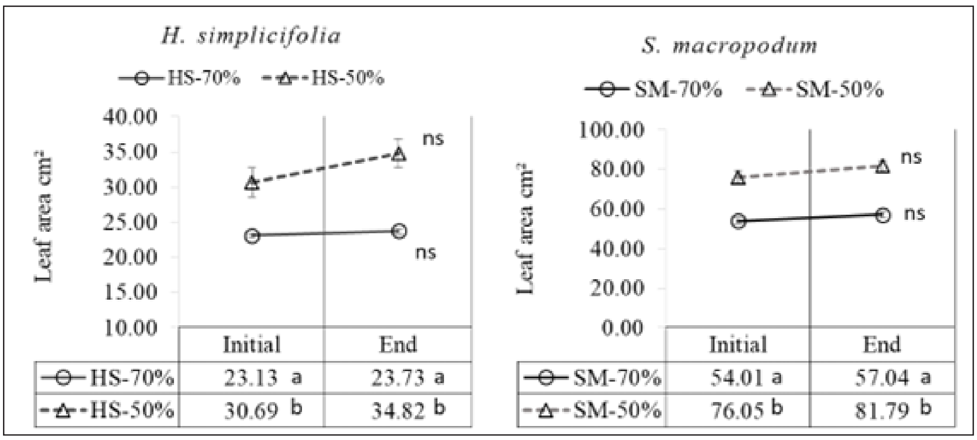


Fig. 13. The leaf area of *H. simplicifolia* and *S. macropodum* wildlings were exposed to different light intensities for two months. Matching letters indicate no significant difference, with p>0.05 (n=40). Different letters indicate a significant difference, with p<0.05 (n=40). For the month comparison, * indicates a significant difference, while 'ns' indicates no significant difference.

The subsoil obtained from the Tembat Forest Reserve contained more nutrients than the subsoil usually used as a potting medium by the forestry nursery in Ajil, Terengganu. Most tropical subsoil is acidic and has adequate phosphorus, which helps to stabilize the subsoil (Lynch, 2011). Table 1 shows that available phosphorus data for the subsoil media indicate that in the Tembat Forest Reserve subsoil control, M1 and M2 had phosphorus levels in the same range as those of the Jerangau Reserve Forest, where the wildlings were collected; while M3 had a much higher phosphorus level. Although the control subsoil had a lower nitrogen level compared to subsoil mixed with sand and additional nutrients, the subsoils used still had adequate nutrients to support growth during the early stages of development for both species.

The 0.5 ratio of additional nutrients of burnt oil palm mesocarp is considered excessive for the wildlings

Wildlings grown in M1 had the lowest growth rates throughout the study for both species; wildlings grown in M3 had the steepest H_{RGR} trend (Figure 3). Wildlings grown in M3 exhibited the highest growth rates in the last four months of the study. These growth patterns are likely related to the amounts of available nutrients in the soil, which would influence plant growth. Based on the results of this study, the addition of burnt oil palm mesocarp at a ratio of 0.5 seems excessive. This is because the phosphorus content in M3 is approximately four times higher compared to P content in Jerangau's soil, subsoil (control), M1, and M2, which leads to excessive nutrients in the early phase of wildlings' growth development and caused low survival percentage. Wildlings had sufficient nutrients during the first month, but the nutrients were subsequently washed out by water easily, especially in media that contained compost (Hurley *et al*., 2017). According to reports by JPSM (2014), the gradual application of a suitable amount of compost was needed to avoid insufficient amounts of nutrients. Meanwhile, the wildling growth rate in M3 became better from month 2 to month 4 as the additional nutrients in burnt oil palm mesocarp were washed out by water in the high-porosity media (Rosenani *et al*., 2016).

Vermicompost improves the physical and chemical soil properties

H_{RGR} trends for both species showed stunted growth in a few of the wildlings due to nutrient depletion in the high soil porosity of mixed media sand (Figure 3). Soil compaction places stress on the root, making it difficult for the root to effectively penetrate the soil (Hakansson & Lipiec, 2000). The subsoil has lower soil porosity which leads to soil compaction (Table 2). Soil compaction restricts nutrient cycling in the rhizosphere by microbes due to less or no aeration (Phogat *et al*., 2015). Throughout the study, wildlings grown in M2 had lower mortality compared to the others with additional nutrients (compost and burnt oil palm mesocarp). This is because vermicompost contains live earthworms, which indirectly increased soil porosity through burrowing and repaired the soil structure, allowing for better aeration and a healthier rhizosphere (Lazcanoa & Domínguez, 2011; Kumar *et al*., 2018). Besides, vermicompost improves the chemical properties in soil by providing more microsites for organisms and allows the nutrient cycle happens naturally in the rhizosphere (Kumar *et al*., 2018). Though the nutrients in the media mixed with vermicompost are probably washed out by the water, unlike compost and burnt oil palm mesocarp, the worms and microorganisms are still there. The worms in vermicompost have been shown to have intestines with unique microflora (Toyota & Kimura, 2000) and to be bioreactors that are the vermicast production sites (Manyuchi & Phiri, 2013), which contribute to the reproduction of microbial communities. Those microbes such as cytokinins *Arthrobacter* and *Bacillus spp* in the soil can produce the cytokinins and auxins naturally, which are needed by any plant to grow (Yong *et al*., 2014).

Shade-tolerant plant mechanisms to greenhouse technique

Higher survival rates with nightly air ventilation

The survival rates of *H. simplicifolia* and *S. macropodum* wildlings were over 80% in both greenhouse treatments (Figure 5). This greenhouse technique was used to maintain the air humidity compared to the uncovered greenhouse technique, especially during the daytime (Huy, 2012). The wildlings were collected on the forest floor, which had a humidity of approximately 80% (Rachel, 2014); they acclimatized to the new, less humid environment in the nursery. Wildlings needed to acclimatize to the sudden shift in the environment. Generally, the optimum air relative humidity for a plant should be between 40% and 80% in the nursery (Fanourakis *et al*., 2013); plant quality is best at a humidity of 70% (Mortensen, 2000). Results of the present study indicate that non-dipterocarp tree species can survive at relative humidity levels of 95–100%.

Both treatments had a constant relative humidity of 100%, but RH1 lacked natural air ventilation at night. As such, the air moisture reached the saturation point and the air held the maximum amount of water vapor (Elovitz, 1999; Hundy *et al*., 2016). This occurs below the dew point and thus condensation appears on cold surfaces (Hundy *et al*., 2016). Elovitz (1999) observed that condensation appears as fog or mist on UV plastic because the plastic is a colder surface than the wildings' leaves. He stated that condensation on the UV plastic walls inside the greenhouse can negatively affect plant growth. This is because high humidity inside the greenhouse can inhibit evaporation and decrease the transpiration rate by decreasing the leaf water potential (Vesala *et al*., 2017).

In addition to relative humidity, plants respond to temperature (Aphalo & Jarvis, 1991). During the day, the air in a greenhouse becomes hotter due to the UV plastic walls and the high humidity; ventilation is needed at night to cool the air. Nightly ventilation in the greenhouse caused more air circulation, which maintained the humidity at a more suitable level for the wildlings (Stanghellini, 1987). Moreover, air circulation is important for reducing plant stress, increasing evaporation and transpiration, as well as regulating water and nutrient uptake (Katsoulas & Kittas, 2008). Air moisture circulation also regulates stomata activity. Stomata must remain open to absorb sufficient CO_2 for photosynthesis, which leads to water loss via transpiration from the leaves (Mortensen & Fjeld, 1998; Hundy *et al*., 2016). Although stomata occupy only about 1% of a leaf's surface area, transpiration rates can reach 50% of the evaporation rate of a free water surface (Kramer & Kozlowski, 1979). When the rate of water loss exceeds the rate of water uptake, internal moisture stress occurs; this stress may eventually become severe and adversely affect metabolic processes such as photosynthesis (Farooq *et al*., 2009; Vesala *et al*., 2017). Therefore, for this study, natural ventilation at night helped optimize the relative humidity and reduced plant stress through respiration.

Morphological mechanisms

Scaphium macropodum wildlings have a higher survival rate than *H. simplicifolia* wildlings (Figure 6). Leaf proliferation as well as greenhouse treatment affected plant survival and growth; wildlings in RH1 from both species experienced a decrease in leaf proliferation from the beginning of the study to the end (Figure 8). Evaporation is one of the most important processes for photosynthesis and respiration mostly occurs on the surface of leaves. Evaporation causes transpiration. However, when the humidity reaches the saturation point, evaporation is inhibited and transpiration cannot occur; the wildlings' leaves lose moisture and the wildlings experience internal water stress (Aphalo & Jarvis, 1991). At some point, stomata conductance is interrupted because there are insufficient water and minerals to open and close the stomata (Jones, 1998; Nepi *et al*., 2010). Elongation, which depends on turgor pressure, slows down and other internal processes are adversely affected (Nepi *et al*., 2010). Things become worse when wildlings begin to shed leaves to survive. Chlorophyll is important for photosynthesis. Without leaves and chlorophyll, it is difficult for *H. simplicifolia* wildlings to photosynthesize. When photosynthesis stops, growth stops. However, *S. macropodum* wildlings have green stems (Huy, 2012), which allowed *S. macropodum* wildlings with no leaves to photosynthesize and survive at the saturation point. Any green plant parts have stomata on them, but stems have fewer stomata than leaves (Kirkham, 2014), hence photosynthesis occurs at a slower rate in wildlings without leaves. This indicates that the green stems of *S. macropodum* wildlings are likely an adaption to extremely high humidity environments, especially when there is no leaf left.

Shade-tolerant plant mechanisms and light intensity

Growth of shade-tolerant wildlings under partial light

The results show that the wildlings grew better under SN50 than under SN70 (Figure 10). Huy (2012) found that, in a nursery, *S. macropodum* seedlings up to 3 months old required 50% shade to sustain growth. Results from this study, as well as results from previous studies, indicate that 50% shade produces the optimal temperature and light conditions for photosynthesis and wildling growth (Lambers *et al*., 2008). For both species, the H_{RGR} of wildlings under SN50 was slightly higher than the H_{RGR} of wildlings treated under the SN70 (Figure 12). This growth rate (SN50) is considered normal for shade-tolerant species, especially for *S. macropodum* (Huy *et al*. 2012). Results show that *H. simplicifolia* wildlings grew faster under SN50, similar to the *S. macropodum* wildlings (Figure 11). Generally, higher light intensity generates more auxins at the apical meristem, maximizes phototropism, and stimulates cell elongation towards the sunlight to gain more light for photosynthesis (Liscum *et al*., 2014). Although phenotypic plasticity tends to be lower in a shade-tolerant tree, plasticity for certain traits, particularly for morphological features that optimize light capture, can be high (Valladares & Niinemets, 2008).

Increases in leaf area from high light intensity

Wildlings grown under SN50 had a higher leaf area compared to wildlings under SN70 for both species (Figure 13). Poorter (2001) stated that shade-tolerant seedlings optimize their light interception by producing larger and darker leaves at lower light intensities (50–70%). Shade-tolerant species also have higher chlorophyll contents in their leaves and a higher photosynthetic capacity in low-light conditions (Valladares & Niinemets, 2008). The leaves have vacant spaces along the cell walls in mesophyll cells so that the leaves can grow wider. The vacant spaces were filled with chloroplast, which increases the photosynthesis rate when exposed to higher light intensities (Oguchi *et al*., 2006).

CONCLUSION

This study indicates that exposure to various environmental factors for six months affects the survival and growth of *Scaphium macropodum* and *Heritiera simplicifolia* wildlings. Shade-tolerant, non-dipterocarp *S. macropodum,* and *H. simplicifolia* wildlings had better growth performance when grown in a greenhouse with night-time ventilation. Though subsoil from Tembat Reserved Forest provided sufficient nutrients for the wildlings according to the constant growth rates, the addition of vermicompost naturally sustained and improved the rhizosphere for the long term. Furthermore, the wildlings exhibited better growth in areas with 50% shade netting; this indicates that the duration for which wildlings stay in the nursery can be shortened by exposing them to partial light.

ACKNOWLEDGEMENTS

The authors would like to thank the wildlife research group at Universiti Kebangsaan Malaysia; Jabatan Perhutanan Kuala Berang, Terengganu; Jabatan Perhutanan Negeri Terengganu, Malaysia; Tenaga National Berhad Research; and everyone who offered assistance and guidance throughout this study. The study was supported by the ST-2017-010 and GUP-2018-022 research grants.

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